



# **LUQ V: UNDERSTANDING ECOSYSTEM CHANGE IN NORTHEASTERN PUERTO RICO**

**A PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION  
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## PROJECT SUMMARY

### Overview

The Luquillo Long-Term Ecological Research Program (LUQ) integrates research, educational activities, and outreach through a focus on disturbance and ecological response in wet tropical forest ecosystems. **The overarching goal of the Luquillo LTER program is to determine how changing climate and disturbance regimes, alone or in concert, drive changes in the biota and biogeochemistry. An enhanced mechanistic understanding of change in natural and human modified landscapes will supply critical information to manage and conserve tropical forest ecosystems globally.** Building on over 90 years of research history in the Luquillo Experimental Forest, LUQ has significantly shaped understanding of climate and climate change, disturbance ecology, biogeochemical cycling, productivity, land use history, and population and community dynamics in wet tropical forest and stream ecosystems. The research proposed here employs a combination of long-term measurements, experimental manipulations, and models to determine the effects of changes in climate and disturbance frequency in forests and stream ecosystems over the remainder of the 21st century.

**Intellectual Merit:** Climate change is resulting in an increase in the frequency of drought and intense hurricanes in the Caribbean, as well as other tropical regions. These changes are resulting in new combinations of species and biogeochemical conditions that create non-analog ecosystems. The conceptual framework guiding our research explores the development of these novel ecosystems resulting from the separate and combined effects of increased drought and hurricane frequency, and mediated by land use legacies. The research proposed stems from the results of long-term measurements and manipulative experiments to answer the following key questions:

**What Are the Short- and Long-Term Effects of Drought on Biota and Biogeochemical Cycling in Tropical Forests?**

**What are the Effects of Increased Frequency of Intense Hurricanes on Tropical Forest Biota and Biogeochemical Cycling?**

**How do Changes in Climate Interact with Hurricane Disturbance, Land Cover, and Land Use Legacies to Shape Ecosystems of the Future?**

We will address these questions using long-term measurements of the tabonuco forest and along the elevation gradient, a climate change analog, as well as new and on-going manipulative experiments. To help test our hypotheses that increased drought frequency will alter species composition and distribution as well as soil carbon storage we propose two new experiments: the Throughfall Exclusion Experiment and the Stream Diversion Experiment. We continue the Canopy Trimming Experiment to test our hypotheses that increased frequency of intense hurricanes will increase the dominance of shade intolerant species with cascading effects through other biota and biogeochemistry. We use models and data-model integration to integrate across scales and forecast future conditions. This will allow us to address the combined effects of increased drought and hurricane frequency as mediated by land use legacies.

**Broader Impacts:** Using integrated theoretical, experimental, and observational approaches LUQ provides an innovative and comprehensive scientific framework for evaluating the management of tropical ecosystems confronting a changing climate. The program will continue to train numerous graduate and undergraduate students, especially members of underrepresented groups, producing a cadre of collaborative, multidisciplinary scientists who can link population, community, and ecosystem approaches to provide a predictive understanding of environmental change. LUQ 5 will capitalize on its recent success in catalyzing major projects in Puerto Rico, such as NEON, STREON, IGERT, CZO, and ULTRA-Ex. Schoolyard LTER in LUQ V will reach teachers and hundreds of middle and high school students through field research and via a web-based middle school curriculum for teaching ecology.

Note – Because of an administrative situation beyond our control and unrelated to the Luquillo LTER award, our project received no funds from the National Science Foundation from December 2013 through November 2014. This hiatus in funding affected our capacity to prepare our renewal proposal, and, in the spirit of fairness, NSF extended the due date for the proposal from 2014 to 2015. NSF instructed us to prepare a proposal to cover three years of work (December 2015 through November 2018) and to include additional funds to cover costs assumed by the University of Puerto Rico and subcontracted institutions during the funding hiatus. Despite the gap in funding, all key long-term measurements continued on schedule as a result of the commitment of investigators, students, and administrators. Investigators continued to conduct fieldwork, publish results, and prepare for the proposal that you have before you.

## 1.0 INTRODUCTION

**The overarching goal of the Luquillo LTER program is to determine how changing climate and disturbance regimes, alone or in concert, drive changes in the biota and biogeochemistry. An enhanced mechanistic understanding of change in natural and human modified landscapes will supply critical information to manage and conserve tropical forest ecosystems globally.**

The foundations of the Luquillo Long Term Ecological Research Program (LUQ), based in the Luquillo Experimental Forest (LEF), Puerto Rico, stem from nine decades of research on forest composition, growth, and management by USDA Forest Service scientists as well as 25 years of work on biogeochemical cycles supported by the U.S. Department of Energy and its predecessor the Atomic Energy Commission. Results from these studies stimulated the formation of LUQ and the choice of an organizing theme focusing on the interplay between disturbance and ecological response. The products of LUQ research have helped shape understanding of montane forest ecosystems in the tropics and globally, and catalyzed complementary research efforts such as the Luquillo Critical Zone Observatory (CZO), the San Juan Urban Long Term Research Areas (ULTRA), and the USGS's Water, Energy and Biogeochemical Budgets (WEBB) program. LUQ continues to use our expanding knowledge of the forests and streams of the Luquillo Mountains to foster a broader understanding of the principles that structure montane forest ecosystems in temperate and tropical environments.

### 1.1 Conceptual Framework for Luquillo LTER V

***We propose to study the effects of climate change, specifically more frequent droughts and hurricanes, on the structure and function of tropical forest ecosystems.*** Our conceptual framework explores the development of novel ecosystems resulting from the separate and combined effects of increased drought and hurricane frequency, and mediated by land use legacies (Fig. 1). These novel ecosystems will differ from earlier and current ones in both structure and function. We use biogeochemistry, productivity, and the composition and structure of biotic populations and communities as the characteristics for quantifying impacts. Our proposed research builds on key questions stemming from results of our previous studies:

**1. What are the short- and long-term effects of drought on tropical forest biota and biogeochemical cycling?** Global circulation models (GCMs) indicate that precipitation will decline by as much as 50% in the Caribbean region over the remainder of the century (Neelin et al. 2008, Comarazamy & González 2011). Our models and empirical data suggest that rainfall is becoming more variable in the Luquillo Mountains (*Scatena 1998, van der Molen 2010, Schaefer 2003, González et al. 2013*). The long-term effect of these trends will be to increase the frequency of droughts as well as to produce an environment with more pronounced seasonality. The rate of these changes is more rapid than earlier believed (Hayhoe 2013). A major question is how the biota and biogeochemistry in historically wet rainforests will respond to increased drought frequency.

**2. What are the effects of increased frequency of intense hurricanes on tropical forest biota and biogeochemical cycling?** Hurricanes affect islands and coastal ecosystems on all continents except Antarctica. Hurricane disturbance is an important factor shaping the biotic and biogeochemical characteristics of the Luquillo Mountains (*Waide & Lugo 1992, Walker & Willig 1999, Scatena et al. 2012, Brokaw et al. 2012*). Our long-term data demonstrate that the effects of hurricanes are contingent on the initial state of the ecosystem (i.e., time since past disturbance) and the particular characteristics of the disturbance (i.e., canopy openness, debris deposition, rainfall intensity). For example, previous land use

mediates the effects of hurricanes (*Uriarte et al. 2009*), and differences in intensity and duration of hurricanes produce correspondingly distinct effects on the biota and ecosystem processes (*Beard et al. 2005*). Climate models predict that the frequency and intensity of hurricane disturbance are changing globally (*Royer et al. 1998, Emmanuel 2005, Trenberth 2005, Webster et al. 2005, Zhao & Held, 2012; Villarini & Vecchi, 2013*). In addition, models based on our long-term data further predict that more frequent hurricanes will lead to changes in species composition (*Doyle 1981, Uriarte et al. 2009*) resulting in alterations in biogeochemistry and productivity (*Sanford et al. 1991, Zimmerman et al. 1995*).

**3. How do changes in climate interact with hurricane disturbance, land cover, and land use legacies to shape tropical forest ecosystems of the future?** Changes in climate will lead to changes in biotic structure and biogeochemistry, and the rate of change will be exacerbated by more frequent disturbances (*Doyle 1981, Sanford et al. 1991, Covich et al. 1991, 1996, O'Brien et al. 1992, Silver 1998, Wang et al. 2002a, b, Erickson & Ayala 2004*). The combined effects of changes in climate and disturbance regimes will result in tropical forest ecosystems characterized by novel community compositions resulting in altered biogeochemistry, productivity, and population dynamics (*Hobbs et al. 2006, Lugo et al. 2012, Willig et al. 2012*).

These three interrelated questions form the basis for hypotheses designed to test ecological theory on disturbance, population and community assembly, and biogeochemical dynamics. Our hypotheses are also designed to explore broad-scale patterns in space and time and facilitate the development of models applicable to Puerto Rico, the Caribbean, and tropical forest ecosystems globally.

## **1.2 The Luquillo LTER as Part of a Global Research Community**

The Luquillo Long Term Ecological Research Program focuses on a forested mountainous landscape on a tropical island in the midst of the Caribbean biodiversity hotspot (*Reagan & Waide 1996, Brokaw et al. 2012*). Mountains create steep environmental gradients that facilitate the study of changes in climate and other critical factors structuring the biota and influencing biogeochemistry. Today, the LEF is an island within an island (Fig. 2). As a preserve of forest and streams only a short distance from a large metropolitan area, the LEF exists in a changing landscape. The region is losing agricultural lands as a consequence of expanding secondary forest and growing urban areas, a pattern common to many tropical regions (*Lugo 1994, Thomlinson et al. 1996, Gould et al. 2012*). Furthermore, the LEF lies in the path of powerful storms including hurricanes arriving from the Atlantic Ocean that define the disturbance regime, as they do in many coastal forests of the world. Thus, LUQ research provides knowledge relevant to understanding and managing forest reserves throughout the tropics.

Tropical forests are the Earth's largest repositories of terrestrial C (*Schlesinger & Bernhardt 2013*). These forests store approximately 52% of the global plant C pool (*Schlesinger and Bernhardt 2013*) and 33% of the soil C stock (*Scharlemann et al. 2014*). Net primary productivity (NPP) and decomposition are the dominant processes driving C dynamics in tropical ecosystems, and changes in the drivers of either of these processes (e.g. climate, local weather patterns, topography, geology, disturbance, biotic communities, and land use history) affect whether ecosystems retain or release C to the atmosphere. The relative proportion of C storage and loss in turn affects global climate through feedbacks to atmospheric CO<sub>2</sub> concentrations.

Extremely high biodiversity characterizes tropical forests, which harbor 68% of described vascular plant species and much higher proportions of other plant and animal groups (*Forseth 2012*). Endemic species are common on islands and mountains, making them most vulnerable to global climate change and changes in disturbance regimes. While high in endemism because of its insular montane nature, the LEF hosts many common higher taxa of plants, animals, and microbes found elsewhere in the Neotropics (*Reagan & Waide 1996*). Puerto Rico's forests are more diverse than biomes from higher latitudes, and they display the preponderance of rare species that are the hallmark of tropical communities (*Connell 1978, Reagan & Waide 1996, Zimmerman et al. 2008*). Mountains harbor some of the most fragile environments in the world, including elfin cloud forests such as those found in the Luquillo Mountains (*Díaz et al. 2003*). Montane systems are being altered significantly by land use change at low elevations (*Becker et al. 2007*) and imperiled by climate change at higher elevations (*McCain & Colwell 2011*). Tropical organisms are expected to respond more strongly to environmental changes along elevation gradients compared to temperate organisms because, from an evolutionary perspective, tropical organisms face little intra-annual variation in climate and, therefore, are more sensitive to other forms of



environmental variability (Janzen 1967). Mora et al. (2013) have recently shown, as a corollary to Janzen's hypothesis, that significant departures from climate norms will be recognized first in the tropics because of their relatively stable climates. Though the magnitude of climate change may already be greater in the Arctic, it will take longer for the departures from normality to be recognized in the Arctic against the background of extreme intra-annual variation.

Together, this intricate web of critical interactions among the climate, disturbance regime, the biota, and biogeochemistry converge to provide an important laboratory for quantifying the impacts of global change. The Luquillo LTER anchors the US LTER Network in the critical biome of wet tropical forests, acting as a nexus of interaction with the U.S. LTER Network as well as with international networks studying tropical forests, islands, and mountains. With its deep research history, long-term data, and robust infrastructure, all associated with an LTER site, the LEF is an ideal place to monitor the pulse of tropical ecosystems in a changing world.

## 2.0 RESULTS FROM PRIOR SUPPORT

The LEF has one of the longest continuous research histories of tropical forest ecosystems globally (Fig. 3). Research and monitoring started in the 1920s with pioneering studies by the US Forest Service and university partners on tropical forest structure and function, timber management, and reforestation (Harris et al. 2012). From 1960-1988, the Atomic Energy Commission (later the Department of Energy) sponsored the Rainforest Project, which provided what was at that time the most detailed understanding of tropical forest metabolism, nutrient cycling, energy flows, and population dynamics (Odum & Pigeon 1970).

The LEF became the only tropical site in the LTER Network in 1988. Our initial approach focused on mid-elevation *tabonuco* (*Dacryodes excelsa*) forest. We then explored climate effects on tropical forests by expanding up the mountain along a climate gradient (Fig. 4; Gonzalez et al. 2013). To address the effects of current and past land uses, we extended our research down the mountain to include the mosaic of active and abandoned farmlands and urban areas surrounding the LEF (e.g., *Thomlinson et al. 1996*, *Grau et al. 2003*, *Herrera-Montes & Brokaw 2010*, *Marin-Spiotta et al. 2009*). The broad range of ecosystems included in LUQ facilitated testing the generality of our early findings, and exploring temporal as well as spatial scaling questions. Products from the last 6 years of LUQ include 168 peer-reviewed publications, 7 books and special features, 39 book chapters, and 10 dissertations and theses. Below, we briefly outline the foci of our early research and detail the goals and accomplishments of our most recent activities. All LUQ publications are in *italics* and the 10 most significant publications from LUQ IV are also underlined.

From its inception, LUQ has focused on understanding the role of disturbance in shaping the biotic communities and biogeochemical cycling of tropical forest ecosystems. Our early work (LUQ I-III) led to three key conclusions that guide our current research (Figs. 4a-c):

1. Disturbance shapes the climatic, biotic, and biogeochemical characteristics of the Luquillo Mountains, but responses to disturbance are mediated by initial conditions and characteristics of the disturbance (*Waide & Lugo 1992*, *Walker & Willig 1999*, *Brokaw et al. 2012*). Thus, the effects of disturbance are contingent on previous disturbance events. Hurricanes exert their primary effects through canopy opening and organic matter deposition, in order of importance (*Shiels & González 2014*).
2. Climate is a primary determinant of the distribution of biota and rates of biogeochemical cycling in the LEF (*Barone et al. 2008*, *González et al. 2013*). Long-term directional change in climate is taking place in the LEF, and rates of change are more rapid than previously realized. Both models and empirical data suggest that rainfall is decreasing and temperature is increasing in the Luquillo Mountains (*Scatena 1998*, *van der Molen 2010*, *Schaefer 2003*, *González et al. 2013*).
3. The interaction between changing climate and disturbance regime will result in ecosystems characterized by novel species compositions, with altered structures, biogeochemistry, and ecosystem services (Doyle 1981, *Sanford et al. 1991*, *Covich et al. 1991, 1996*, *O'Brien et al. 1992*, *Silver 1998*, *Wang et al. 2002a, b*, *Erickson & Ayala 2004*, *Dodds 2006*, *Bouskill et al. 2013*). Determining how these new ecosystems will develop and evolve under dynamic climate and disturbance regimes is a long-term theme of LUQ.

## 2.1 Luquillo LTER IV

During LUQ IV (2008 – 2014), we examined how disturbance interacts with changing climate to drive changes in tropical ecosystems and the services that they provide using long-term datasets, models, and new experiments (Fig. 4d). Our research focused on three themes: 1) how disturbance and associated environmental characteristics influence long-term ecosystem response; 2) how climate variability determines the diversity and distribution of plants and animals, soil C storage, and greenhouse gas dynamics; and 3) how land use and its legacies modify forest composition as well as the quantity and quality of water, aquatic food webs, and subsequent land cover. The following sections summarize our results and indicate key questions that have arisen from our research.

**Disturbance:** Intense hurricanes (category 2 and higher) are among the most severe natural disturbances that repeatedly impact many tropical forests in ecological timeframes, and thus play a central role in the structure and function of these ecosystems (*Scatena et al. 2012*). Following Hurricane Hugo, which struck the LEF in 1989, some forest processes such as soil nutrient cycling and stream chemistry, returned to near pre-hurricane levels quickly, exhibiting a high degree of resilience (*Zimmerman et al. 1996*, *Brokaw et al. 2012*, *McDowell et al. 2013*; Fig. 5). Others factors, such as forest structure, stream-water exports of coarse particulate matter, and abundances of some plants and animals have never fully recovered their pre-storm values (*Heartsill-Scalley 2010, 2012*, *Willig et al. 2011*). We compared results from research following Hurricane Hugo with responses to Hurricane Georges, an intense storm that occurred almost a decade later. The two hurricanes differed in their effects on both terrestrial (*Canham et al. 2010*, *Royo et al. 2011*, *Willig et al. 2012*) and aquatic ecosystems (*Crowl et al. 2012*). Hurricane Georges resulted in much less structural and compositional change, largely because the branch structure of the forest had not fully recovered, reducing the impact of the second storm on the forest canopy and the amount of woody debris generated. These results demonstrate contingency (*Scheiner & Willig 2011*), that response to disturbance is dependent upon pre-existing conditions. This is a key principle of the conceptual framework for our research (*Waide & Willig 2012*), and shows how disturbance history is an important determinant of subsequent disturbance effects (*Boose et al. 2004*, *Ostertag et al. 2005*).

Data from the two hurricanes suggested that canopy opening and detrital inputs were the dominant drivers of ecosystem response to disturbance (*Walker et al. 1991, 1996*, *Zimmerman et al. 1996*, *Brokaw et al. 2012*, *Crowl et al. 2012*, *Shiels & González 2014*). We used a large-scale manipulation experiment (the Canopy Trimming Experiment – CTE; Fig. 6) to explore the separate and combined effects of canopy opening and detrital deposition. In general, canopy openness was a more important predictor of ecological response. For example, the abundance of seedlings of woody plants increased as a result of canopy opening (*Shiels et al. 2010*), while the abundance of litter arthropods, gastropods, and coqui frogs decreased at least initially (*Richardson et al. 2010*, *Klawinski et al. 2014*). Additional results from the CTE are discussed in sections below. We will repeat the CTE hurricane treatment once a decade to monitor the impacts of frequent intense disturbance on tropical forest biota and biogeochemistry; the second set of experimental hurricane treatments was completed in late 2014.

**Climate:** Ample evidence documents that the Luquillo Mountains, like many regions in the tropics, are changing from very wet, warm, and relatively aseasonal to drier, warmer, and more seasonal ecosystems (*Christensen et al. 2007*, *Comarazamy and González 2011*, *Waide et al. 2013*). Models predict a significant increase in extreme storm events (*Hayhoe 2013*), interspersed with longer and more frequent periods of drought. Models also predict an increase in cloud-base height by 200 m (*van der Molen et al. 2010*) as a result of changes in transpiration and albedo caused by reforestation, a dominant trend in Puerto Rico over the last 60 years (*Zimmerman et al. 2007*). Urbanization, another dominant trend in the area surrounding the LEF, can also have pronounced effects on cloud-base height due to urban heat island (UHI) effects (*Wu et al. 2005*, *Comarazamy et al. 2010*). Preliminary analyses from National Weather Service data in Puerto Rico indicate an increase in cloud height has occurred, and similar changes have been reported in Hawaii (*Diaz et al. 2011*). Understanding how these changes are affecting the upper elevations of the Luquillo Mountains, particularly unique elfin woodlands, is a core goal of our long-term research (*González et al. 2013*).

In LUQ IV, we confirmed our hypothesis that UHI effects on air temperature in eastern Puerto Rico would be similar in magnitude to those predicted from global warming (*Murphy et al. 2011*). Long-term data

showed temperature increases from 1.78 to 2.15 °C at the base of the Luquillo Mountains, and a decreasing precipitation trend in Puerto Rico (*Waide et al. 2013*). However, data from stations within the Luquillo Mountains show variable patterns (*Greenland and Kittel 2002, Heartsill-Scalley et al. 2007, van Beusekom et al. 2015*), suggesting significant local variation in long-term precipitation trends. These local patterns in rainfall will result in highly variable runoff in the drainage network (*McDowell et al. 2012, Jones et al. 2012*). One future challenge, therefore, will be to link the effects of global, regional, and local drivers to forecast future climate scenarios in the Luquillo Mountains and their impacts on the biota and biogeochemical cycling.

The predicted increase in the frequency of drought is likely to impact biota and biogeochemical cycling strongly in wet tropical forests. Preliminary studies suggest that dry periods significantly increase soil O<sub>2</sub> availability, lower soil P availability, decrease greenhouse gas emissions, and alter microbial diversity and community structure (*Liptzin et al. 2011, Wood & Silver 2012, Bouskill et al. 2013, Silver et al. 2014*) and significantly influence habitat structure and trophic dynamics in streams (*Covich et al. 2003, 2006*). Knowledge of the regulation of ecosystem structure and function by climate, particularly precipitation, along the elevation gradient in the Luquillo Mountains provides the means to anticipate the effects of future climate changes (*González et al. 2013*). A key question yet to be addressed is how much drying can tropical forests withstand before biota and biogeochemistry are affected and whether these changes will be gradual or reach a threshold of rapid or unpredictable change.

**Biogeochemical Dynamics:** Tropical forests cycle more C annually than any other terrestrial ecosystem on Earth. Disturbance disrupts patterns in C and nutrient cycling, and can lead to different trajectories of ecosystem response (*Lugo et al. 2012*). For example, aboveground biomass and nutrient content were still recovering 15 y after Hurricane Hugo, and species composition and distribution had changed (*Heartsill-Scalley et al. 2010*). In the CTE, canopy opening resulted in the decline of an important functional group of fungi that likely contributed to accelerated P losses from decomposing litter (*Lodge et al. 2014*) and slowed leaf litter decomposition (*González et al. 2014*). Litterfall production was slow to recover, resulting in a decline of 9 Mg C/ha over the first 4 yr (*Silver et al. 2014*). In contrast, C losses via soil respiration recovered rapidly and remained high (1.5 yr, *Silver et al. submitted*), likely resulting in significant C losses from soils. Stream NO<sub>3</sub><sup>-</sup> and K<sup>+</sup> exhibited transient peak concentrations following hurricanes (*McDowell et al. 2013*; Fig. 5d), while stream-water exports of particulate organic matter during intermediate and high flow events were still depressed 16 y after Hurricane Hugo (*Heartsill-Scalley et al. 2012*). Results from the CTE showed patterns in N loss from soils (*McDowell & Liptzin 2014*) that closely paralleled those observed following Hurricanes Hugo and Georges (*Schaefer et al. 2000, McDowell et al. 2013*). This confirmed the hypothesis that increased N in streams following hurricanes is likely derived from terrestrial sources rather than from in-stream processes.

**Land Use:** In LUQ IV, our work in streams highlighted the importance of conservation of headwater catchments for fish and shrimp species in an urbanizing environment (*Hein et al. 2011*). We tested the hypothesis that urbanization increases the magnitude and variability of discharge, light and nutrients that influence in-stream ecosystem processes (*de Jesús-Crespo & Ramírez 2011a,b, Ramírez et al. 2011, Phillips & Scatena 2012, Potter et al. 2014*), thus demonstrating the existence of a tropical equivalent of the Urban Stream Syndrome (*Ramírez et al. 2009*). This work contributed to the establishment of the Urban Long Term Research Area (ULTRA) project in San Juan focused on the Rio Piedras Watershed (*Muñoz-Erickson et al. 2014*). We hypothesized that water withdrawals for human use would increase over levels in 2004 (*Crook et al. 2007*) and 1994 (*García-Martínó et al. 1996*). Estimation of the decadal change in water withdrawals to 2014 supports this hypothesis. Our work in forests showed that the effects of hurricanes are contingent on legacies of previous land use, but that the mechanisms underlying this effect are complex (*Uriarte et al. 2009, Comita et al. 2010*). The diverse responses observed, even among species deemed “shade intolerant” (*Uriarte et al. 2012*), suggest that the interaction between logging and hurricanes will result in a non-analog or novel community composition as species favored by the intermediate disturbance of logging spread through unlogged forest (*Lugo & Helmer 2004, Uriarte et al. 2009, Willig et al. 2012*). Our work led to new questions: how long will the effects of previous land use persist in this system, and how will prior land use affect responses to climate change?

**Populations and Communities:** We used long-term measurements from the Luquillo Forest Dynamics Plot (LFDP) to advance our understanding of forest community dynamics and the factors that determine species richness (*Willig et al. 2007, Kress et al. 2010, Uriarte et al. 2010, Swenson et al. 2012*).

Phylogenetic relatedness explained little of the neighborhood dynamics of juvenile and adult trees (*Uriarte et al. 2010, Swenson et al. 2012*) compared to ecological traits such as wood specific gravity, leaf succulence, and maximum height. Phylogenetic relatedness was more important in explaining spatial patterns of seedling dynamics (*Comita et al. 2009, unpubl.*), where secondary chemistry and, therefore, pathogen and herbivore resistance, was likely to be conserved phylogenetically. This suggests that species-specific enemies may be important in maintaining species diversity (*Zimmerman et al. 2008*). Long-term tree community dynamics in the LFDP also revealed evidence for life history trade-offs important in maintaining tree, shrub, and liana diversity (*Uriarte et al. 2012, Muscarella et al. 2013*).

A key factor influencing community diversity is disturbance (Connell 1978, *Willig & McGinley 1999, Willig et al. 2007, Waide & Willig 2012, Walker and Wardle 2014*). Our modeling efforts suggested that cyclical high hurricane activity (50 yr periodicity; Goldenberg et al. 2001) fosters the establishment of species that would be rare in the absence of major storms, emphasizing the potential importance of storm frequency in controlling species composition over long time periods (*Uriarte et al. 2009*). In the CTE, canopy opening caused heavy recruitment of pioneer, shade intolerant trees, shrubs, and ferns (*Sharpe and Shiels 2014, Shiels et al. 2010, Zimmerman et al. 2014*), slightly increasing species diversity.

The gradient in precipitation and temperature in the Luquillo Mountains provides a surrogate for changing climate and facilitates understanding of how such change may influence the biota (*González et al. 2013*). We hypothesized in LUQ IV that distributions of terrestrial organisms over 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). Surveys provided evidence of clumping in the upper boundaries of tree species along the elevation gradient, evidence of a compartmentalized metacommunity structure (*Barone et al. 2008; Presley et al. 2010*). The gastropod metacommunity exhibited a compartmentalized structure through these same forest types, but showed an un compartmentalized (i.e., Gleasonian) structure along a paired elevation transect through nearby riparian forest dominated by a single species of palm, *Prestoea acuminata* (*Willig et al. 2011, Willig et al. 2013*). *Richardson & Richardson (2013)* used this same approach for their studies of invertebrate distributions with elevation. *Prestoea acuminata* occurs throughout the Luquillo Mountains except on the most exposed ridges where elfin woodland occurs. It lacks ecotypic differentiation (*Fetcher et al. 1999*), likely because of the small physical distance over which the environment changes relative to gene flow. Thus, it provides an ideal focal species to study long-term changes in consumer relationships and trophic dynamics along the elevation gradient; it is a common garden for decomposer and consumer studies (Clausen et al. 1948).

**Productivity:** Primary productivity in LEF headwater streams is exceedingly low (*Merriam et al. 2002, Potter et al. 2010*), and thus secondary productivity is tightly linked to inputs of riparian leaf litter, linking terrestrial and aquatic ecosystems. Both primary and secondary productivity are affected by nutrient cycling associated with large populations of benthic invertebrates, especially freshwater shrimps (*Benstead et al. 2010*). However, secondary productivity of headwater stream consumers is relatively slow and dependent on a mix of detrital and periphyton food resources. Consequently, our observations and models demonstrate that up to seven years are required for the dominant omnivorous shrimp to become reproductive adults (*Cross et al. 2008*). Rates of terrestrial net primary productivity (NPP) in the LEF, like most tropical forests, are among the highest on Earth, and decline with increasing elevation (Fig. 7). Recent research suggests that NPP and plant and soil C stocks in these forests may be more sensitive to climate than previously believed (*Wood et al. 2014*). Nitrogen is abundant in the forests of the LEF (*Silver et al. 2011*), and does not limit NPP (*Cusack et al. 2010*). Variation in production along elevation gradients in the Luquillo Mountains is tightly coupled with variation in population, community, and metacommunity structure in gastropods (*Willig et al. 2011, 2013*), providing strong support for the “more individuals hypothesis” (Srivastava & Lawton 1998). How these relationships change under altered precipitation and disturbance regimes is a key focus of our long-term research going forward.

## 2.2 Cross Site Activities, Supplemental Funding, and Broader Impacts

LUQ contributes to many collaborative activities. These include cross-site, Network-level databases on climate and hydrology (ClimDB, HydroDB, StreamchemDB), and participation in LIDET (Long-term Intersite Decomposition Experiment Team, *Parton et al. 2007, Cusack et al. 2009, Currie et al. 2010*) and LINX (Lotic Intersite Nitrogen eXperiment, *Webster et al. 2003, Findlay et al. 2011, Potter et al. 2010*).

Cross-network collaborations are conducted with NEON (National Ecological Observatory Network), STREON (Stream Experimental and Observatory Network), LCZO (Luquillo Critical Zone Observatory), IGERT, and San Juan ULTRA-Ex. LUQ is a member of NeoSelvas and Cloud Forest Research Coordination Networks (RCN) as well as Smithsonian's Center for Tropical Forest Science – Forest Global Earth Observatories (CTFS – ForestGEO; *Anderson-Teixeira et al. 2015*). We recently spearheaded an effort to document the broader impacts from participation in the LTER Network on a broad cross-section of the LTER community. We assembled a suite of ~ 40 introspective essays, followed by analyses by social and behavioral scientists and a historian, to understand how participation in the LTER Program has changed the nature of scientists (*Willig & Walker 2015*).

We used **supplemental funds** during LUQ IV (total \$543,664) for Schoolyard LTER, Research Experience for Undergraduates (REU) and Research Experience for Teachers (RET); international research; network-level activities in IM and landscape studies; and research equipment and sample analyses. The Schoolyard LTER program included workshops for students and teachers at El Verde Field Station, and research symposia for students and teachers. LUQ REU and RET involved nine students and three teachers (one from Puerto Rico, two from mainland US) studying stream and forest ecology. International research included three workshops on comparing results and standardizing methods for research on hurricane effects, held in Mexico, Florida, and Colorado. A supplement supported an LTER Network-level workshop on incorporating social science into LTER, as well as studies of how specific institutional arrangements affect human decisions about the landscape surrounding the LEF. LUQ participated in a cross-site LTER study of land-cover and land use change and in Network-level IM efforts on managing sensor data, incorporating GIS into IM, and improving EML with DRUPAL. Supplemental funds also paid for meteorological, stream sampling, laboratory, and computer equipment and for sample analyses.

As part of our **broader impacts**, 55 graduate and 83 undergraduate students have been involved in LUQ over the last 6 yr. Our Schoolyard LTER program reached 1050 students in Puerto Rican high schools, and 954 teachers and 1662 students via our interactive teaching website Journey to El Yunque. The leveraged funds included a \$1,100,000 grant from the US Dept. of Education for an ongoing evaluation of how Journey to El Yunque affects motivation and learning. Since 2008 a site REU program based at El Verde Field Station, and strongly connected to LUQ, has involved 56 students, 55% of whom represent minorities, and produced 12 publications, eight with the student as first author. The LFDP, CTE, and other LUQ field projects have been supported by volunteer internships for recently graduated students seeking experience in tropical research. Since 2008, 60 students have participated (over 50% women and 30% minorities), and many have gone on to pursue academic studies.

### 3.0 RESEARCH APPROACHES

#### 3.1 Long-term Measurements and Experiments in *Tabonuco* Forest

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. Chief among the long-term measurements are the **Luquillo Forest Dynamics Plot** (LFDP; Fig. 8) and the **Bisley Experimental Watersheds** (BEW) located in *tabonuco* forest (200 – 600 m asl) on windward and leeward sides of the LEF. The LFDP covers 16 ha in which >110,000 woody plant stems  $\geq 1.0$  cm dbh have been studied over two and half decades (*Thompson et al. 2002, Zimmerman et al. 2010*). A large plot is needed to study species-rich communities where rare species are frequent, and to examine mechanisms promoting species diversity and coexistence (Condit 1995, Wills et al. 2006, *Zimmerman et al. 2008*). In the LFDP, we conduct spatially explicit censuses of trees, shrubs, seedlings (since 1999), and phenology/seed rain (since 1992) at time intervals relevant to their dynamics. Addition of dendrometers to the largest trees and annual measurements of CWD in the plot allows us to estimate C storage in the plot as well. In 2010, we began monitoring soil moisture monthly (0-10 cm depth) in 320 m<sup>2</sup> plots. Intensive soil moisture measurements are made during dry periods ( $\geq 3$  days without rainfall). The abundance of key heterotrophs, including gastropods and phasmids, as well as lizards, frogs, and birds are measured at forty locations placed on a 60 x 60 m grid in the LFDP. The BEW are two adjacent watersheds that total 13 ha. Forest composition and soil and plant nutrient content are monitored in 83 permanent 10 m diameter plots on a 40 x 40 m grid every 5 years. Throughfall, litterfall, and stream

chemistry are measured weekly, along with coarse particulate export (*Heartsill-Scalley et al. 2007, 2010, 2012*), which is measured every two weeks.

**Stream Monitoring** is conducted in three streams of the BEW and in two streams in the El Verde Research Area, the Quebrada Sonadora and the Q. Prieta. Chemistry is measured weekly in these streams (since 1983), as well as in additional streams gauged by the USGS. In the Q. Prieta, we have monitored decapod shrimp weekly at 19 locations (pools) since 1988. Decapod abundances are also measured twice yearly in two BEW streams. Algal abundance, ecosystem metabolism, chlorophyll a, and insect abundance are measured biannually in the Q. Prieta and one BEW stream. The upper section of the Q. Prieta is where we will locate a new Stream Drought Experiment (see below and Fig. 9).

The **Canopy Trimming Experiment (CTE)** was established in the El Verde Research Area in 2002. Initially, this experiment was designed to separate the two principal effects of hurricanes, canopy opening and debris deposition (*Shiels & González 2104*). The CTE has helped us distinguish the effects of microclimate, detrital inputs, and different functional groups of decomposers in detrital processing and ecosystem resilience after hurricanes (*Shiels & González 2014*). Thereafter, through a series of repeated canopy manipulations, the CTE will allow us to assess the effects of a projected increase in the frequency of intense hurricanes (Knutson et al. 2012) on forest composition, soil C storage, and nutrient dynamics (Sanford et al. 1991). The experiment originally included four treatments in each of three blocks. Each treatment covers a 30 x 30 m area and includes: 1) canopy trimmed, with trimmed biomass distributed on the forest floor, changing microclimate, forest floor mass, and nutrient content, 2) canopy trimmed, with trimmed biomass removed changing microclimate, 3) canopy not trimmed, but canopy biomass from a trimmed plot distributed on the forest floor, changing forest floor mass and nutrient content, 4) untreated control. To simulate an increased frequency of intense hurricanes, treatments 1 and 4 (hurricane and control) are being repeated every 10 years for at least 50 years total. The first of the repeated disturbances, the second canopy trimming treatment, took place in late 2014; measurements are continuing (Table 1).

**Table 1.** Continuing measurements in the CTE and scientists charged with their collection.

<b>Abiotic</b>	<b>Frequency</b>	<b>Lead(s)</b>
Temp (air and soil)	Hourly	Ramírez & González
Soil & litter moisture	Bi-weekly-annually	Ramírez & González
Canopy openness	Quarterly	Zimmerman
Throughfall	Biweekly	Ramírez
<b>Biotic</b>		
Plants except ferns	Annually	Zimmerman
Ferns	Annually	Sharpe
Soil microbial biomass/classification	Biweekly-annually	Cantrell/Lodge
Litter fungi connectivity	Monthly-annually	Lodge
Density of frogs	Bi-annually	Shiels
Density of anoles	Bi-annually	Shiels
Density of litter/litterbag arthropods	Bi-annually	González/Cantrell
Density of understory spiders	Bi-annually	Shiels
Canopy arthropod density/structure	Bi-annually	Schowalter
Density of gastropods and phasmids	Bi-annually	Willig & Bloch
<b>Ecosystem Processes</b>		
Litterfall mass & chemistry	Biweekly	Ramírez
Tree diameter increments	Annually	Zimmerman
Litter decomposition rates	6 mos post-trim	Cantrell, Barbarena
Understory herbivory rates	Annually	Prather
Soil nutrients (total & avail)	Quarterly	Lodge/González
Soil carbon pools and fluxes	Annually/periodically	Silver
Soil solution chemistry	Weekly - quarterly	McDowell

During the next three years, the **Throughfall Exclusion Experiment** (TEE) will be used to determine the impact of multiple short-term droughts on soil biogeochemistry as well as on microbes, seedlings, and litter organisms. Small (3 x 3 m) clear plastic structures significantly reduce soil moisture without causing significant changes in other environmental conditions (e.g., temperature or light; *Wood & Silver 2012*, *Bouskill et al. 2013*). Replicate shelters will be placed in ridge, slope, and valley positions, and paired with untreated controls. Roofs are removed weekly to deposit collected litterfall on the soil surface. Throughfall amount and chemistry will be measured according to *Wood & Silver 2012* allowing us to determine both water and nutrient removal as a result of simulated drought. We will use volumetric moisture and temperature sensors, a Hydrosense CS620 for gravimetric moisture (Campbell Scientific, Logan, UT), and soil psychrometers (Wescor PST-55, Logan, UT) to convert soil moisture measurements to soil water potential. Soil O<sub>2</sub> sensors (Apogee Instruments, Logan UT) will be installed in a subset of plots in each topographic position. Each shelter will be divided into quadrats to minimize any sampling effects across different measurements (i.e. seedlings, sensors, soil, litter organisms). Results of the TEE will be incorporated into models to investigate potential long-term effects and will help us evaluate feasibility of future large scale throughfall exclusions, which are logistically challenging in the forested ecosystems (Meir *et al.* in press).

We will also establish a **Stream Drought Experiment** (SDE) in two 150-m long stretches of tributaries of the Q. Prieta (Fig. 9). Our long-term data provide a basis for the selection of these two study reaches: the Prieta has been studied for over 25 years (Schaefer *et al.* 2000). We will construct a dam and weir to divert 50% of stream flow (excepting high flow events) to below the de-watered reach between June-Aug (predicted by downscaled climate models to show the largest increase in drought) over three consecutive years during this funding cycle and three additional years in the future. An un-manipulated arm of the stream with similar slope, width (1-3 m), biota, and chemistry will serve as a reference reach. We will add riparian leaf litter to the stream in pulses during the drought treatment to simulate increased leaf drop. We will use Randomized Intervention Analysis (RIA, Carpenter *et al.* 1989), a design well suited to the analysis of un-replicated whole-ecosystem manipulations. RIA requires a manipulated system and a reference system. As required for RIA, all measurements will be conducted concurrently in both streams to create a time-series for each characteristic. Similar to other whole-stream manipulations using RIA (Wallace *et al.* 1997), we will collect 2 y of pre-manipulation data (2016-17) before the beginning of the reduced-flow manipulation, resulting in 1 y of post treatment data (2018) for the current proposal, to be continue to complete at least 6 y of post treatment data. A future manipulation (LUQ VI) will include litter inputs and canopy opening in both tributaries of the Q. Prieta. Mapped trees in the 1 ha area will allow estimation of litter inputs during experimental studies (*Uriarte et al.* in press).

### 3.2. Long-term Monitoring of the Elevation Gradient

The Luquillo Mountains, ranging to 1075 m in elevation, 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). Forest communities vary along the gradient from mid-elevation (200-600 m asl) *tabonuco* forest, *palo colorado* forest (600-900 m), and elfin woodland (900-1075 m; Fig. 10). Palm forest, an edaphic formation, occurs at all elevations. Every six years we measure emergent ecosystem properties in three series of **Long Term Elevation Plots** (LTE) placed at 50 m intervals along the gradient. In one of these series (Sonadora transect) we compare upland forest types to adjacent palm forest (Table 2). We also monitor climate, rainfall chemistry, diameter increment, and litterfall. Soil properties and plant species composition have been measured in these plots; we have also conducted decomposition experiments as part of previous LTER research (*Silver et al. 1999*, *McGroddy & Silver 2000*, *Dubinsky et al. 2010*). The infrastructure for the LTE, where we will continue long-term monitoring of community changes, was established for vegetation in LUQ III (Barone *et al.* 2008) in three watersheds (Mameyes, Icacos, and Sonadora).



**Table 2.** Measurements along the elevation gradient in the Luquillo Mountains. Measurements are divided into those measured every six years at a spatial scale of 50 m elevation intervals versus those measured at daily to monthly time scales in plots placed at elevations along the gradient (roughly corresponding to tabonuco, palo colorado, and elfin woodland). Lead scientist for each set of measurements appears in parentheses.

Long-Term Elevation Plots
<p><b>Climatic characteristics (continuous)</b></p> <ul style="list-style-type: none"> <li>• Meteorology and micro-meteorology along mixed forest and palm forest transects in the Sonadora watershed. (Ramírez)</li> <li>• Rainfall, air temperature, and soil temperature. (González &amp; Silver)</li> </ul> <p><b>Biotic communities (every 6 y)</b></p> <ul style="list-style-type: none"> <li>• Trees (adults and seedlings) and ferns along the Sonadora, Mameyes, and Icacos watershed transects. Trees (adults and seedlings) and ferns in the Sonadora (Zimmerman &amp; Heartsill-Scalley)</li> <li>• Gastropods in the Sonadora Watershed (Willig)</li> <li>• Litter invertebrates in the Sonadora Watershed (González)</li> <li>• Canopy invertebrates in the Sonadora watershed (Schowalter)</li> <li>• Stream insects along an elevational gradient in the Sonadora watershed (Ramírez)</li> <li>• Stream decapods in the Sonadora watershed (Crowl &amp; Covich)</li> <li>• Birds, reptiles, and amphibians in the Sonadora watershed (Waide)</li> <li>• Microbes in the Sonadora watershed (Cantrell)</li> <li>• Stream algae in the Sonadora watershed (Pringle)</li> <li>• Grazing and Detrital Trophic Webs (or Networks) based on <i>Prestoea acuminata</i> (Sierra Palm) in the Sonadora Watershed (Waide &amp; Willig)</li> </ul> <p><b>Biogeochemical Cycling &amp; Ecosystem Processes (periodic)</b></p> <ul style="list-style-type: none"> <li>• Production (estimated by tree growth) every 6 y (Zimmerman)</li> <li>• Decomposition rates (using popsicle sticks and palm leaf litter) over 1-3 y (Silver &amp; González)</li> <li>• Nutrient (N, P, Ca) fluxes in litterfall quarterly (González &amp; Silver)</li> <li>• Soil descriptions 1 time (González &amp; Silver)</li> <li>• Litterfall every 2 weeks (González &amp; Silver)</li> <li>• Rainfall chemistry weekly (González &amp; Silver)</li> </ul>

**3.3. Modeling** – We employ a suite of models to integrate our understanding of the impacts of a changing climate and disturbance regime on ecosystems in the LEF (Fig. 11A) and forge predictions of future change. We used the Century model (e.g., Sanford *et al.* 1991, Zimmerman *et al.* 1995, Wang *et al.* 2002, Johnson *et al.* 2011, Lash-Whitney *et al.* 2013) and, more recently, the daily time-step version, DayCent (Silver *et al.* *in prep*) to understand biogeochemical dynamics in LEF ecosystems under different disturbance and climate scenarios. We developed the spatially-explicit forest demography model SORTIE (Uriarte *et al.* 2004, 2005, Canham *et al.* 2010) to make predictions of novel community assemblages arising from the interaction of land use legacies and hurricane disturbance in the LFDP (Uriarte *et al.* 2009). SORTIE includes a litterfall submodel (Uriarte *et al.* *in press*) used to estimate the influence of litterfall on soil nutrients (Uriarte *et al.* *in press*), seedling establishment (Muscarella *et al.* 2013), and inputs to streams.

During LUQ V we added statistical downscaling of global circulation models to understand global climate variation as a regional driver of change. During the remainder of LUQ V, we will implement the Ecosystem Demography model (ED2) in the LEF (Moorcroft *et al.* 2001, Medvigy *et al.* 2009). By aggregating species into functional groups, ED2 accounts for detailed, mechanistic representations of C and water fluxes between the forest and the atmosphere in response to climate variability and soil properties. ED2 explicitly incorporates climate and can inform or corroborate the belowground processes from DayCent, where SORTIE cannot. During LTER V we will develop and parameterize ED2 to incorporate 1) tree data along the elevation gradient to model their dynamics, 2) a hurricane disturbance

model, and 3) downscaled climate and hurricane scenarios (e.g., Uriarte & Papaik 2007) to predict impacts of future climate. Finally, we will develop a consumer/decomposer trophic dynamics model for streams and adjacent riparian areas to complement the stream-water diversion and elevation studies. We will begin with a terrestrial component based on the common, well-studied riparian palm *P. acuminata* (Presley et al. 2011, Willig et al. 2011, 2013, Richardson & Richardson 2013). These modeling efforts span the range of temporal and spatial scale relevant to montane tropical ecosystems (Fig. 11B) and give us the ability to construct a synthetic understanding of tropical forest ecosystem dynamics confronted with a changing climate and disturbance regime.

#### 4.0. PROPOSED RESEARCH

##### 4.1 Question I: What Are the Short- and Long-Term Effects of Drought on Biota and Biogeochemical Cycling in Tropical Forests?

Global circulation models predict that the majority of the Caribbean will be much drier by the end of the century, suffering as much as a 50% reduction in annual rainfall (Neelin et al. 2008, Comarazamy & González 2010). This reduction will be accompanied by changes in the timing of rainfall, i.e., increased seasonality that will depart significantly from recent 30-year (i.e., climatic) patterns (the precipitation regime). Increased frequency of drought predicted to take place during this century will likely have profound effects on biotic communities and biogeochemical cycling within the Luquillo Mountains. The effects of projected drying trends may vary among ecosystems with different initial environmental characteristics. Elevation, topography, historical land use, and current distribution of plants, animals, and microbes contribute to environmental characteristics and define the axes along which studies of drying will be conducted.

The effects of drought are expected to manifest progressively (Smith et al. 2009). Small organisms (e.g., microbes, invertebrates, seedlings, juvenile amphibians and crustaceans) are likely to respond rapidly (e.g., days to months) to decreased moisture with increased mortality rates and demographic changes. Some biogeochemical processes are also likely to respond rapidly due to direct physical effects (e.g., improved aeration, decreased hydration) and indirect effects associated with changes in the composition, abundance, and activity of biota. Over longer (e.g., annual to decadal) periods, more frequent and longer droughts will decrease NPP, lead to more pulsed litterfall inputs, and increase light levels below forest canopies (e.g., Beard et al. 2005). These changes in environmental conditions will in turn feed back on the abundance of organisms and community structure. By 2100, we expect to see significant shifts in species composition and associated community structure, lower C storage, and generally slower biogeochemical cycling.

We tailor our hypotheses, experiments, and measurements to address changes expected over both short and long temporal scales. We will explore the effects of drought through ongoing measurements of species composition and habitat associations in the LFDP and along the elevation gradient, and through manipulative drought experiments in the *tabonuco* forest. Results from these experiments will provide data on the consequences of drought, and allow us to test models of long-term consequences of a changing precipitation regime. These manipulations also lay the groundwork for expanded precipitation manipulations in future funding cycles. Our long-term measurements of precipitation, plant and animal populations and communities, and biogeochemical cycling in the LFDP and BEW will allow us to follow the consequences of climate drying for these communities. Similarly, spatially extensive vs. temporally intensive monitoring of climate, biogeochemistry, productivity, and species distributions along the elevation gradient will allow detection of any key alterations in these attributes resulting from a change in precipitation regime. Note that the first name after each hypothesis will serve as coordinator, while the others are primary contributors.

**Hypothesis 1a.** *Over the short-term, droughts will alter the spatial dynamics of seedling survival and growth along catenas. Drought effects will be exacerbated on well-drained ridges favoring drought tolerant species, while in poorly drained valleys drought will improve soil aeration and generally enhance survival and growth. (Zimmerman, Uriarte, Thompson, Walker)*

**Hypothesis 1b.** *Over the long-term, increasing frequency of drought will lead to changes in community composition as drought-sensitive wet forest species become locally extinct or restricted to moist soils environments. High elevation forests may suffer more rapid changes in community composition, once a critical threshold of drying has been reached. (Uriarte, Waide, Willig, Zimmerman)*

**Background** – Topography is a strong driver of plant demography in forest ecosystems through effects on microclimate, edaphic conditions, and disturbance (Franklin 1995). Species distributions vary predictably along catenas (e.g. ridge, slope valley toposequences) in the LEF, following patterns in soil moisture and drainage (Wadsworth and Bonnet 1951, Frangi & Lugo 1985, Scatena & Lugo 1995, Willig *et al.* 2013). Differential drought tolerance of seedlings along catenas could lead to large shifts in community composition and structure over the longer term (Engelbrecht *et al.* 2007, Muscarella *et al.* 2013). We predict that drought will increase seedling survival and growth for all species in high soil moisture environments (low topographic zones) due to alleviation of anoxic soil conditions (Silver *et al.* 1999). Seedlings of species associated with well-drained ridges may be more vulnerable to periodic drought (O'Brien *et al.* 2013), although it is also possible that these species will exhibit drought avoidance mechanisms such as deep roots and deciduousness (Brenes-Arguedas *et al.* 2013).

Elevation is also an important driver of population and community structure through effects on climate, soils, and disturbance regime. Mountains represent important model systems (Garten *et al.* 1999) for conducting natural (i.e., observational) experiments (Körner 2003) because their global distribution across all continents and latitudes allows comparative studies of broad-scale ecological patterns (Grytnes & McCain 2007, McCain & Grytnes 2010). The rapid rate of change in environmental characteristics within relatively short geographic distances along elevation gradients provides insight into the mechanisms that mold species distributions and community assembly (Whittaker 1960, Terborgh 1971) that can then be contrasted among taxa (Presley *et al.* 2012), or over time (Rowe 2007, Moritz *et al.* 2008). Climate changes along elevation gradients strongly challenge species tolerances in both evolutionary and physiological contexts (Grubb 1977, Cavalier 1986). Theory predicts that tropical organisms will respond more strongly to environmental changes along elevation gradients compared to temperate organisms (Janzen 1967). If true, then environmental responses to global change drivers on tropical mountains may provide an early indication of what the future holds for many of the world's ecosystems.

Over the long-term, a drier climate characterized by more frequent and severe droughts could increase tree mortality and lead to localized extinctions, although few data exist for wet tropical forests. Studying the effects of periodic droughts on adult trees and whole forests is difficult because natural droughts are infrequent relative to most research timespans, and most tropical trees are inherently long-lived (DOE 2012). Observational studies in Panama, the Amazon, Borneo, and Africa found that seasonal and drier tropical forests suffered increased mortality associated with drought events (Feeley *et al.* 2011, Phillips *et al.* 2009, 2010, Fauset *et al.* 2012). Over time in *tabonuco* forest, we expect significant changes in the distributions of plant and animal species as influenced by spatio-temporal variation in soil moisture (as influenced by topography and soil type) (Johnston 1992, Silver *et al.* 1999, 2013). Few studies have explored effects of habitat specificity with regard to drought tolerance in the tropics, and patterns are unclear (e.g., Butt *et al.* 2013, O'Brien *et al.* 2013, but see Fauset *et al.* 2012). We predict that more frequent and persistent dry periods will restrict moisture-loving species to valleys. Rare species more common at higher elevations could disappear, while species from lower elevations may become more common.

**Work Plan** – To predict how a changing precipitation regime leads to population and community changes over time, we need to determine the susceptibility of species to drought. We will begin with a seedling experiment of 24 tree species selected based on their abundance in the LFDP (Thompson *et al.* 2002, Zimmerman *et al.* 2010) and their life history characteristics (Zimmerman *et al.* 1994, Muscarella *et al.* 2013). Seeds of target species will be germinated in individual plastic tubes in a shade house under moderate light and transplanted to replicate treatment and control plots on ridges, slopes, and valleys (e.g., redox gradient, Silver *et al.* 1999). After planting, the seedlings will be allowed to establish in the forest for about 6-9 months before the rainout shelters (Section 3.1) are erected over them. Shelters will be left in place for three months (June-August), which corresponds with the predicted increase in seasonality from global circulation models. Seedling and environmental measurements will follow Engelbrecht *et al.* (2005, 2007) and Engelbrecht & Kursar (2003). Hemispheric photographs will be taken

above each shelter so that potential differences in light availability can be incorporated as a covariate in statistical analyses.

The relative survival rates of species in experimental conditions will open a window for further investigation using the LFDP database. We can determine, for example, (1) the degree to which experimental drought tolerance explains spatial patterns of seedling mortality in the field; (2) how this relates to other measured demographic characteristics such as growth and mortality rates of saplings and adults; and (3) and how drought tolerance relates to other measured ecological traits such as wood density and leaf characteristics (e.g., LMA). The latter, already measured for all species found in the LFDP for both seedlings and adults, offers the opportunity to understand and model the long-term impacts of a changing precipitation regime on the entire tree community.

We will use measurements in the LFDP, BEW, and LTE as well as modeling to explore the long-term impacts of drought on plant communities and associated C storage. Addition of dendrometers to the largest trees in the LFDP combined with annual measurements of coarse woody debris contributes to estimates of C dynamics over time. Beginning in 2016, we will monitor changes in the distribution of key biota in the LTE every 6 years. This will allow us capture any important changes occurring over the long-term (i.e., over the remainder of the century) while being logistically feasible. More frequent monitoring will occur following important events such as intense hurricanes or severe droughts because they will likely cause rapid changes in biotic distributions. Vegetation will be monitored along all three transects, but we will only measure animal populations (Table 2) in the Sonadora watershed. Primary forest extends to the lowest elevation along the Sonadora transect (300 m, *Foster et al. 1999*), which intersects the LFDP and other studies in the El Verde Research Area, providing a direct link between long-term data from *tabonuco* forest and the gradient studies.

We will use a modeling approach to explore the long-term and large-scale impacts of changes in precipitation and associated mortality in SORTIE. Measured drought tolerance in the throughfall exclusion experiment will be compared to field measurements of seedling mortality and juvenile and adult mortality and growth as described above. These data will provide a starting point for establishing parameters for drought impacts on species demography. More severe drought scenarios can be extrapolated by assuming juvenile mortality operates in parallel to seedling mortality at progressively lower relative rates among larger ontogenetic classes (*Lasky et al. in press*). Our future goals are to use data on the presence or absence of species along the elevation gradient and associated environmental characteristics (e.g., physical [slope, aspect, soil type]; climatic [mean temperature and precipitation; variability of temperature and precipitation]) to parameterize a suite of models to explore alternative drought scenarios. We anticipate that the interaction between changing climate and physical variation will produce new biotic communities that will fundamentally change biogeochemical cycling. Trophic models calibrated for these new communities will provide a tool to predict community dynamics and the effect of change on growth and decomposition. Results from this work will inform biogeochemical models (e.g., DayCent, ED2) that will predict stand and forest-level changes in carbon and nutrient stores. In LTER VI we will expand our rainout shelter experiments along the elevation gradient to test model predictions.

**Hypothesis 2a.** *Increased frequency of drought will enhance soil C storage in the short term due to slower decomposition rates associated with changes in the activity, abundance, and community composition of microorganisms and litter fauna. Greater soil oxygen availability during drought will increase soil P retention over the short-term, and decrease nitrous oxide and methane emissions resulting in a negative feedback to climate change. (Willig, Bloch, Cantrell, Gonzalez, Lodge, McDowell, Pett-Ridge, Schowalter, Silver, Waide)*

**Hypothesis 2b.** *Over the longer term, greater drought frequency in tropical forests will decrease soil C storage. This will result primarily from lower NPP and associated C inputs in response to plant water stress and decreased P availability. (Silver, Lugo, McDowell, Wood)*

**Background** – Soil and litter organisms play a key role in C storage and nutrient dynamics of terrestrial ecosystems (Lavelle et al. 1997, *González & Seastedt 2001*, Hattenschwiler et al. 2005), but little is known about how these organisms are responding to climate change. Microbial activity often responds rapidly (days to months) to environmental change in tropical forests, leading to highly dynamic patterns in biogeochemical cycling (*Silver et al. 2001*, Cleveland and Townsend 2006, *Wood & Silver 2012*). In wet

tropical rainforest environments, periodic drought represents a significant perturbation that is likely to alter community structure (*Bouskill et al. 2013*, Waring & Hawkes 2015) and activity (*Cleveland et al. 2010*, *Wood & Silver 2012*, *Wood et al. 2014*) of soil microorganisms. Although it is difficult to link changes in microbial communities directly to biogeochemical cycling at the field scale, laboratory assays of LEF soils showed that soil respiration, microbial biomass, and microbial diversity all declined under static aerobic conditions (one impact of soil drying) relative to fluctuating redox conditions (Pett-Ridge et al. 2006). Long-term observations suggest that soil microbial communities in the LEF are very sensitive to drought (*Lodge et al. 1994*, *Lodge 1993*, *Lodge & Cantrell 1995*). Experimental drought in the LEF decreased soil microbial diversity by 40% in the LEF, and led to dramatic changes in microbial community composition, functional potential and enzyme expression (*Bouskill et al. 2013*). We predict that shifts in the activity of bacteria relative to fungi with drought (*sensu* Fuchslueger et al. 2014) could have significant implications for C storage and C turnover in the LEF.

Even less is known about how soil and litter fauna respond to drought in the wet tropics, although evidence from other ecosystems suggests a high degree of sensitivity (Wheeler & Levings 1988, Caldwell & Vitt 1999, Liiri et al. 2002, Schlaghamersky et al. 2014). This is particularly true for gastropods and frogs, which are considered sentinel species in the LEF because of their sensitivity to soil moisture conditions and their effects on litter processing and nutrient dynamics (*Beard et al. 2002, 2003*). Long-term data and experimental manipulations document that gastropod populations and communities responded to local-scale variation in environmental conditions along catenas (*Alvarez & Willig 1993*; *Secrest et al. 1996*, *Willig et al. 1998, 2007 2014*, *Bloch & Willig 2006*). Because most gastropod species are adapted to high levels of moisture, we predict decreased species dominance in drought treatments. Similarly, the abundance and survival of frogs was strongly linked to patterns in rainfall in the LEF (*Stewart 1995*). Long-term data showed that frog abundance was negatively correlated with the number of days with  $\leq 3$  mm rainfall, as well as the number of dry periods throughout the year. We predict that the abundance of small frogs sampled from litter will decrease in the rain out treatment.

The majority of research on the biogeochemical effects of drought in the tropics has been conducted in seasonally dry environments. For example, NPP and heterotrophic respiration were resistant to natural droughts in seasonal Amazonian forest, but autotrophic respiration was not (Doughty et al. 2015). Methane consumption increased and N<sub>2</sub>O emissions decreased during an experimental drought, presumably due to increased soil aeration, although soil O<sub>2</sub> was not measured (Davidson et al. 2008). Less work has been done on the biogeochemical effects of drought in aseasonal wet tropical forests, where the absence of prolonged dry periods leads to near constant high soil moisture availability. Theory predicts that soil respiration follows a humped-shaped distribution with regard to soil moisture, with lower rates in saturated soils due to anoxia and diffusion limitation and low rates in dry soils due to moisture stress (Davidson et al. 2006). Preliminary research in the *tabonuco* forest showed that a short-term (3 month) partial drought significantly decreased soil respiration on ridges and slopes, but not in waterlogged valleys (*Wood & Silver 2012*). Both roots and microbial activity contribute to soil respiration, and there are several ways in which droughts could affect their C dynamics. In well-drained soils, live root biomass and associated autotrophic respiration may decline in response to localized drying; alternatively root biomass and respiration could increase if drought increases aeration in poorly drained soils. Roots are thought to be a dominant source of soil C in many ecosystems (Rasse et al. 2005), and thus both the activity and fate of roots during drought are likely to significantly impact soil C stocks.

Drought is also likely to affect N and P cycling and retention in LEF soils. Higher redox potential could lead to increased Fe-P bonding (Chacon et al. 2006), slower P cycling (*Wood & Silver 2012*), and lower P exports. Drying of waterlogged soils could increase nitrification (*Silver et al. 2001*) and stimulate denitrification or nitrate leaching during subsequent storm events (*McDowell et al. 2013*). Overall, we expect that higher redox potential in these soils will result in lower production of CH<sub>4</sub> and N<sub>2</sub>O (*Liptzin et al. 2011*, *Wood & Silver 2012*), although hot spots and hot moments of denitrification could continue to play an important role across the landscape (*sensu* McClain et al. 2003).

Carbon mineral interactions could also affect soil C storage following droughts. In the LEF and highly weathered tropical forest soils elsewhere, Fe is the most abundant anaerobic terminal electron acceptor (*Hall & Silver 2013*), and supports short-term rates of anaerobic CO<sub>2</sub> production that are similar to rates under well-aerated conditions (*McNicol & Silver 2014*). As soil redox increases, lower rates of Fe-induced

C respiration (*Hall & Silver, 2013*) and higher rates of Fe-C bonding (Kleber et al. 2005, Torn et al. 1997) could lead to increased C storage. However, Fe oxidation can also lead to C oxidation through Fenton reactions and the stimulation of DOC production via soil acidification (*Hall & Silver 2013*). On-going complementary work in the LEF is exploring Fe-redox dynamics in relation to C cycling as part of the Critical Zone Observatory and related NSF and DOE sponsored research.

Over the longer term, drought impacts on soil C storage are affected by patterns of C inputs and outputs. In ecosystems with distinct dry seasons, even short-term droughts can lead to increased tree mortality, though the specific mechanisms driving this are not well understood (Meir & Grace 2005, Phillips *et al.* 2009, Doughty *et al.* 2015). The forests of the LEF receive more rainfall and more evenly distributed rainfall than in seasonally dry tropical forests. This, together with clay-rich soils contributes to relatively high soil moisture throughout the year (*Silver 1992*). Repeated droughts and associated water stress will likely decrease plant litter production and litter C and nutrient inputs to the forest floor. Thus we hypothesize that over the long-term, C cycling in wet tropical forests will be most strongly impacted by lower C inputs associated with decreased NPP. Some species have the ability to alter C allocation patterns, increasing root biomass at the expense of leaf area index in response to drought (Doughty *et al.* 2015). Increased C allocation to root biomass could partially or fully offset declines in aboveground C inputs. The impacts of plant reallocation on soil C pools are poorly understood. Net primary productivity is commonly limited by P availability in highly weathered tropical forest soils (*Cleveland et al. 2011*). Lower litterfall rates could slow rates of P circulation, and decrease soil P stocks. Furthermore, the clay-rich soils of the LEF have the propensity to form strong bonds between P and Fe (oxyhydr)oxides. Soil aeration during drought is likely to increase Fe oxidation and associated binding with P, decreasing P availability. Thus lower P availability is a potential mechanism leading to lower C storage during drought. Finally, recent work suggests that microbial respiration per unit biomass may increase during droughts in wet tropical forests (Waring & Hawkes 2015). This could further stimulate soil C losses.

**Workplan** – We will use the TEE to study short-term effects of drought on land (Section 3.1). Decomposition will be measured during the drought in treatment and control plots using litter bags retrieved at 0, 7, 28, and 90 days from placement. Litter will be dried, weighed, and analyzed for C, N, and P. Invertebrates will be extracted from litter bags using Tullgren funnels, sorted, counted, and identified to the lowest taxon possible (*González and Seastedt 2001*). To sample gastropods and frogs, we will use modifications of the protocol for nocturnal sampling of these species employed on the LFDP. For all taxonomic groups, we will calculate changes in functional, phylogenetic, and taxonomic diversity over time and among samples to evaluate the effect of drought on litter trophic webs. We will also relate decomposition rates to invertebrate diversity and microbial community analyses (see below).

Soil and litter will be sampled for microbial communities at the beginning of the experiment and annually thereafter. High-throughput amplicon sequencing of DNA using recommended best practices such as hot-start Taq polymerase and low number of amplification cycles (Smith & Peay 2014) will be conducted using 16S and ITS Illumina iTags (targeting bacteria, archaea, and fungi), followed by quality control screening including backward and forward sequence matching, and chimera and short sequence removal in QIIME, UPARSE and USEARCH. qPCR will be used to enumerate functional groups (denitrifiers, ammonia oxidizers, methanogens, methanotrophs) and total bacteria/archaea (Fierer *et al.* 2005) and fungi. Trace gas fluxes (CO<sub>2</sub>, N<sub>2</sub>O, and CH<sub>4</sub>) will be measured every two weeks using surface flux chambers (*Wood & Silver 2012*). Porous cup tension lysimeters will be used to measure dissolved organic C, N and P and dissolved inorganic N and P as an index of leaching losses. Soils will be sampled for total C and N and extractable soil P concentrations before and after drought treatments (Tiessen & Moir 1993). Soil cores will be sampled for fine live and dead root biomass at the beginning of the experiment (n = 2 per plot) and at the end of each drought period thereafter (Silver & Vogt 1993). Although our small plots are not expected to induce stress on whole trees, we do expect root response to localized drying, providing an index of drying effects on C inputs from roots. Patterns in soil biogeochemistry, root biomass, and microbial communities will be explored over time and space using ANOVA (repeated measures for the temporal dynamics). We will use robust regression analyses to identify relationships among soil C pools, P availability, greenhouse gas fluxes, in relation to biotic communities and root dynamics.



We will use long-term measurements of C and nutrient pools and fluxes along the elevation gradient (Table 2) to identify responses to natural variation in rainfall as a test of Hypothesis 2b. To inform future work, we will begin with modeling experiments to identify potential gaps in knowledge and help guide the design of future research. We will use the DayCent biogeochemical model to determine the potential impacts of repeated drought on soil C storage and biogeochemical cycling. We will use the model to test the effects of increasing drought frequency based on climate scenarios for the region (see Hypothesis 7), as well as a worst-case scenario defined as two times the frequency and/or severity of the predicted future conditions for 2080. We will use this as a benchmark against which to evaluate relative change between present conditions and potential future ones. Model runs will consider both short-term and long-term effects on soil C pools, plant productivity, and a suite of C, N, and P fluxes in litterfall, gas emissions, leaching, and internal cycling. Field data gathered as part of Hypothesis 2a will be used to validate results and should allow us to improve model performance and predictive capacity.

**Hypothesis 3a.** *Increased frequency of drought will be accompanied by decreased stream discharge, increased leaf-litter subsidies and patchy anoxic conditions in stream pools, resulting in: (i) changes in stream trophic dynamics; (ii) increased rates of leaf decomposition; and (iii) increased production and evasion of CH<sub>4</sub> and N<sub>2</sub>O due to higher nutrient and DOC levels and periodic development of anoxic conditions. (Covich, Crowl, Heartsill-Scalley, McDowell, Pringle, Ortiz, Ramirez)*

**Hypothesis 3b.** *Longer-term, cumulative effects (3-6 y) of increased drought frequency will occur despite brief high discharge events that “reset” the system (in-between droughts), resulting in: (i) reduced subsidies of emergent aquatic insects to forest food webs; (ii) enhanced algal primary production; and (iii) extended periods of increased leaf-litter storage. (Crowl, Covich, McDowell, Pringle, Ortiz, Ramirez)*

**Background** – A short-term consequence of droughts is that progressively pulsed leaf litter inputs become concentrated in increasingly shallow pools along with invertebrate consumers (shrimps, crabs, and aquatic insects), resulting in increased leaf-litter processing rates, stronger predator-prey interactions, and alteration of in-stream nutrient cycling. Predatory shrimp (*Macrobrachium* spp.) disperse farther upstream into pools during low-flow conditions and are expected to increase their consumption of those benthic species that lack predator avoidance adaptations, such as use of spatial refuges and inducible morphological defenses (Covich *et al.* 2009, Kikkert *et al.* 2009, Ocasio *et al.* 2014, 2015). Increased prey vulnerability occurs, in part, because in-stream chemical communication regarding the presence of predators is a less-effective adaptation among prey species in avoiding predators when flow ceases and shoreline refuges are left high and dry (Crowl & Covich 1994). The resulting changes in the community composition of stream consumers are likely to further alter rates of decomposition, nutrient cycling, and periphyton production (Hein *et al.* 2011, Pérez-Reyes *et al.* 2015). Consequently, the cumulative effects of increased drought frequency are expected to alter the composition and dominance of these species assemblages, with decreases in densities of detritivore and grazer species that are most vulnerable to increased predator densities. Preliminary data in small streams in the LEF also suggest that during extended periods of low rainfall, low discharge, and pulsed leaf-litter inputs, dissolved oxygen levels can decrease to physiologically intolerable levels for detritivores and predators.

The reciprocal exchange between streams and riparian ecosystems (i.e., inputs of leaf-litter, woody materials, and insects) are likely to shift during wet and dry periods. These bi-directional changes in energy and nutrients have not yet been comprehensively studied in tropical rainforest streams, making it difficult to predict how increased drought could affect these tightly coupled ecosystems. While enhanced leaf-litter inputs serve to increase detrital resources for stream consumers, decreased discharge reduces the amount of available stream habitat and enhances their vulnerability to predation. We thus predict changes in the transfer of energy and nutrients to the riparian forest through aquatic insect emergence, with overall decreases in rates of this subsidy transfer in response to longer-term cumulative increases in drought frequency. Decreased stream-riparian resource subsidies, in the form of both aquatic insects and amphibious crabs, can have cascading effects on terrestrial predators such as spiders (Pfeiffer 1996), bats (Gannon *et al.* 2005), tree frogs (Woolbright 1996), and anolis lizards (Reagan 1996). These previous studies of foraging in the LEF suggest that emergence of aquatic insects from the streams can function as a subsidy to these abundant terrestrial predators. Our recent preliminary studies in the LEF documented that adult aquatic insects emerge from streams and are consumed by spiders (Kelly *et al.* *in press*). Stable isotope analyses demonstrated that the  $\delta^{13}\text{C}$  signatures of aquatic insects consumed by



spiders are distinct from their terrestrial insect prey in the LEF (*Kelly et al. in press*). Other preliminary studies showed that the percent of N derived from aquatic insects by spiders was approximately 20% and that aquatic insects were trapped up to 67 m from the stream channel. Studies in temperate ecosystems demonstrate that foraging by spiders (Marczak & Richardson 2007, Iwata 2007), bats (Fukui et al. 2006, Hagen and Sabo 2011), lizards (Sabo and Power 2002), and birds (Nakano & Murakami 2001) is coupled to consumption of invertebrate prey emerging from streams (Sabo & Power 2002, Baxter et al. 2005, Ballinger & Lake 2006, Marcarelli et al. 2011).

Our past long-term observations demonstrate that drought results in pulses of leaf litterfall, especially by those riparian tree species that lose their leaves in response to periods of water stress (*Beard et al. 2005*). This increase in leaf litter provides a pulsed input of material that is partially decomposed by microbes and stream invertebrates (*Crowl et al. 2001, Crowl et al. 2006, Wright and Covich 2005a, 2005b, Bobeldyk and Ramírez 2007, Rincón and Covich 2014*), with resulting increased C storage (accumulation of biomass of consumer and low-quality litter) and altered detritivore growth rates (Pérez-Reyes et al. 2015). Our previous short-term experiments demonstrate that, at the reach scale (50 -100 m), nutrient cycling is affected by the consumer community (*Crowl et al. 2001, Benstead et al. 2010*). The presence of abundant shrimp consumers in a stream results in a decrease in the quantity and increase in the quality (> C/N ratio) of benthic organic matter (*Pringle et al. 1999*). Experimental manipulation of shrimp community composition shows that composition can determine the effects of leaf-shredding shrimp on water quality, because the inclusion of filter feeders reduces the FPOM in transport following leaf shredding (*Crowl et al. 2001*).

Over the longer term (e.g. decades) climate change induced droughts are expected to result in changes in plant community structure (Hypothesis 1), including displacement of riparian tree species. The associated changes in light regime, litterfall, and nutrient and C dynamics (Hypothesis 2) will result in major shifts in the dominance of consumer species and nutrient cycling. Some non-native consumer species are likely to disperse upstream and create a “hybrid ecosystem” that alters carbon storage and nutrient cycling. Thus our long-term goals for future LTER research are to continue drought experiments and long-term measurements of environmental conditions and stream food web responses to determine the nature of cascading effects at both the community and ecosystem level.

**Work plan:** We will test Hypothesis 3a and 3b using a whole-stream manipulation (Stream Diversion Experiment, SDE) designed to reduce stream flow (Section 3.1). Stream food webs and rates of ecosystem processes (whole-stream metabolism, leaf decomposition, primary production, secondary production, and nutrient uptake) will be compared between the dewatered and control stream. Most variables will be measured weekly during manipulations, increasing the power of our analysis. We will measure the effects of flow reduction on biodiversity, biomass, and productivity of all major food web components in the streams. Microbial and algal biomass will be measured by sampling benthic biofilms along the experimental reach, using a modified Loeb sampler according to methods described by Pringle (1996). Previously described methods will be used to assess rates of leaf decomposition (*Wright & Covich 2005a, 2005b, Crowl et al. 2006, Bobeldyk & Ramírez 2007, Rincón & Covich 2014*) and biomass-specific primary production (Connelly et al. 2008) within the experimental reach. Whole-stream respiration and nutrient uptake ( $\text{NH}_4$  and  $\text{PO}_4$ ) will be measured at the reach scale (*Potter et al. 2010*). Greenhouse gas production will be assessed by grab samples to determine stream  $\text{N}_2\text{O}$ ,  $\text{CO}_2$ , and  $\text{CH}_4$  concentrations and propane addition to determine the re-aeration rates that are needed to calculate gas evasion (*Potter et al. 2010*). Aquatic insect composition and biomass will be measured monthly by sampling riffles (using a Surber sampler) and pools (using a core sampler). A series of emergence traps will be used to assess effects of decreased stream flows on insect emergence and isotope studies will elucidate food web pathways of this subsidy (e.g., consumption by spiders) in the riparian forest (*Kelly et al. in press*). Sticky traps (clear plastic sheets coated with Tangle-Trap adhesive, Tanglefoot, Grand Rapids, MI) and malaise traps will be used to track aquatic insect dispersal and densities in the surrounding riparian forest relative to terrestrially produced insects. Movements of crabs, bats, and lizards will be determined using standard protocols (e.g., mark-recapture, radiotelemetry). Aquatic insect secondary production will be estimated monthly using the instantaneous growth method (Benke 1984), with growth rates for major taxa determined *in situ* in growth chambers. Shrimp and crab populations will be sampled in pools using minnow traps, following standard protocols (*Zimmerman & Covich 2003, Covich et al. 2006*). Shrimp secondary production will be measured following previously used methods

(Cross et al. 2008). Movements of adult crabs out of the stream and into the forest as flows are reduced will be determined using traps and drift fences at different distances from the stream channel to measure transfer of energy and nutrients to the surrounding forest. We will also monitor standing crops of detritus in the streambed at the same time that we collect benthic samples for insects. Changes in stream dissolved organic matter and nutrients will be monitored weekly at both study streams. Oxygen, temperature, water level, and specific conductance will be measured continuously with HOBO Onset loggers. These data will be integrated into a general model to link in-stream population dynamics to levels of riparian subsidies that in turn distribute aquatic insects and amphibious crabs back to the forest. The balance of subsidies is expected to shift toward the stream food web as a result of increased leaf litter and light inputs to accelerate in-stream detrital production and primary productivity.

#### **4.2 Question II: What are the Effects of Increased Frequency of Intense Hurricanes on Tropical Forest Biota and Biogeochemical Cycling?**

Hurricanes are an important factor structuring forests in many parts of the world, and thus increases in the frequency of intense storms have serious implications for forest composition, structure, and C and nutrient dynamics (Lugo 2000, 2008, McDowell et al. 2013, Shiels & González 2014). Increased sea surface temperatures (SST) make it likely that the frequency of the most intense hurricanes will increase over time (Bender et al. 2010, Knutson et al. 2012). We will address how an increase in the frequency of major hurricanes influences plant and heterotrophic communities in terrestrial and aquatic ecosystems, as well as implications for C storage and nutrient dynamics.

We will employ a combination of long-term measurements, modeling, and ongoing (CTE) and new experimental manipulations. Disturbance effects generally include a complexity of impacts from damage and mortality of vegetation to litter deposition and changes in physical and microclimatic conditions. Most research designs are unable to tease apart these interrelated effects to isolate mechanisms of change. The initial design of the CTE allowed us to explore the short-term effects (0-10 y) of canopy opening and litter deposition associated with intense hurricanes on plant survival and growth, microclimate, detrital inputs, decomposition, biotic population and community characteristics, and biogeochemical cycling (Shiels & González 2014). To determine the long-term effects of increased frequency of hurricanes, the hurricane simulation treatment (trim+debris deposition) will be repeated every ten years for at least 50 years. The second trim took place in late 2014 with on-going measurements on physical, biotic, and ecosystem-scale processes (Table 1).

We will examine the long-term effects of increased frequency of extreme storms on streams using a combination of modeling, long-term measurements, and manipulation experiments with pre-treatment data collected over the next three years. During the next two years, we will simulate the effects of increased hurricane frequency on riparian vegetation using models already parameterized for the LEF to inform treatments for the proposed experiment. We will also expand our regular monitoring of streams to include measurements of changes in litter inputs, canopy gaps, and light levels to provide baseline data for the new experiment. We will utilize the stream flow modification experiment described under Hypothesis 3 to collect pre-treatment measurements for a stream canopy trimming treatment parallel in design to the CTE, which will be implemented in LUQ VI.

**Hypothesis 4.** *An increased frequency of severe storms will increase the dominance of shade intolerant, pioneer plant species. Changes in vegetation composition will induce changes in heterotroph communities, including animals and microbes. (Willig, Lodge, Cantrell, Shiels, Uriarte, Zimmerman)*

**Background** -- Increased frequency of hurricanes in *tabonuco* forest should shift species dominance to shade intolerant (or "pioneer" species) versus slower-growing, shade tolerant species (Doyle 1981, Uriarte et al. unpublished). Evidence of this has already been found in the CTE resulting from the first set of experimental treatments (Shiels et al. 2010), as well as in response to disturbance caused by Hurricane Georges in 1998 (Zimmerman et al. 2014). Dominance of pioneer species and more frequent canopy opening will favor heterotrophs associated with shade intolerant plant species, and the more frequent hot and dry conditions. These, in turn, will have cascading effects on C and nutrient fluxes (Shiels et al. 2015; Hypothesis 5) and streams (Hypothesis 6).

It is unclear which shade intolerant species will respond to the second experimental trim in the CTE. Following Hurricane Hugo, there was widespread recruitment of the pioneer trees *Cecropia schreberiana* and *Psychotria berteriana* in *tabonuco* forest (Walker 1991, Zimmerman *et al.* 1994). The response to Hurricane Georges differed, with much lower recruitment by *C. schreberiana* (Zimmerman *et al.* 2010). We expect that this was due to priority effects, i.e. the presence of species at the time of disturbance that dictate the species composition following disturbance and through succession. Thus, the second trim in the CTE allows us to experimentally test for priority effects due to the presence of pioneer species from the first trim (Belyea & Lancaster 1999). Similarly, the identity of species of invertebrates and the magnitude of their responses to disturbance was not the same after Hurricanes Hugo and Georges (Bloch & Willig 2006, Willig *et al.* 2010), perhaps because of differences in residuals after the two storms and cross-scale interactions (Willig *et al.* 2007). The second trim in the CTE will facilitate an assessment of the legacies of previous disturbances on population and community level responses to subsequent disturbances.

**Work Plan** – In the fall of 2014 we conducted a second experimental trim in the CTE, reducing the experimental design to two treatments, a hurricane-like treatment and an unmanipulated control or reference treatment. To test Hypothesis 4 we will continue to follow recruitment and mortality of seedlings, ferns, and all trees  $\geq 1$  cm DBH on an annual basis. These measurements will allow us to determine changes in species composition during the next 10-year cycle. In addition, we record elements of microclimate, forest floor mass, and soil chemical and physical properties (Table 1). For animal heterotrophs, we will continue our focus on the gastropods and phasmids, as well as herpetiles. These are being recorded quarterly to biannually since the latest (second) trim; we will return to annual censuses following the first year after the latest trim. For microbes, we will sample bacteria and fungi using the methods for Hypotheses 2a and 5. We will use the SORTIE model to predict changes in terrestrial vegetation over multiple decades under increased frequency of major hurricanes, and evaluate the predictions of the model using long-term data from the LFDP. We will use this information to inform modeling of riparian zone plant dynamics under the same scenarios (Hypothesis 6). Moreover, we will continue to use novel Bayesian statistical techniques (e.g., intervention analysis and transformed Gaussian Markov random fields) to explore spatial and temporal dynamics of populations and communities of animals in response to repeated disturbances (Prates *et al.* 2010, Ravishanker *et al.* 2014, Prates *et al.* submitted).

**Hypothesis 5.** *Soil C stocks will decrease with increasing hurricane frequency because of a lag in recovery of plant litter and woody debris production relative to heterotrophic respiration. Decreased woody litter inputs with increasing frequency of severe storms will change the composition of soil microbial communities and lead to faster turnover times of C in soils. (Lodge, Cantrell, McDowell, Silver)*

**Background** -- Using the Century model and debris mass data from Hurricane Hugo, Sanford *et al.* (1991) predicted that a 60-year return interval for hurricanes would result in increased soil C storage due to large inputs of coarse woody debris with slow decomposition rates. We propose that an increase in hurricane frequency above the 60-year background return interval will reverse this trend and lead to lower soil C storage. Our long-term experiments and observations show that hurricanes transfer a large mass of litter from the canopy to the forest floor (Lodge *et al.* 1991), and that five or more years are required for recovery of litterfall productivity (Scatena *et al.* 1996, Ostertag *et al.* 2003, Silver *et al.* 2014). In contrast, soil respiration rates increased following disturbance and returned to the relatively high baseline values within two years (Silver *et al.* submitted). The short-term increase in soil respiration rates following canopy disturbance corresponds to rapid rates of surface litter decomposition. For example, forest floor necromass had returned to pre-disturbance levels within 2-10 months following Hurricane Georges in the LEF (Ostertag *et al.* 2003). Higher temperatures and moisture in surface soils, together with increased C and nutrient availability from litter deposition (Silver *et al.* 2014) can stimulate microbial activity and associated decomposition rates. The high background soil respiration rates relative to lowered litterfall inputs and rapid decomposition of hurricane debris suggest the potential for soil C losses. This potential loss is further supported by the likelihood that autotrophic respiration was reduced due to a decrease in live biomass. As storm frequency increases, the rapid decomposition rates typical of wet tropical forests may exceed rates of C inputs via litter production leading to a net loss of C storage in the ecosystem.

This effect is likely to be strengthened by changes in post-disturbance plant communities and associated effects on soil microbial communities. The predicted increase in the proportion of early successional

species and generally younger vegetation will lead to lower inputs of coarse woody debris with successive storms; small wood and wood of successional species are more easily decomposable (Eaton & Lawrence 2006). We predict that changes in the structure and chemical composition of litter inputs will decrease fungal to bacterial ratios in the soil and alter enzyme activities. Changes in the distribution of microbial functional groups and their associated enzyme activities could result in different proportions of dissolved organic carbon (DOC) and particulate organic carbon (POC) entering the soil. If fungi that produce delignifying enzymes and DOC in the form of ferrulic acid are inhibited in the hurricane treatment, more POC and less DOC may enter the soil thereby increasing the light soil carbon fraction. Soils in the *tabonuco* forest are currently characterized by a large pool of mineral associated C and relatively small pools of particulate and occluded C (Hall *et al.* 2015). An increase in POC could potentially shift the distribution of soil C storage to more particulate C relative to mineral associated pools, which may in turn increase rates of C turnover and lead to lower soil C storage overall. Although we expect overall fungal biomass to decrease relative to bacteria, the abundance of some key fungal groups such as Basidiomycetes may not decline. Basidiomycete fungi play a particularly important role in the LEF through their ability to produce lignin- and lignocellulose-degrading enzymes. Based on our previous research (Lodge & Cantrell 1995), we expect this group to be resilient to increased hurricane frequency, and thus stimulate rates of decomposition of woody debris.

**Work Plan** – We will use the DayCent model to explore the effects of increased hurricane frequency on soil C storage, changes in plant community composition, NPP, and structure and quality of litter inputs. To determine if soil C storage and the distribution of C in soil fractions (Hall *et al.* 2015) have changed over time, we will use archived soil samples from 1988 (pre Hurricane Hugo), 1990 (post Hugo/Pre-Georges), 1992 (post Hurricane Georges) and fresh soils all collected from the same locations and depths (0-10 cm, 10-35 cm, 35-60 cm) in the BEW. A subset of samples will be selected for <sup>14</sup>C analyses to estimate turnover times (Hall *et al.* 2015). We will do the same analyses on samples collected from the CTE experiment using archived samples from 2002 (pre-treatment), 2008 (post-treatment), 2014 (pre-treatment round 2), and 2019 (five years post treatment round 2). We predict that the proportion of light fraction C will increase after storms, and that the proportion of light fraction C after Hurricane Georges and CTE round 2 will be larger than after the initial (Hugo/CTE) disturbances. We will explore mechanistic drivers by comparing soil C data with ongoing measurements of microbial communities (see methods from Hypothesis 2a), POC, and DOC dynamics (McDowell and Liptzin 2014 and Table 1).

We will use the CTE experiment to explore changes in microbial community and DOC dynamics associated with repeated disturbance. Short-term responses will be measured during the first year. Microbial biomass will be measured and fungal:bacterial ratios will be inferred from qPCR and DNA amplicon frequencies (Fierer *et al.* 2005; Hu *et al.* 2014) and C:N ratios using chloroform fumigation-extraction method as modified by Fierer & Schimel (2003). Microbial biomass will also be measured using the fumigation-incubation method (Vance *et al.* 1987). Changes in hydrolytic and oxidative enzymatic activity will be measured directly using a BioTek Synergy 2 with a Multi-Mode Microplate Reader (DeForest 2009, German *et al.* 2011, Sinsabaugh *et al.* 1999) and also using RNA amplicon abundances. These will be compared to changes in soil microbial communities indicated by within-block comparisons of DNA amplicon abundances in hurricane treatment versus control plots and correlated with DOC measurements in lysimeters (Table 1).

**Hypothesis 6.** *Increased frequency of intense hurricanes could result in higher-elevation streams shifting from consumer-controlled to producer-controlled ecosystems, due to the increase in stream nutrient concentrations, litter inputs, and light inputs that re-configure terrestrial-aquatic linkages in these headwater streams and riparian forests. (Pringle, Covich, Crowl, McDowell, Ortiz, Ramirez)*

**Background** – Twenty years of research on stream chemistry and biology shows that there is a strong response to hurricanes, which alter the riparian forest-stream connections, increase some nutrients, and change food web dynamics for months to years (Brokaw *et al.* 2012, Crowl *et al.* 2012, McDowell *et al.* 2013). After hurricanes, nitrate concentrations remain elevated for 18 months or more (McDowell *et al.* 2013), large litter inputs enter the stream but are rapidly decomposed (Crowl *et al.* 2001, Beard *et al.* 2005), and light levels increase because of increased canopy openness. In many ways, the Luquillo Mountain streams have been very resilient in response to the past two major hurricanes.

Increased frequency of intense storms is likely to have profound effects on stream communities, bi-directional subsidy exchanges, and biogeochemistry. Shifts in riparian vegetation toward more shade intolerant trees will alter both the transient light regime (more frequent periods of high light due to repeated hurricane disturbance) as well as the baseline light regime (lower LAI with more drought-tolerant species), and the quality, quantity, and timing of leaf-litter inputs. We will focus on species that are most likely to enter or leave the riparian forest community (Hypothesis 4) and their effects on subsidy dynamics. Following Hurricane Hugo, we observed a  $1 \text{ kg/m}^2$  input of detrital material across the forest including the streams (Lodge et al. 1991). We experimentally demonstrated that this input resulted in an increase in dissolved C, N, and particulate C production and export (Crowl et al. 2001).

In the longer term, we expect that our relatively unproductive communities, limited by light and predation, will switch from being consumer controlled to being producer controlled, resulting in increased microbial, algal, insect and decapod and fish densities, total biomass and secondary production, as a consequence of increased nutrients, allochthonous inputs, and light. In addition, the increased inputs of coarse woody debris and palm fronds will result in a significant increase in debris dams, leaf-litter storage, and habitat heterogeneity. This increased habitat complexity will most likely result in more spatial refugia for prey species and decreased predation by larger consumers (*Macrobrachium* spp) resulting in a decrease in top-down control on insects and smaller shrimp species. Taken in aggregate, we hypothesize that the increased frequency of severe storms in the LEF will fundamentally alter the stream ecosystems, resulting in increased primary productivity, standing stock biomass, and tighter nutrient cycling during extended periods between less-frequent, high-discharge events.

**Work plan** – We will enhance our existing stream monitoring to include monthly litter inputs, light and light gap measurements and microbial responses. In addition, nutrients, algal standing crop as well as insect, decapod, and fish densities and biomass will be sampled twice a year in six headwater streams (four of which are currently sampled as LTER focal streams; two additional higher-elevation streams). Sampling periods will include during the driest time of the year (Feb-March) and the period of the most severe storms (late September) to capture the effects of dry periods on stream biota. Sampling methods will follow protocols from our long term measurements (Section 3.1) and already established within the LUQ framework. Light gaps, coarse woody debris, and leaf-litter inputs will be mapped and quantified in replicate 100 m reaches in the study streams.

We will simulate hurricane impacts on the riparian vegetation using the SORTIE and Demographics models already parameterized for the LEF. Simulations will be used to model both short-term (annual) as well as long-term (decadal) impacts on riparian canopy composition and structure. These simulation results will guide future experimental manipulations of riparian canopy cover and increased light on the stream ecosystem components. Our future goals (LUQ VI) are to conduct a canopy trimming experiment for streams using a similar design as the CTE. We will explore the separate and combined drought (stream-water diversion, SDE) and hurricane disturbance through direct manipulations and modeling.

#### **4.3 Question III: How do Changes in Climate Interact with Hurricane Disturbance, Land Cover, and Land Use Legacies to Shape Ecosystems of the Future?**

Changes in global climate, hurricane frequency, and land cover, three critical forcing functions for tropical ecosystems, will interact to create the environment that will determine changes in structure and function of forest ecosystems in the LEF over the next century. Moreover, the response of the biota and biogeochemistry to this new environment will be contingent on conditions created by legacies of prior land use. Understanding and predicting the response of forest ecosystems to these new conditions will require the application of ecological theory informed by our detailed knowledge of past responses to climate, disturbance, and land use legacies. Over the next three years, we will refine our understanding of future trends and variability of climate in the LEF, and apply that understanding to developing predictions of forest behavior that will inform our future research.

We will use a downscaling approach to link predictions of future climate from GCMs to climate at spatial scales that are ecologically relevant to the forest ecosystems of the Luquillo Mountains. This approach is enabled by the existence of multiple long-term records of climate in and around the Luquillo Mountains. In addition, we will examine the importance of predicted changes on land use-land cover as a local forcing

on precipitation variability. We will use the results of these analyses and our knowledge of plant traits to inform simulation models that will assess the future structure of forests in the LEF.

**Hypothesis 7.** *A greenhouse gas-enhanced climate will drive changes at the global-to-regional scales, resulting in new, unique climate regimes forcing ecological change. Land use and land cover change (LULCC) will exacerbate the global-to-regional forcing. The additive effect will result in decreased rainfall and increased cloud heights on average but greater extremes in precipitation for the LEF. (Mote, Zimmerman)*

**Background** -- Climate variability throughout the Caribbean region is strongly associated with global scale wave patterns, tropical cyclones, orographic effects, sea breeze circulations, regional scale wind patterns (primarily the easterly trade winds), and intense solar heating (Taylor et al. 2002). Generally speaking, the Caribbean has two distinct “rainy” seasons (Taylor et al. 2002, Chen and Taylor 2002, Angeles et al. 2010); April - July and August -November, the latter partly associated with hurricanes and tropical storms (Taylor et al. 2002). This first period is interrupted beginning in May and lasting until July in some locations by what is commonly called the midsummer drought (MSD) (Taylor et al. 2002; Curtis and Gamble 2008; Gamble et al. 2008; Angeles et al. 2010). This annual dry period is expected to intensify in the 21<sup>st</sup> Century as greenhouse warming is enhanced (Rauscher et al. 2008).

The effects of a greenhouse gas-enhanced climate and LULCC adjacent to the forest are predicted to lead to a wide-range of climate changes (Comarazamy & González 2011). Deviation in the intensity and direction of near-surface winds relative to the topography will redistribute areas of local convergence (low pressure) and divergence (high pressure), leading to spatial redistribution of areas of upward and sinking motions. These changes in local convergence, coupled with changes in surface and atmospheric temperature and moisture, should lead to changes in cloud cover, cloud base heights, and precipitation (Comarazamy & González 2011). Cloud base within the forest will increase in height, leaving reduced areas shrouded in cloud for shorter duration. Light and moderate rainfall days will decrease in number, accompanied by an increase in the number of dry days and the number of consecutive dry days. Days of heavy rainfall, including days with rainfall exceeding the 99<sup>th</sup> percentile, will increase in frequency (Hayhoe 2013).

**Work Plan** -- Analyzing the historical precipitation climatology of northeast Puerto Rico will involve the use of spatially interpolated, continuous gridded products, and station observations from rain gauges, including long-term observations from the LTER. Due to coarse spatial resolution of global climate models (GCM), downscaling is needed to produce future climate scenarios at the scale desired. This will involve developing self-organizing maps (SOM) to categorize the large-scale synoptic conditions (e.g. sea-level pressure, wind) from reanalysis products or GCM output into “synoptic types”, or “synoptic patterns.” SOMs improve our understanding of transition zones between synoptic types, which is particularly helpful in the tropics (Reusch et al. 2005). We will produce a frequency distribution of “synoptic types” for historical atmospheric data for the Caribbean and assess the historical precipitation variability for northeast Puerto Rico based on synoptic types. Probability density functions will be developed between the synoptic type and the historical record of precipitation. This will allow for a particular synoptic type to be associated with a precipitation distribution for each observation point. We will create a series of site-specific artificial neural networks to model the observed precipitation using a suite of atmospheric variables. These models will help determine which atmospheric variables have the largest control on precipitation in the Luquillo Mountains.

To examine local anthropogenic forcing mechanisms on precipitation variability, LULCC impacts on precipitation in northeast Puerto Rico will be assessed. An epoch approach will be utilized in order to take advantage of the long-term precipitation records available in the study area. The early epoch will assume less LULCC than the later period. We will use the prevailing circulation to ascertain the downwind effects of the LULCC. The findings from this study will provide insight into the impacts that can be expected in the LEF as LULCC change continues from the coast to the mountains.

Determining future climate scenarios of precipitation variability in the study area will involve the use of downscaling GCM future simulations with SOMs. GCM validation will be carried out by analyzing historical simulations and the ability of the CMIP 5 GCM simulations to reproduce the historic synoptic types. To produce future simulations of synoptic types, SOMs will be created using an ensemble of the best performing GCMs. Scenarios of future precipitation regimes in northeast PR will involve using the

change in frequency of projected synoptic types to the frequency of observed synoptic types. The changing frequencies of synoptic types are indicative of shifts in climate. An emphasis will be placed on the shifts in synoptic types that produce PDFs representing extreme rainfall events (wet and dry).

Future, long-term changes in cloud properties will be examined by downscaling CMIP 5 GCM simulations. A climatology of the spatial distribution of rainfall will be developed and 'downscaled' to stream flow in the LEF in an effort to better understand how rainfall distributed across space is related to stream flow. This study will take advantage of the extensive stream flow data from the streams and rivers in the LEF and adjacent areas. Stream flow data for each mode will be combined to form PDFs of stream flow, which will allow for an understanding of how the spatial patterns of rainfall are related to stream flow. Establishing this climatology will inform subsequent studies on how future changes in the spatial distribution of rainfall in the LEF will impact stream flow.

**Hypothesis 8.** *Interactions between increased frequency of hurricanes and drought, mediated by land use legacies, will lead to novel biotic communities with altered biogeochemistry. This results from idiosyncratic responses of shade intolerant species to hurricane disturbance and drought, and their feedbacks on heterotroph communities, carbon storage, and nutrient cycling. (Zimmerman, whole group)*

**Background** -- A central tenet of our research is that responses to disturbance are contingent upon legacy effects of previous disturbance events (Scheiner & Willig 2011, Waide & Willig 2012). When the interval between disturbance events is great, succession acts to reduce legacies of previous disturbance. However, when disturbance events are frequent, legacies accumulate and can perpetuate the persistence of new ecosystem states. Therefore, the frequency of disturbance is important in determining forest dynamics, the composition of communities, and associated rates of ecosystem processes.

The kind and magnitude of a disturbance determines the characteristics of its legacies. Thus, hurricanes and landslides have very different legacies, as do category 1 and category 5 hurricanes. The order of successive disturbance events is also important in determining forest response. A weak hurricane followed by a strong hurricane has a very different collective effect than a strong hurricane followed by a weak one. Land use history produces widespread legacy effects in tropical ecosystems due to broad scale patterns of deforestation, agriculture, abandonment, and forest regrowth (Chazdon 2014). Legacies of land use in *tabonuco* forest include distinct plant (Thompson *et al.* 2002), consumer (Willig *et al.* 1998, 2007), and microbial communities (Willig *et al.* 1996, Bachelot *et al.* submitted), as well as altered patterns in litterfall and soil chemical properties (Uriarte *et al.* 2015). Hurricanes imposed on land use legacies promote the persistence of shade intolerant tree species associated with human disturbance (Uriarte *et al.* 2009) because post-hurricane light conditions favor the establishment of their seedlings, even in primary forests (Comita *et al.* 2010).

Increasing frequency of hurricanes and droughts will create combinations of legacies that have heretofore been infrequent in the LEF. How changes in vegetation composition will proceed under these conditions depends, in part, on the relationship between shade- and drought-tolerance (Engelbrecht *et al.* 2007, Valladares & Niinemets 2008), which is unknown in our forests. It is also unclear if heterotrophic community composition will follow patterns in plant species composition, or become decoupled from plant dynamics with increased drought and intense hurricane frequency. Soil C and nutrient pools will likely reflect the combined effects of changes in disturbance regimes, community shifts, and legacy effects, increasing the variability across the landscape. Some combinations of disturbance may lead to such extreme conditions that forest communities cross a threshold and rapidly shift to new ecosystem states.

**Work Plan** -- We will use data collected from Hypotheses 1, 2, 4, and 5 to parameterize the SORTIE and DayCent models. We will use the SORTIE model to investigate scenarios of increased hurricane and drought frequency across a range of plant community compositions. Modeled responses to normal and elevated drought and hurricane frequency scenarios will investigate how the disturbance regime influences both the overall abundance and spatial patterning of tree species within the LFDP in *tabonuco* forest as well as other forest types in the LEF. We will use existing data sets on plant species distributions (Thompson *et al.* 2002, Hogan *et al.* in prep.) and variation in soil resources (Uriarte *et al.*, in press) to partition variation in consumer communities (Willig *et al.* 2007) to predict the degree to which consumers will respond to changes in tree species composition. Evidence suggests that producers and consumer species should be coupled (Secret *et al.* 1996). However, Bachelot *et al.* (submitted) found that soil



fungus communities were only weakly associated with tree species in the LFDP; most variation was associated with soil variables. We will use the results from SORTIE modeling to parameterize the DayCent model for NPP, litter chemistry, and soil characteristics. We will run DayCent with the same scenarios as above to determine potential impacts on C, N, and P cycling. These studies together should provide predictions on how interactions between drying, hurricane disturbance, and land use have the potential to structure biotic communities and biogeochemical cycling of the future. Our future goals (LUQ VI) are to test these predictions against field data and to refine the predictive ability of our models as observations and results of manipulative experiments improve our understanding of the development and dynamics of novel forest ecosystems.

#### 4.4 Synthesis

We will continue to conduct synthesis in LUQ through integrative publications (books, special issues), via thematic workshops for LUQ personnel and scientists unaffiliated with our site, through interactions at annual meetings, and via electronic communication, as well as with collaborators from other LTER sites and networks (e.g., the PARTNERS RCN and the CloudNet RCN). We are an active participant in Drought-Net, a network to assess the sensitivity of terrestrial ecosystems to drought. We plan to host a workshop of key scientists and engineers to investigate the potential for a large-scale rainfall exclusion experiment. We recently convened a workshop of LUQ and non-LUQ scientists and students to explore the use of a suite of species distribution models (including multi-species models) to understand the current distribution of key groups of species (e.g., trees, birds, amphibians) throughout the island, with a goal of predicting broad scale changes in biotic associations in light of climate change and to inform future hypotheses about biotic change in wet tropical rainforests. We will convene a follow-up workshop to refine ways in which we can integrate LUQ data with that available elsewhere to execute an integrated research program. Development of downscaling techniques for Puerto Rico will allow us to more deeply understand how a changing precipitation regime can influence rainforest ecosystems, which will allow researchers, educators, and policy makers in Puerto Rico and elsewhere in the Caribbean to understand the implications of climate change for the region. This is one aspect of the **Broader Impacts** of LUQ research.

#### 5.0 RELATED RESEARCH PROJECTS

A project related strongly to this LTER proposal is a warming experiment being conducted at a nearby site by collaborators in IITF, USGS, and at Michigan Tech University (TRACE, 2014). This pilot project, mounted with funding from USDA Forest Service and the Department of Energy, seeks to test the utility of infrared heaters for increasing temperatures to a projected increase of 4° C (Cavaleri et al. in press). LUQ has collaborated with this effort so far by providing scientific input and field help. In addition, LUQ provides funding for graduate students working with UPR researcher Olga Mayol on the impacts of dust arriving from Africa on elfin woodlands. UPR researchers Qiong Gao and Mei Yu are investigating how land use changes (reforestation and urbanization) in Puerto Rico, interacting with climate changes (drought and sea level rise), have impacted coastal wetlands during the past three decades. Kathleen McGinley of IITF, an international relations specialist, working in collaboration with Alejandro Torres Abreu, an environmental sociologist, is addressing how, when, and why specific institutional arrangements affect decisions about the landscape surrounding the LEF. It will lay the groundwork for conducting scenario analysis of future land cover changes (*Thompson et al. 2012*). We are collaborating with the Earth Sciences Division - DOE as it embarks on the Next Generation Ecosystem Experiments – Tropics. The goal of this program is improve understanding of disturbance on C and related water and energy exchanges between tropical forests and the atmosphere by reducing sources of uncertainty in modal representations of these interactions and their influences on the Earth's future climate. Finally, LUQ collaborates closely with the Caribbean Landscape Conservation Cooperative. CLCC is a partnership among research and management agencies, organizations and individuals interested in sustainability issues in the Caribbean.

#### 6.0 EDUCATION AND OUTREACH

LUQ education and outreach programs, another aspect of **Broader Impacts**, are led by a professional educator, in collaboration with LUQ researchers. Steven McGee, an educational researcher and President of *The Learning Partnership*, guides the LUQ Education and Outreach Program, with help from Noelia Báez (Education Coordinator), Jess Zimmerman, Jorge Ortiz and Eda Meléndez (Information

Manager). The components of this program are detailed below.

**Schoolyard LTER** -- For over 20 years, the US Forest Service and the University of Puerto Rico-Río Piedras have collaborated to develop K-12 curriculum in science and mathematics throughout Puerto Rico. These efforts led to the development of the LUQ Schoolyard LTER program that now involves high schools in four rural municipalities. Teachers and their students have established long-term plots on public and private lands near their schools to study forest structure and dynamics. During LUQ IV we institutionalized Schoolyard LTER by hiring an Educational Coordinator for the project. This project has strengthened our relationship with schools, and helped guide teachers and students as they monitor their long-term plots and record biological and environmental data. Each year, schoolyard teachers have (1) participated in a summer planning meeting, (2) brought five students each to a weekend internship at El Verde, (3) supported students in collecting similar data at their schools, and (4) enabled students to submit their research to be presented at an annual symposium at UPR. At the weekend internship, students contributed to and analyzed an ongoing dataset about the Schoolyard plot at El Verde. During LUQ V, we will revise our Schoolyard model to expand the number of schools involved in the program. The primary change is to reduce the Schoolyard internship at El Verde from a weekend event to a daylong field trip. The current schools will continue to be supported through the new daylong internship and data collection at their schools. As a prerequisite for new schools to participate in the Schoolyard LTER, teachers must first participate in a data jam workshop and subsequently implement a data jam with their students. During the data jam workshop, teachers will work with LUQ data housed on the EcoTrends web site to investigate a basic ecology question using the claim-evidence-reasoning framework (McNeill & Krajcik, 2008). Those teachers who successfully implement the data jam with their students in their schools will be invited to participate in a training workshop and internship in the subsequent school year.

**Journey To El Yunque** -- During LUQ III & IV, we supported the development of a 4-wk bilingual middle school curriculum unit called *Journey to El Yunque* (<http://elyunque.net/journey.html>). Students use LUQ data to investigate the effects of Hurricanes Hugo and Georges on the Luquillo Mountains and consider the long-term implications of increased hurricane activity. Steven McGee and Jess Zimmerman have leveraged LUQ NSF funding for a 4-yr grant of over \$1,100,000 from the U.S. Department of Education (Ed) to conduct basic research, in collaboration with an educational psychologist, on how the program affects motivation and learning. The results of this research project will be the basis for additional funding from the Ed and NSF to significantly revise the web site materials based on new ways to support student learning as well as to incorporate more recent research findings from LUQ.

**Natural Resource Career Tracks** -- This program is funded in Puerto Rico by USDA National Institute of Food and Agriculture via a subaward from New Mexico State University. With annual funding of roughly \$350,000, the program, directed by Zimmerman, has involved more than fifty students from Puerto Rico in summer internships, and other career enhancement activities, at USDA National Forests and other USDA agencies as well as other potential employers.

**Research for Undergraduate Students** -- Two undergraduate students are selected each year from UPR or collaborating institutions for a summer research experience. Students and projects are suggested by LUQ researchers or selected as part of a site REU at El Verde Field Station. All REUs are integrated in the undergraduate research training program and share their results at a poster presentation held at the UPR campus in Río Piedras.

**Volunteer Research Interns** -- LUQ has been very successful at recruiting volunteer research assistants to perform field research in the LFDP and CTE. Students are oriented to research goals and trained in field protocols, data entry and management, and identification of tropical biota. Field trips and seminars by local and visiting scientists enhance their field experiences. Working for 4-mon stints, students receive per diem, lodging and free travel to the site in exchange for their research assistance. Approximately 200 students have worked at LUQ since 1995, about a third of them from underrepresented minorities.

**Graduate Students** -- There are 41 graduate students involved in LUQ research at 14 institutions. Twenty-two percent are underrepresented minorities, mostly of Puerto Rican origin. Students select a representative who organizes student activities at the annual meetings and sits on the Science and Education Advisory Council (see Project Management). A recent dissertation created a bilingual portion of our website (Pérez-Reyes 2014) on water-related research that continues to attract users from many countries.

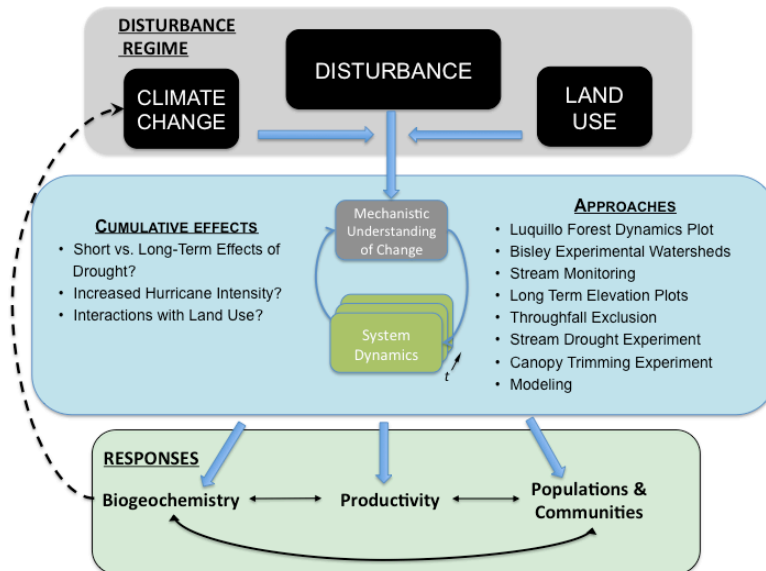


Figure 1. During LUQ 5, we will explore how a changing disturbance regime (grey shaded box) elicits responses in interlinked aspects of dynamic ecological systems (green shaded box) of the Luquillo Mountains (i.e., biogeochemical dynamics, productivity, and biotic dynamics), as well as feedbacks of biogeochemical dynamics on climate changes (dashed arrow). We do so by employing observational experiments, manipulative experiments, and modeling to characterize historical and current system dynamics, thereby enhancing the mechanistic understanding that allows us to predict altered system dynamics in light of a changing disturbance regime (i.e., predictive understanding; blue shaded box). The critical aspects of the changing disturbance regime that we will consider include aggregate effects of multiple disturbance elements (frequencies of intense storms and droughts as they interact with land use) and the various mechanisms of change that might produce novel communities and altered ecosystem dynamics.

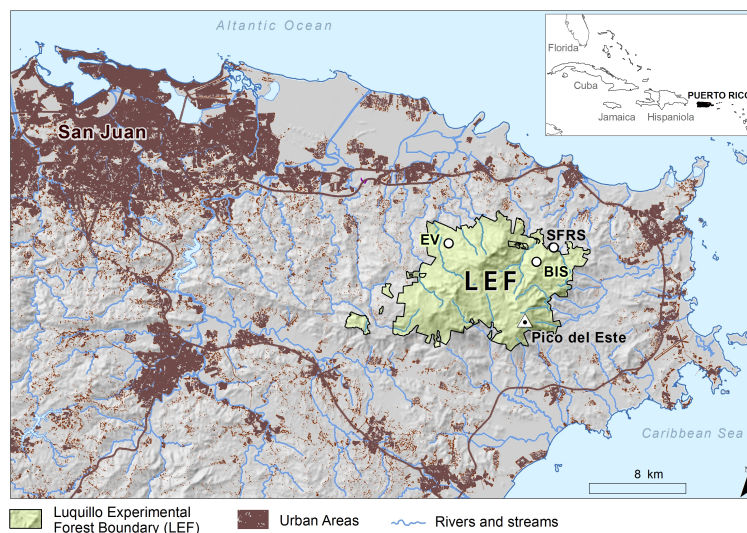


Figure 2. Map of the Luquillo Experimental Forest in northeastern Puerto, showing the Luquillo Experimental Forest (LEF) in relation to the San Juan Metropolitan Area and surrounding urban centers. Key study locations in the LEF include El Verde Field Station (EV), Sabana Field Research Station (SFRS), Bisley Experimental Watersheds (BIS) in *tabonuco* forest (200 – 600 m elevation) and Pico del Este (PE) in elfin woodland (> 900 m elevation).

	Forest Service Research	Radiation Experiment	DOE Cycling Studies	Establish Long-Term Measurements	Hurricane Response	L-T Experiments & Gradient Analysis	Ecosystem Function & Services	Altered Ecosystems
Disturbance	Selective Thinning	$\gamma$ -Radiation Gap Effects	1988 Flood	Hugo 1994	Drought Georges	Canopy Trim Experiment	Disturbance Interactions	Increased Drought & Hurricane Frequency
Climate	Monitoring	Cloud Forest Climate		Monitoring	Modeling and Isotope Studies Cloud Forest Climate		Urban Heat Island	Downscaling Studies
Land Use	Forest Restoration			Land Use Characterization	Land Use Legacies		Urban Streams	Effects on Precipitation Variability
Biogeochemistry Dynamics		Mineral Cycling	Decomposition	Watershed & stream monitoring Soil ecology		Climate Effects		Effects of Precip Variability
Populations & Communities		Radiation effects	Species Pop <sup>2</sup> Models Habitat Selection	Response to Disturbance		Elevation Gradient	Novel Communities	
Productivity	Growth & Yield	Forest Metabolism & Energy Flows		Disturbance effects		Elevation Gradient	Monitoring	Drought & Redox
Conceptual Framework	Forestry Management	Steady State Dynamics		Patch Dynamics	Ecological Space	Detrital Dynamics Gradients	Resilience, Ecosystem Services	Cumulative Disturbance Effects
USDA Forest Service 1940s 1950s		AEC 1960s	DOE 1970s	LUQ I 1988	LUQ II 1994	LUQ III 2000	LUQ IV 2006	LUQ V 2012

Figure 3. Research history in the Luquillo Experimental Forest, showing key long-term studies in relation to fundamental components of LUQ activities (horizontal bars). Disturbance and factors which modify the disturbance regime (see Fig. 1) are color-coded gray and measured responses are green. Evolving projects and, since 1988, LTER goals are shown in columns. Information includes the changing conceptual underpinnings of the research programs (blue) as well as administrative history since the 1940s (white at bottom).

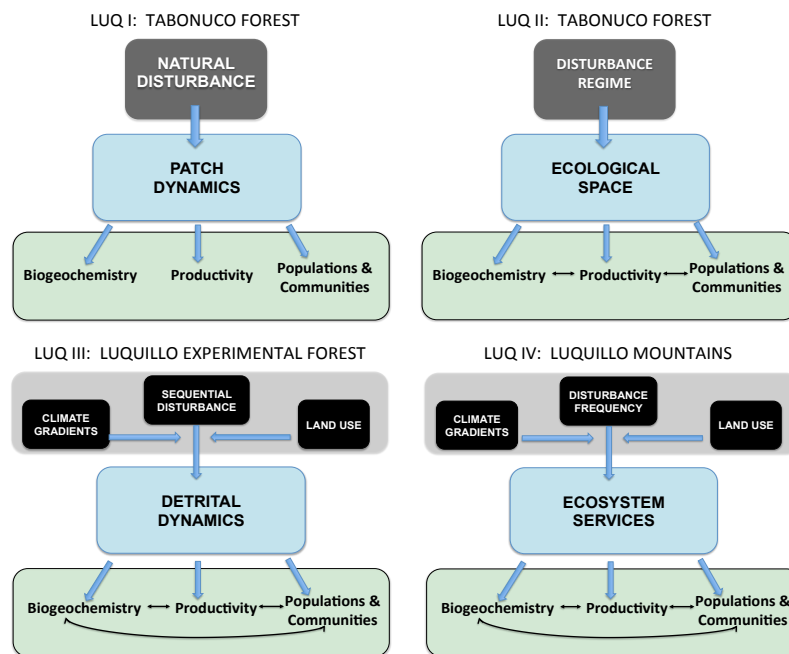


Figure 4. The evolution of the conceptual framework of LUQ. We initially focused on patch dynamics in one forest type (*tabonuco* forest) as a unifying theme (LUQ I). In LUQ II we developed the concept of “ecological space” (see Waide & Willig 2012 for history) to describe how antecedent and current conditions influence the biota and biochemical dynamics responding to the disturbance regime. In LUQ III we focused on detrital dynamics as our unifying theme, while expanding our studies to include all of the LEF, including life zones at elevations above *tabonuco* forest. We studied ecosystem services in LUQ IV, extending our studies to urban and other zones at the base of the Luquillo Mountains.

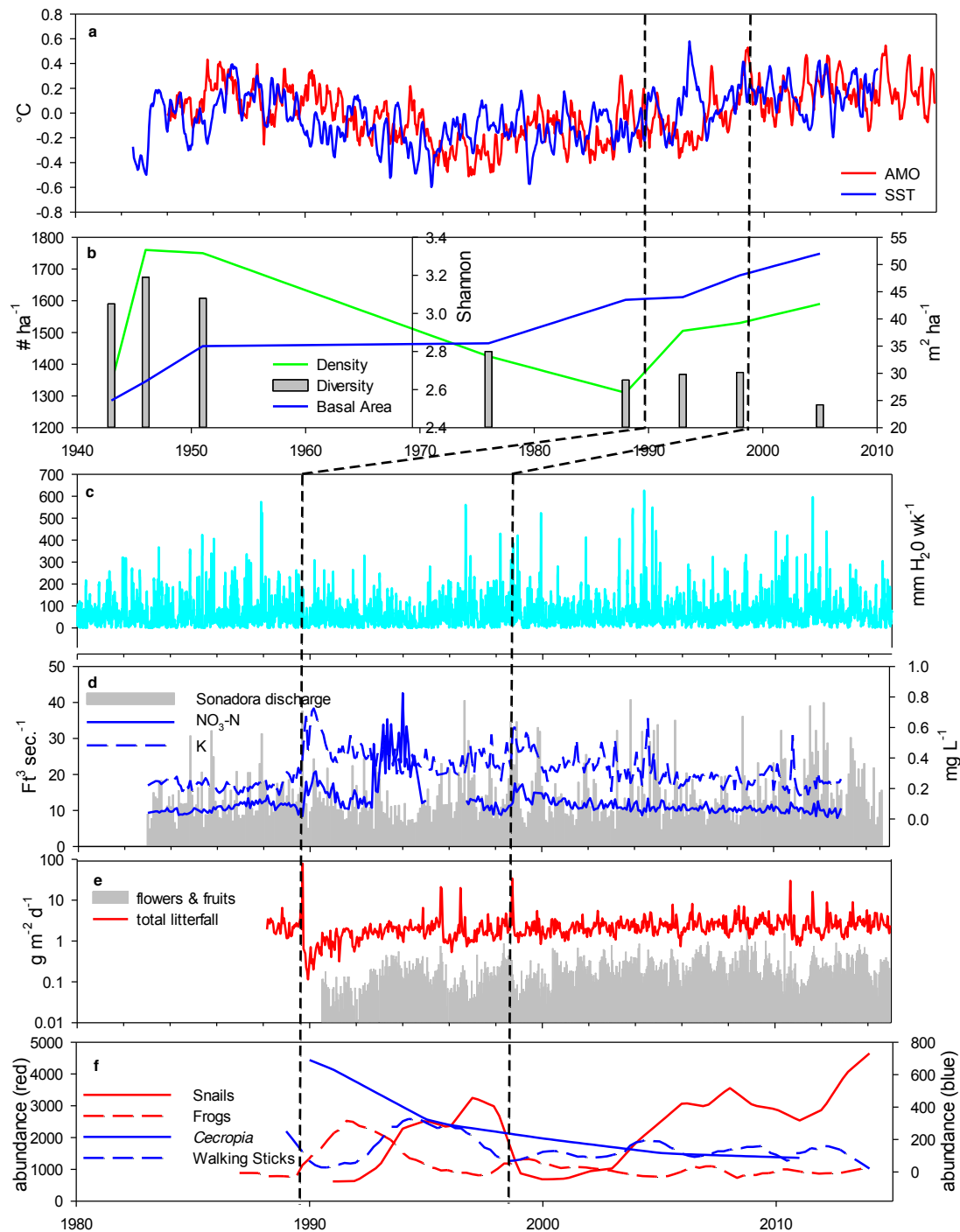


Figure 5. Long-term data sets collected in the LEF that contribute to LUQ research. Climate variability is strongly related (a) to the climate index Atlantic Meridional Oscillation (AMO) and sea surface temperatures (SST), which influence temperature and precipitation. Forest plots established by the Institute of Tropical Forestry in 1943 (b) show that *tabonuco* forest was recovering basal area after human and hurricane disturbance in the early 19<sup>th</sup> Century; tree density and diversity (Shannon-Weiner Index) show distinct responses to hurricane disturbance then and in response to Hurricane Hugo in 1989, but not in response to Hurricane Georges in 1998. Since the inception of LUQ in 1988, litterfall in the Bisley

Experimental Watersheds (c) responded strongly to damage by H. Hugo, but less so to that of H. Georges.  $\text{NO}_3^-$  and  $\text{K}^+$  in the Quebrada Sonadora responded to hurricane disturbance (d) by showing distinct increases following storms. Again, this was more evident following H. Hugo than after H. Georges. Nitrate was also high during a drought in 1994 when stream flows were very low. Monitoring of populations and communities of key organisms by LUQ (e) show diverse responses to hurricane disturbance (Zimmerman et al. 1996, Shiels and Gonzalez 2014). The pioneer, shade intolerant tree (*Cecropia schreberiana*) recruited heavily following H. Hugo, but not H. Georges. The coqui, a frog, increased in abundance following H. Hugo in response to the increased forest floor debris (which promotes survival and reproduction). The snail *Nenia tridens* showed a decline following hurricanes but then increases with the abundance of plant species that are favored forage or habitat. The walking stick, *Lamponious portoricensis* was very abundant before H. Hugo, but, in a surprise, never recovered its former abundances.



Figure 6. One of the hurricane treatments in the Canopy Trimming Experiment. Plots are 30 x 30 m with an inner 20 x 20 m measurement plot. Arborists trimmed all large (>10 cm diameter) branches and the tops of trees over 3 m (removing fronds from palms) to simulate the impact a major hurricane. The resulting debris was sorted into categories, weighed, and then distributed evenly on each 5 x 5 m subplot to homogenize the debris treatment. Hurricane treatments and unmanipulated controls are replicated in three separate blocks. The photo was taken on November 19, 2014. This same plot was trimmed using the same protocol in November of 2004. Thus, we are following a schedule of increasing intense hurricane disturbance to *tabonuco* forest every ten years. See Research Approaches for further details on the project, including data collected.

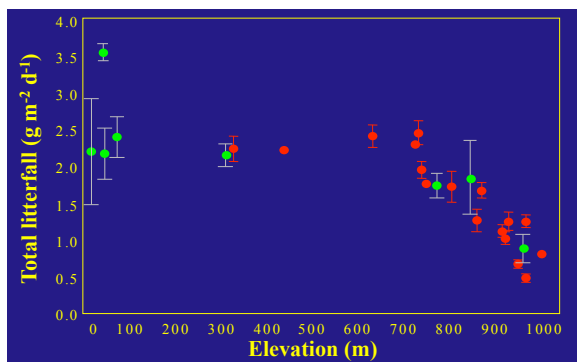


Figure 7. The decline in total litterfall with elevation in the Luquillo Mountains. Green symbols are from a set of plots ranging from coastal forests (including fresh water *Pterocarpus* swamp showing the highest productivity) to elfin woodland at the summit (González, unpublished). Red symbols represent higher elevation plots distributed in *palo colorado* forest (700 – 900 m) and elfin woodlands (Silver, unpublished, Weaver and Murphy 1996).



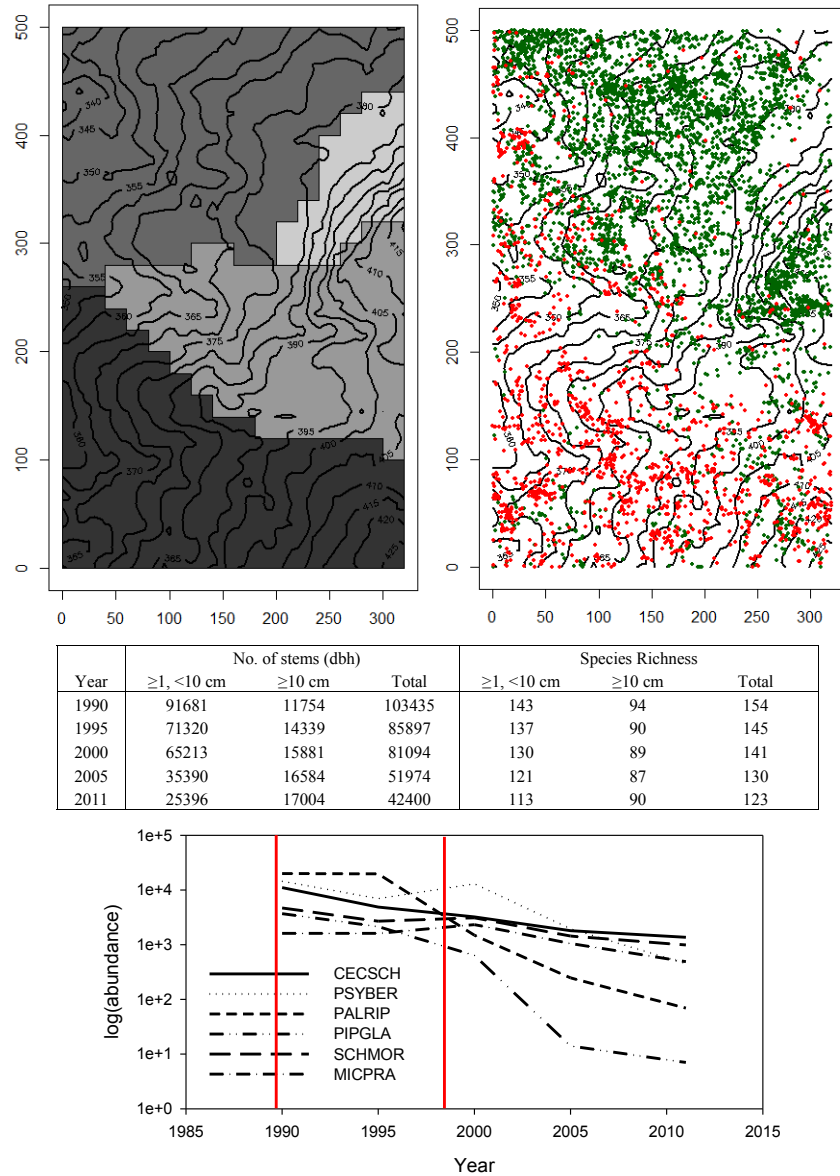


Figure 8. The Luquillo Forest Dynamics Plot (LFDP): maps of (upper left) land use (LU) history (canopy cover in 1936 aerial photograph such that darkest shading represents >80% cover; remaining classes are 50 – 80%, 20 – 50%, and <20%, %, represented by decreasingly lighter shades of grey [Thompson et al. 2002]), showing impacts of logging and other land uses; (upper right) distributions of shade-tolerant *Dacryodes excelsa* (*tabonuco*; red symbols) and anthropogenic pioneer *Casearia arborea* (green symbols), such that the two tree species that illustrate responses to > 80 vs. <80 % canopy cover (i.e., high vs. low LU intensity). Changes over time show (center) numbers of species in small (1-10 cm diameter at breast height [DBH] and large tree diameter classes (>10 cm dbh). The near or complete loss (lower) of some shade-intolerant, pioneer species (with their six letter species codes) whose recruitment occurred after Hurricane Hugo (1989) but whose numbers were not influenced by Hurricane Georges (1998; red lines). Species loss from the plot was also due to local extinction of very rare species.



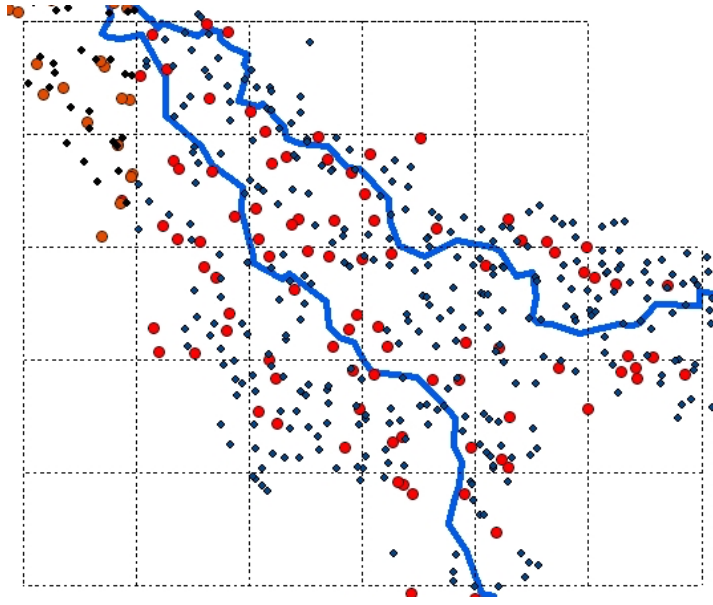


Figure 9. Map of the Stream Decomposition Experiment, showing two tributaries of the Quebrada Prieta. One tributary will be (randomly) chosen for a 50% reduction of stream flow to simulate drought effects. Grid has 20 m intervals. Preliminary mapping of trees in the riparian is also shown, with palms marked by red symbols and non-palms by black symbols.

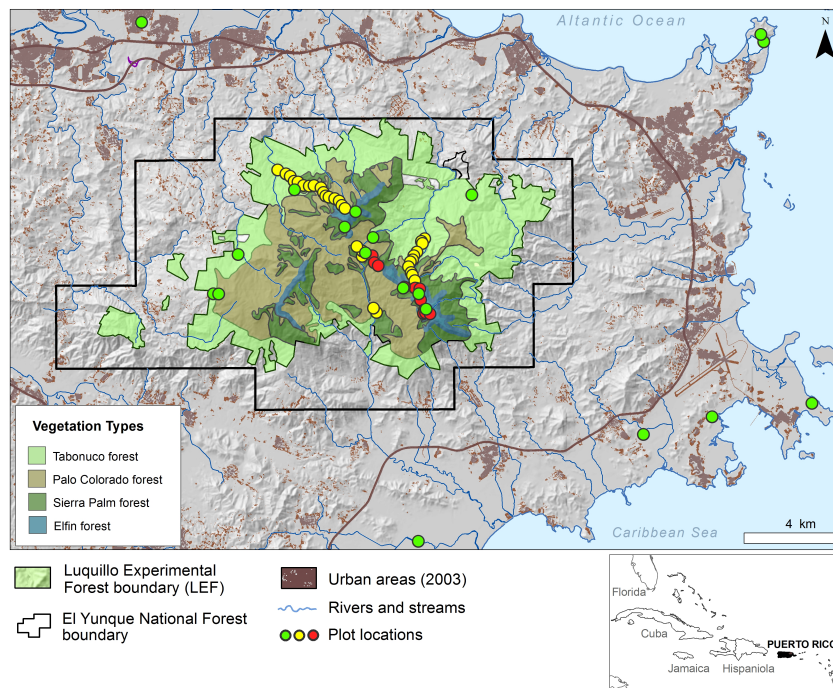


Figure 10. Location of forest plots used to sample the elevation gradient, shown in relation to historically recognized forest types. In yellow symbols are the Long Term Elevation Plots, which are sampled a six-year intervals for changes in characteristics shown in Table 2. Other sets of plots that sample the elevation gradient are shown in green and red (see Figure 7).

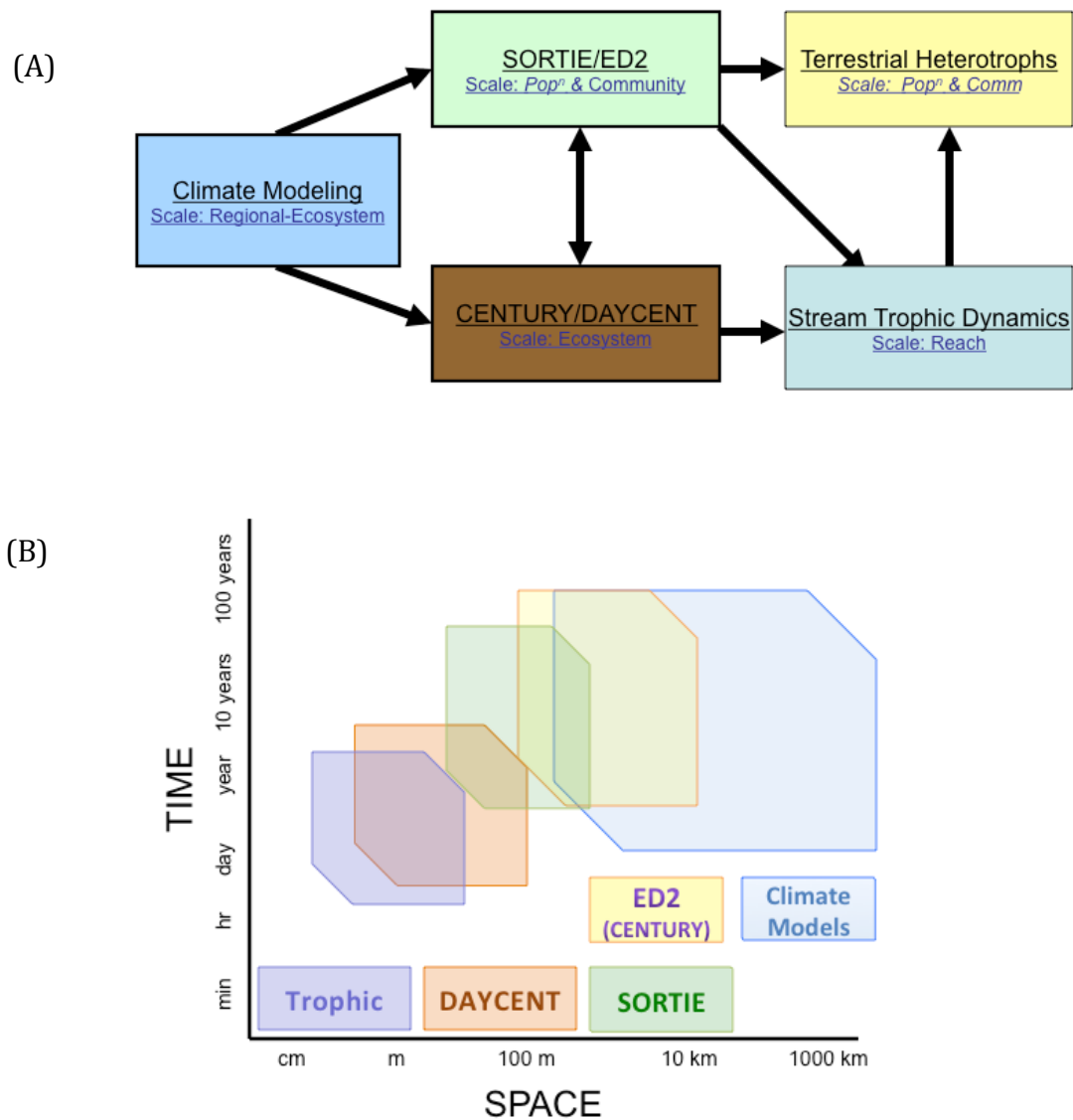


Figure 11. Modeling scheme for synthesizing information gathered in long-term modeling and experiments, and short-term experiments. Information (A) will flow among models, starting with climate downscaling of precipitation from GCMs and scenarios of changes in hurricane intensity on the left. Downscaling studies are currently underway and hurricane scenarios are taken from the literature. These feed into vegetation dynamics (SORTIE and ED2) and soil biogeochemistry (DayCent, Century) models. SORTIE and DayCent/Century are currently used by LUQ. ED2 is being implemented currently, which incorporates functional groups of species modeled by SORTIE and utilizes a soils model based on Century. Century, in turn, can inform stream biogeochemistry. During the remainder of LUQ V, we will develop trophic dynamics models to trace the flows of carbon and nutrients from stream to riparian habitats. These models together (B) span the range of spatial and temporal dynamics at our site.

## PROJECT MANAGEMENT

A Management Committee (MC) consisting of the PI and four co-PIs undertakes project management in the Luquillo LTER program (LUQ). Jess Zimmerman is the Lead PI of LUQ, and Nick Brokaw, former Lead PI, will continue to serve as co-PI at UPR. The remaining co-PIs are Grizelle González (USDA Forest Service), Whendee Silver (University of California, Berkeley) and Michael Willig (University of Connecticut).

The MC was established under bylaws approved by LUQ Senior Personnel (SP) in December of 2014 and consists of a Lead PI and four Co-PIs from UPR, IITF and two off-island collaborating institutions. This structure was chosen to (1) provide sufficient administrative support at UPR where the program is managed while (2) allowing sufficient input in to the management of the program by collaborating institutions. Brokaw will assist Zimmerman with the implementation of the current proposal, thus providing institutional memory from his time served as PI. Zimmerman will remain in a leadership position for the next decade. During the next three years, UPR will conduct a national search for a senior faculty member to serve as Co-PI, replacing Brokaw and eventually taking over the Lead PI position. The leadership transition is expected toward the end of LUQ VI.

Zimmerman has 24 years of experience as an administrator and researcher at UPR. He is the former Director of The Institute for Tropical Ecosystem Studies (merged into the Department of Environmental Science in 2012) and was Lead PI for LUQ before this position was separated from the Directorship of ITES in 2002, when Brokaw became Lead PI. Zimmerman served as a Program Officer at the National Science Foundation from 2004-2006 before returning to UPR to become Project Leader of the Luquillo Forest Dynamics Plot. Zimmerman also served as co-PI of the IGERT Program at UPR and was the Founding Coordinator of the Graduate Program in Environmental Sciences at UPR.

Grizelle González serves as Project Leader at IITF, where she has worked for 15 years, and represents the IITF – USDA Forest Service on the MC. González supervises researchers and support staff from IITF who conduct research at the Bisley Experimental Watersheds and at Pico del Este as part of LUQ. González also provides support for LUQ through her management of the Sabana Field Station. González plays a key role in coordinating IITF's contribution to LUQ, and has contributed greatly to its success by leading several synthesis efforts (e.g., González et al. 2013, Shiels and González 2014).

Whendee Silver is Professor of Ecosystem Ecology and Biogeochemistry and has the Rudy Grah Endowed Chair in Forestry and Sustainability in the Department of Environmental Science, Policy, and Management at U.C. Berkeley. She was a graduate student with LUQ at its inception and has been LUQ senior personnel since 1994. She is a productive leader in biogeochemistry at our site. She is co-PI on the Luquillo CZO project, providing a critical link with this sister project.

Mike Willig is Director of the Center for Environmental Sciences & Engineering, and Professor in the Department of Ecology & Evolutionary Biology, at the University of Connecticut. He has been with LUQ since its inception in 1988. Willig is a distinguished animal community ecologist and worked at NSF as a program officer and the Director of the Division of Environmental Biology.

The MC is in charge of the administration of the project, including managing the budget, reviewing the progress of the science, making changes in administrative policy, and suggesting changes to the bylaws. The MC has regular monthly meetings to discuss the management of the project and at more frequent intervals as necessary. The two PIs at UPR are in charge of day-to-day administration including liaison with the SRO of UPR, Río Piedras to ensure smooth and efficient administration of the LTER award. Experience has shown that regular meetings between the UPR PIs and the Coordinator of the Post-Awards Office under the Dean of Grants and Research make this possible. In the current proposal, we have streamlined administrative processes by reducing the number of subawards managed at UPR from 12 to 7.

The MC is advised by a Science and Education Advisory Committee (SEAC; Table 3-1) who are nominated by LTER researchers (SP and Associate Researchers) and chosen by the MC for a three-year renewable term. Former co-PIs Pringle and Ramírez were retained on the SEAC for a three-year term as agreed to in the bylaws. The Information Manager, one student representative, and the Education Coordinator are *ex-officio* members of the SEAC, along with the founding PIs, Robert Waide and Ariel Lugo. A number of the members of the SEAC (Bloch, Heartsill-Scalley, Shiels, Wood) are junior scientists and thus represent the new generation of LTER researchers.

The SEAC meets quarterly to review progress in achieving scientific and education goals established in the most recent proposals and exchange ideas on new research initiatives. With the SEAC, the MC conducts regular reviews, via the submission of annual reports, of the contributions of each of the SP. The SEAC may recommend changes to the membership of the SP based on these reviews, which then goes to the MC for approval.

A complete list of SP (Table 3.2) also describes the role of each person in governance and provides institutional affiliations. The SP are also listed under individual hypotheses for which they bear responsibility in the Project Description.

External advisors are utilized to maintain an objective perspective on the development and performance of LUQ. Three external advisors are appointed by the MC, with the advice of the SEAC, and serve 3-year renewable terms. The External Advisory Committee reviews the entire LUQ program annually and makes a written report to the MC on strengths and weaknesses of LUQ and potential improvements. With this proposal, the Advisory Committee will consist of Aaron Ellison (HFR), Tim Fahey (HBR), and John Porter (VCR).

Interactions among the SP occur frequently via email, web site announcement of recent events and publications, upcoming events, and via teleconference. Monthly meetings are held with the LUQ scientific community via the web and in person at UPR. The MC organizes virtual research seminars to keep the LUQ community informed of scientific progress. An annual LUQ All-Scientists Meeting is held each June, consisting of a day of seminars and posters (sometimes held in conjunctions with other organizations), a day of review of scientific progress and future planning, and one-half day of a business meeting among the SP.

The MC, with the advice of the SEAC, appoints Associate Researchers that have research programs that complement LUQ but are funded from other sources. Associates are normally appointed for the duration of the six-year funding cycle. Associate Researchers may be supported by LUQ with travel funds, student support, or similar funding. Currently, they are Daniella Cusack (UCLA), Tania del Mar López (Rutgers), Dennis Fernandez (UPR – Humacao), Qiong Gao (UPR), William Gould (IITF), Gary Greer (Grand Valley SU), Charlie Hall (retired), Erika Marin Spiotta (U. Wisconsin), Krista McGuire (Barnard College), Sabastian Martinuzzi (U. Wisconsin), Bob Muscarella (Columbia U.), Jennifer Petit-Ridge (Lawrence Livermore Nat. Lab.), Chelse Prather (U. Va), Steve Presley (U. Conn), Luis Santiago (UPR), Sheila Ward (independent), Larry Woolbright (retired), Joe Wunderle (IITF), and Mei Yu (UPR).

Table 3-1. Composition of LUQ leadership, including the PIs who constitute the Management Committee and the members of the Science and Education Advisory Committee (SEAC). Members of the SEAC serve a three-year term until renewed or replaced by new members.

Name	Role	Institution
<i>Management Committee</i>		
Zimmerman, Jess	PI	University of Puerto Rico
Brokaw, Nick	Co-PI	University of Puerto Rico
González, Grizelle	Co-PI	IITF, USDA Forest Service
Silver, Whendee	Co-PI	University of California, Berkeley
Willig, Mike	Co-PI	University of Connecticut
<i>Science and Education Advisory Committee</i>		
Báez, Noelia	Education Coordinator <sup>1</sup>	University of Puerto Rico
Bloch, Chris	Selected 2015	Bridgewater State Univ.
Covich, Alan	Selected 2015	University of Georgia
Heartsill-Scalley, Tamara	Selected 2015	IITF, USDA Forest Service
Hogan, Aaron	Student Representative <sup>1</sup>	University of Puerto Rico
Lugo, Ariel	Founding PI <sup>1</sup>	IITF, USDA Forest Service
Meléndez, Eda	Information Manager <sup>1</sup>	University of Puerto Rico
Pringle, Cathy	Co-PI LTER 5a <sup>2</sup>	University of Georgia
Ramírez, Alonso	Co-PI LTER 5a <sup>2</sup>	University of Puerto Rico
Shiels, Aaron	Selected 2015	Natl. Wildlife Res. Ctr. USDA
Uriarte, Maria	Selected 2015	Columbia University
Waide, Bob	Founding PI <sup>1</sup>	University of New Mexico
Wood, Tana	Selected 2015	IITF, USDA Forest Service

<sup>1</sup>*Ex-officio* <sup>2</sup>Retained to serve on SEAC according to 2014 By-laws.

Table 3-2. Additional Senior Personnel (Institution)

Ford Ballantyne (University of Georgia)	Kathleen McGinley (IITF, USDA Forest Service)
Sharon Cantrell (University of Turabo)	
Todd Crowl (Florida International University)	Jorge Ortiz (University of Puerto Rico)
D. Jean Lodge (Forest Products Laboratory, USDA Forest Service)	Barbara Richardson (retired)
Olga Mayol (University of Puerto Rico)	Timothy Schowalter (Louisiana State University)
William McDowell (University of New Hampshire)	Jill Thompson (Center for Ecology & Hydrology, UK)
Steven McGee (Learning Partnership, Inc., Chicago)	Lawrence Walker (University of Nevada – Las Vegas)

## **Long-Term Experimental Research (LTER) Information Management System (IMS) for the Luquillo LTER site (LUQ)**

**Overview.** LUQ IMS is committed to support research at the site and LTER Network level. In LUQ IV we made significant changes to our IMS by implementing DEIMS (Drupal Ecological Information Management System), a web-based system for managing all LTER data products and generating compliant metadata in the Ecological Metadata Language (EML), the metadata standard used by the LTER. Now LUQ has an efficient framework-website system for collecting metadata, generating EML and providing public access to our data. DEIMS represents a significant improvement over previous methods for data documentation, access and archival. In LUQ V we will further develop this framework to provide more ways to improve data discovery and access and will train the community on its features and resources for data sharing and conducting data synthesis.

Below, we will describe the fundamentals of our current system, and discuss the additional functionality we will add in LUQ V to improve data discoverability and accessibility, and to provide more resources for researchers. We also plan incorporating spatial data into the system.

### **LUQ IM Description**

**Data Products description.** The LUQ Data Catalog lists all the LTER-sponsored data sets created by LUQ scientists in their research to understand the effects of changing climate and disturbance regimes on tropical forest and stream ecosystems. The main categories of data reflecting our historical and current research are Disturbance, Climate, Water and Land Use, Populations and Communities, Carbon & Biogeochemical Dynamics, and Productivity. The main LUQ V proposal provides a thorough description of the research related to these data products.

**IT Resources.** The LUQ Office is supported by two mini-LAN networks. The mini-Lan located in the San Juan area contains four Windows desktop computers (two with an additional internal 1-TB hard drive), three Unix-based servers and a laptop. Two servers are UNIX Apache web servers using PHP server-side scripting language, MYSQL database and Drupal, a content management system (CMS). The other server contains DEIMS, the information management system framework using the profile developed for the management of LTER ecological information. The laptop holds the files that provide the original information uploaded to the LUQ website. A 500 GB external USB-drive holds old versions of metadata and data. The second Apache web server contains a Plone CMS that is used as the online LUQ Intranet for LUQ scientists. Another mini-LAN is located in the El Verde Field Station (EVFS) facilities containing a Linux server with the downloaded EVFS sensor data. A standalone computer contains backups of these data. Our backup policy and methods are described later in this data plan

**Human Resources.** LUQ IM team is composed of a full time Information Manager, Eda

Melendez (1989-present), a system administrator, and a data entry person. The Information Manager supervises the digital entry and quality control procedures and assures that the data entered in the system complies with LUQ Data Policies and the LTER Network standards and best practices. The information manager also assures that all data is uploaded to the LTER Network Information System (LTER NIS) and assists LUQ scientists and graduate students beginning with initial planning of projects in data structure design, data entry sheet generation and data documentation. The system administrator supports all IM and El Verde Station servers. A part-time student assists in the entry of data and metadata into the LUQ-IMS.

### **Data generation and Processing**

***Supporting Network Standards.*** LUQ-IMS complies with the LTER Network standards and requirements by contributing all its data sets (146) to the LTER NIS Data Portal, which uses PASTA, the Provenance Aware Synthesis Tracking Architecture, as the framework for dynamically harvesting and archiving site-based data and metadata. This is performed through the use of DEIMS, designed originally by the LTER Network Office (LNO) staff and enhanced by a private Drupal expert working with seven Information Managers from the LTER community. The seven information managers pooled LTER supplement funds to hire the Drupal development company. DEIMS produces PASTA-compliant Ecological Metadata Language (EML) packages on the fly. The LUQ EML packages are then manually verified in the NIS Data Portal for quality control processes. DEIMS also generates an EML list of packages that are dynamically harvested by PASTA periodically. Furthermore, DEIMS 2 enhances the LUQ-IMS ability to promote data discovery and synthesis activities by utilizing the LTER Standard Unit Registry for describing and naming the variable units and the LTER Controlled Vocabulary as the official keyword set for LUQ data sets. DEIMS represents a major step towards standardizing LTER information management systems across sites.

### **Supporting all phases of Luquillo Research Cycle**

***Data Project Planning.*** Methods for gathering data, data entry, quality control and data documentation are decided at the beginning of each project and are mostly determined by the data type. Data sheets and the data base structure for all manually collected ecological data are developed at the project planning stage, prior to data collection. The IM also supports researchers writing data management plans for proposals.

***Data Gathering.*** Several mechanisms for data gathering are employed at LUQ. Most of the non-climate ecological data are collected by hand, and protocols developed for data entry and QAQC are overseen by the IM. Protocols have also been developed and published on the website for the entry of some of the data collected in the Luquillo Experimental Forest, including manually collected rainfall data (since 1975) and water chemistry. Meteorological data are gathered both manually and using Campbell Scientific CR1000 dataloggers. Meteorological data from El Verde Field Station located at the top of a 30m tower over the forest canopy are downloaded to a Windows computer using a wireless connection. The distant location Canopy Trimming Experiment plots and the thickness of the rain forest canopy attenuates wireless connectivity so the data is instead manually collected every 2 weeks. We use a wifly dongle to convert the datalogger rs232 serial port to a WiFi signal which is downloaded to an iOS device running LoggerLink. The data is then uploaded to Dropbox and then downloaded to a windows computer and then a backup is stored on the Linux server.

**Data Entry.** Data are entered in a relational database management system table for each project and are maintained and backed up at the El Verde Field Station and at the Information Management facility in San Juan. The entry of manually collected data is also done at different locations. Manual data from El Verde and vegetation data from the Canopy Trimming Experiment are entered in digital media by the LUQ-IM data entry staff. Project managers and volunteers for major data collections like the Luquillo Forest Dynamics Plot enter the data to digital media located at their laboratories. All data entry is coordinated by the LUQ Information Manager.

**Quality control.** The procedures to assure correct collection and entry of data also depend on the type of data. Basic summary functions for averaging and graphing are used on sensor data. The accuracy of manually entered data is tested with a set of data base management system scripts to look for data entry errors. Also, double data entry and programmed procedures are used for assuring the quality of other types of data. A spreadsheet template for the generation and quality control of the El Verde rainfall and temperature daily data has been developed and shared in the website by the LUQ-IM. The spreadsheet also prorates rainfall data collected with one or more days of gap, assigning the averaged values to all days in the gap, including the collection day. The insertion of data into the NIS Portal provides a form of quality control at the file and data structure level.

LUQ scientists and project managers are responsible for the quality assurance of the data collected at the field, and the IM team is responsible for the quality control of the data entered in the digital media. Non-public views for the administration and quality control of metadata content have been developed in DEIMS to make revisions.

**Archiving.** The LUQ and the Forest Service computers, a website server, an Intranet server, a sensor data server and an external 500 GB drive serve as the LUQ archival system holding historical data and metadata. All original data is distributed in the computers where the data were entered. The LUQ-IMS website exposes all scientific data, following our data management policies of sharing and to assure investigators' intellectual rights. The sensor data servers at El Verde Field Station hold the El Verde sensor data and the Plone server holds individual investigator's data files to share with other LUQ scientists. An external 500 GB drive holds a history of all the data and metadata published in the website.

Guidelines for submission of metadata and data to be published in the Information Management System of LUQ are posted on the website. References of publications are maintained in EndNote software for distribution among the LUQ Scientists and as backup of the list of publications. EndNote imports are easily uploaded into DEIMS.

**Documentation and cataloguing:** By using DEIMS, LUQ has achieved a highly structured and databased information management system that allows us to document in detail all our data sets following the Network and LUQ standards. DEIMS provides a framework for metadata (data sets, variable names, persons, research sites, research projects, and publications). In addition, every piece of information can be related to another by the use of theme keyword taxonomies (network and LUQ site-specific sets of keywords). Views have been designed to display various



subsets of the metadata and allow the user to search for data using different criteria. A data catalog lists all data sets by order of incorporation into the system providing an abstract, contact person and a link to the rest of the metadata and data files.

**Backups.** Backups are performed on two types of media and in three time-frames. Individual data files backups are performed on three USB drives and an internal 1-TB drive every time a data file is created or updated. One of these USB drives is carried home and safely kept by the data entry person. The data entered by the student are saved in a USB drive and copied to a Dropbox folder temporarily to then be transferred to the computer hosting the database of origin (information manager's or data entry person's desktop). All the data and metadata entered in the website is maintained in the information manager's laptop which is carried home daily and safely kept. The entire data file system on the information manager's laptop is copied to the information manager's desktop additional 1-TB hard drive on a weekly basis. The file system of the data entry person's computer is copied every month to the same 1-TB drive. The server's Drupal file system is copied every month to another drive of the server. A backup of the Mysql data base is performed using the web tool "phpmyadmin". The resulting sql script containing all the database structure and data is then transferred to the Information Manager 1-TB hard drive.

**Publication and sharing.** LUQ complies with the NSF directives of sharing data with the general public as it publishes all the data generated with the LTER program funds in the website following the Data Management Policy described herein. In addition, it uploads all the data sets to the NIS Data Portal. Four non-LTER data sets are also documented following the LTER Network standards and shared in the LUQ website-IMS.

### **Data Sharing Practices and Policies**

**Data Management Policy (revised and updated in 2015).** The LUQ Data Management Policy establishes the obligation of the scientists to release data collected with LTER funding after two years. The LUQ information manager is responsible for assuring the documentation of data following the LTER Network standards and its publication on the LUQ Website.

**Users Agreement and Disclaimer.** Data users responsibilities are stated in the "User's License and Agreement, Acknowledgement, and Disclaimer" posted on the website.

**Policies for Re-Use, Re-Distribution, and Production of Derivatives.** All templates and protocols used by LUQ-IM for the management and sharing of data are publicly available in the LUQ website. This includes a list of LUQ IM publications, presentations and reports, the template for the data entry and conversion of the rainfall and temperature read at the El Verde Research Station, rules and templates to file metadata to into the LUQ IMS and a private, not publicly available Graduate Students' Project Online Form to enter and display graduate students research Information in the LUQ Graduate Student web page.

**Network activities.** The information manager is an active member in the LTER IM community and has originated and chaired workgroup activities such as the IM / LNO Partnerships and Collaborations WG (originator, 2008), LTER IMC Governance WG (original group member from 2008 to 2010 and 2013) and the Drupal Ecological IMS (DEIMS) WG (original group member, 2011 to present). She has also worked with the Mentoring Database of Expertise, the

Common relational schema for metadata and online EML editor, and the Controlled Vocabulary (2010) WGs and is currently participating in the organization of the Communications WG.

***Schoolyard and community schools and graduate students.*** Since 1999, the LUQ information manager has collaborated with the teachers of the LUQ Schoolyard Program to offer data management workshops to students and teachers on site. She has also participated in the Summer Internships offered annually. She has developed web pages for Schoolyard schools and LTER graduate students. She has organized activities with the LUQ Remote Sensing Lab Director and a local Middle School and has offered a class on LTER and IM standards and methods to UPR's IGERT students on three occasions.

***Information Management related publications.*** The LUQ information manager has authored one paper and collaborated in the publication of two others. She has presented posters at different Annual Meetings and given classes to High School and graduate students. She has been three times co-editor of Databits, the LTER IM Newspaper, and has also collaborated as an author.

***Other outreach activities.*** Since 2014, the LUQ information manager has been part of the Science on Drupal group and has participated in two Drupal Conventions where the Drupal profile for LTER data (DEIMS) has been presented. The Science on Drupal members of developers from and outside the United States and their main goals is "to enable data sharing, build tools for data science, and visualize science data in a meaningful way."

***Local administration resources.*** The LUQ information manager has developed several data tables for the administration of the research programs managed at ITES and the preparation of administrative workflows.

***Integration of Information Management with site science.*** The integration of information management with science involves many aspects of the management of data since collection to analysis, including manipulation, storage, dissemination and protection of data. It also encompasses the interaction of people collecting and analyzing the data and those who disseminate it. LUQ data is complex and varies in terms of subject of study and structure. Date format, species coding and data keyword assignment are some of the aspects that LUQ scientific and IM communities have standardized to facilitate the discovery and merging of data. LUQ scientists have adopted a six-letter code for the vegetation identification since early 1990s. Two mayor lists of these codes, one from the 1990s and another from 2012, are posted in LUQ website. LUQ IM integrated the use of the LTER Controlled vocabulary as the standard few years before it was incorporated into DEIMS. By adopting an information management framework, DEIMS, which incorporates the LTER units, metadata and keyword vocabulary standards, LUQ IM is facilitating data and science integration. Finally, LUQ has provided a common information management platform were all the elements of an LTER IMS, like standards, data, metadata and people lists co-exist and are easily related. By doing so, LUQ IMS have become a bridge between the variety if data collected by LUQ scientists.

## **Future Projects**

***Developing standards for Model Data.*** A review of the ecological models developed by the Systems Ecology Lab at SUNY-ESF for the Luquillo Experimental Forest (LEF) in northeastern

Puerto Rico is accessible on line. Models predicting changes in precipitation, biodiversity, C storage, and plant and animal populations have been used and described in our proposals and websites. During LUQ V, the information manager will cooperate with other ILTER information managers to develop a strategy for documenting models and model output.

***Collaborating with other Networks.*** The LUQ LTER is also part of the Latin-American (LA) community giving us an excellent position to interact with LA scientific and technical groups. Participation in the Drupal working group “Science on Drupal” will give us the opportunity to network with non-LTER groups. We will start in Puerto Rico by networking with DRUPAL technical groups to establish partners in order to collaborate with and support the local science community. By developing a local Drupal group we can reach out and share our LTER culture in and outside Puerto Rico.

***Improve data discovery and access.*** Develop more dynamic tables in DEIMS where users can discover different sources of data using keywords, species codes or any other common data type. Incorporate data bases of widely used precipitation and temperature data of El Verde Station in the DEIMS platform and provide a search engine to the user to extract and download the data.

***Training people from different areas of our LTER community on using the LUQ IMS.*** DEIMS provides straightforward and user friendly mechanisms that allow users of many levels to keep the website-IMS up to date. The LUQ information manager plans to organize training for administrative staff, students and scientists who have expressed their willingness to learn how to update their data sets and other content online.

***Developing a DEIMS-based site for the Education component of LUQ.*** The existing web page for the LUQ Scholyard component needs to be updated to follow the new structure and plans of the LUQ Educational component. With the collaboration of the program coordinator and a local web master we will develop a website that will serve as a resource for the teachers and students participating in our educational activities.

#### ***Publications:***

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## **Luquillo LTER: Facilities and Equipment**

The facilities available to support Luquillo LTER (LUQ) research in the Luquillo Mountains provide the needed equipment and conditions for a vigorous, long-term ecological research program. Moreover, there is institutional commitment for continued upgrading and maintenance of these facilities. Our primary facilities are located Department of Environmental Sciences (DES), University of Puerto Rico-Río Piedras (UPR), and at the USDA International Institute of Tropical Forestry, San Juan, Puerto Rico. DES has received grants from NSF to upgrade facilities at El Verde Research Station and laboratories at UPR.

### **University of Puerto-Rico Río Piedras**

The DES is dedicated to tropical ecosystems research in Puerto Rico and the tropics. DES has offices, laboratories, and collections on the UPR campus in San Juan and a field station at El Verde Research Area in the Luquillo Mountains.

#### UPR campus

- The tropical limnology laboratory is dedicated and equipped for the study of tropical freshwater ecosystems, focusing on understanding factors controlling ecosystem dynamics and processes. The laboratory is equipped with water chemistry analysis equipment (ion chromatographic and spectrophotometry equipment), and field equipment for stream sampling.
- The aquatic ecology laboratory is dedicated and equipped for the study of tropical stream ecosystems, focusing on understanding factors controlling ecosystem processes, the role that biota play in those processes, and the relation between biodiversity and ecosystem function. The laboratory is equipped with dissecting and compound microscopes, and field equipment for stream sampling (e.g., of insects, decapods, fishes).
- The Geospatial Laboratory is located in the library of the College of Natural Sciences. The laboratory was established with funds from USDA. It is equipped with 18 high-performance desktop computers and 8 GPS units. The laboratory has licenses for ArcGIS with the extension modules of spatial analysis, 3D analysis, and geostatistical analysis, ENVI, and ENVI EX remote sensing software. A 44" plotter is available for map printing.
- The Atmospheric Science Laboratory provides a temporary structure for sampling air at East Peak in El Yunque National Forest and many state-of-the art instruments for sampling at East Peak and analysis on the UPR campus.
- The information management facilities are equipped with two UNIX servers hosting both the public website and an Intranet, two desktop computers for data entry and quality control and another for system administration. One additional desktop is used for archival and to back-up the two data entry computers and the information management laptop. Two laptops, one used for remote system administration and another for performing information management tasks and holding all original data and metadata files filed by the LUQ investigators, are safely guarded by the system administrator and information manager.
- Botanical collection.

#### El Verde Field Station

- Living facilities for 40 scientists.
- A brand new laboratory that provides workspace for 10 researchers, and meeting and conference space.

- Library containing publications relevant to the Luquillo Mountains and access through the UPR main library to all holdings on the island.
- Comprehensive collections of local flora and fauna for the following groups: fungi, ferns, dicotyledons, myriapods, arachnids, insects, amphibians, and reptiles. (Extensive reference collections of invertebrates are also accessible at the USDA Experimental Station, San Juan, and Biology Departments on the Río Piedras and Mayagüez campuses of the UPR.)
- A wireless internet backbone from the field station to the Río Piedras campus, using voice over ip (VOIP) to connect to the university's PBX (telephone) for local and long distance calls.
- Dell GIS Server running ERDAS and ARC/INFO GIS software, over 10 windows workstation computers connected via a local area network (LAN)
- Direct access to UPR mainframe computers and electronic mail, with uninterruptible power supplies.
- Conference room.
- An NADP wet deposition station, and several weather stations based on Campbell microloggers.
- A laboratory with balances, microscopes, dissecting scopes, fiberoptic light sources, pH meters, and a diesel backup generator.
- Sample preparation and nutrient analysis laboratories, including sample drying, grinding, and extraction equipment, electronic balances and microbalances, and related equipment.
- Outdoor and indoor animal-holding facilities with light and temperature control and one-way observation windows.
- Electrical and carpentry shops.
- Facilities for field-drying of specimens.

The University of Puerto Rico makes available numerous office staff who serve LUQ, including an Executive Officer who manages an administrative staff composed of a secretary, an administrative assistant, a purchasing/equipment manager, and information management personnel.

### **International Institute of Tropical Forestry, Puerto Rico**

The USDA International Institute of Tropical Forestry (IITF) is a research branch of the USDA Forest Service housed in San Juan and in the Luquillo Mountains at Sabana Field Research Station. The resources available to LUQ through IITF are:

- Headquarters building with facilities for meetings, photocopying, office and audiovisual equipment.
- Tropical ecology and forestry library with more than 55,000 documents, 10,000 bound volumes, 100 journal subscriptions, map, film, and slide collections, microfilm of the entire Oxford Forestry Institute collection, FAO documents and journal listings from larger libraries in microfiche, and computerized literature searching facilities.
- Apparatus needed to measure photosynthesis, respiration, transpiration, and stomatal resistance in the field.
- Large convection ovens.
- Analytical laboratory for soils and vegetation including ICP and GC/MS.
- Research nursery with automatic watering system.

- State-of-the art geospatial analysis tools and expertise in the IITF GIS Remote Sensing Laboratory. This facility offers the most complete set of geospatial data for the region and expertise to support geospatial aspects of LUQ 5 research goals.
- Several microcomputers on a local area network and hook-up with USDA Forest Service computer system.
- Federal telecommunication system (FTS) facilities.
- Access to GSA vehicles.
- Internet 2

IITF provides sample processing for LUQ in a USDA-FS Analytical Laboratory, maintains field facilities used by LUQ collaborators, arranges cooperative agreements for LUQ scientists to conduct complementary research, and pays salaries of IITF technicians and scientists who work on LUQ projects. In addition, other projects funded by IITF contribute in non-material ways to the LUQ program.

### **Other institutions**

LUQ activities and analyses of LUQ samples also take place at facilities of the University of Connecticut Center for Environmental Sciences & Engineering (workshops, invertebrate studies), University of California-Berkeley (soil and gas analyses), the University of New Hampshire (water chemistry), and the University of Turabo, Puerto Rico (microbial studies).

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