



LUQ VI: 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) combines long-term measurements, experimental manipulations, and models to determine the effects of changes in climate and disturbance frequency on wet tropical forest and stream ecosystems. **The overarching goal of the Luquillo LTER program is to determine how changing climate and disturbance regime, alone or in concert, drive changes in the biota and biogeochemistry. An enhanced mechanistic understanding of change in natural and human-modified landscapes will improve our theoretical understanding and inform management of tropical forest ecosystems globally.** Since LUQ began in 1988, multiple hurricanes (1989, 1998, 2017) and droughts (1989, 1994, 2015) have impacted the Luquillo Mountains; this, coupled with a 90-year research history on forest ecology in natural and human-modified forests has provided opportunities to study the response of forests and streams to disturbance. The conceptual framework arising from our work has significantly shaped understanding of climate change, disturbance ecology, biogeochemical cycling, productivity, population and community dynamics, and legacies of land use in wet tropical forest and stream ecosystems.

Intellectual Merit: Global climate change will lead to an increase in the frequency of intense hurricanes and droughts in the Caribbean as well as other tropical regions. We hypothesize that changing climate and disturbance regimes interacting with the effects of past disturbance events will result in new combinations of species and biogeochemical conditions that have the potential to create ecosystems with no prior analog. These new ecosystem states will arise from material and information legacies of multiple disturbances, as well as immigration of species adapted to drier and more open conditions. We rely on a dynamic conceptual framework to guide our research and explore these altered ecosystems as they develop from the combined effects of increased hurricane frequency and/or drought. We will address the following key questions:

How will increased frequency of intense wind storms shape the structure and function of tropical forests now and into the future?

In the context of frequent intense hurricane disturbance, how do severe droughts and climate drying affect biota and biogeochemical cycling?

How do large-scale factors such as climate change interact with hurricanes and drought to shape tropical forest ecosystems of the future?

Our research is guided by hypotheses that address the ultimate and proximate drivers of change in a tropical forest, and the impacts of legacies of past disturbance on current and future disturbance response. We will continue to monitor *tabonuco* forest in the Luquillo Forest Dynamics Plot and the Bisley Experimental Watersheds and use elevation as a climate proxy in the Long-Term Elevation Plots to provide context for our experiments. The continuing Canopy Trimming Experiment will test our hypotheses that more frequent intense hurricanes will increase the dominance of shade intolerant species with cascading effects through other biota and biogeochemistry. Two new experiments, the Throughfall Exclusion Experiment and the Stream Flow Reduction Experiment, will address hypotheses that increased drought frequency will alter species composition and distribution as well as soil carbon and nutrient storage in catenas and streams. Models and data-model integration will allow us to address the combined effects of increased drought and hurricane frequency on tropical forest ecosystems, to synthesize across scales, and to forecast future ecosystem conditions.

Broader Impacts: Using integrated modeling, experimental, and observational approaches, LUQ provides an innovative and comprehensive scientific framework to develop and evaluate theory relevant to managing tropical ecosystems confronting a changing climate. LUQ VI will capitalize on our recent success in catalyzing major projects in Puerto Rico, such as NEON, IGERT, CZO, and ULTRA-Ex. 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. Schoolyard LTER in LUQ VI 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.

1.0 INTRODUCTION

The overarching goal of the Luquillo LTER program is to determine how changing climate and disturbance regime, alone or in concert, drive changes in the biota and biogeochemistry. An enhanced mechanistic understanding of change in natural and human-modified landscapes will improve our theoretical understanding and inform management of tropical forest ecosystems globally.

The Luquillo Long Term Ecological Research Program (LUQ) builds on over 90 years of research history in the Luquillo Experimental Forest (LEF), Puerto Rico and has shaped understanding of tropical forest structure and function. LUQ emerged from a strong collaboration with the U.S. Forest Service's International Institute of Tropical Forestry (IITF) and the Department of Energy (previously the Atomic Energy Commission), and has been a leader in the development of theory on tropical forest disturbance and recovery (e.g., *Walker et al. 1991, 1996, Brokaw et al. 2012, Uriarte et al. 2012, González et al. 2013*), food web dynamics (*Reagan & Waide 1996, Covich et al. 1999*), and biogeochemical cycling effects of, and feedbacks to, climate change (*Lugo & Brown 1993, Silver et al. 2004, Silver et al. 2013*). Leadership by LUQ scientists and collaborators has catalyzed a host of complementary large-scale research efforts including the Luquillo Critical Zone Observatory (CZO), the Next Generation Ecosystem Experiment in the Tropics (NGEE-Tropics), the San Juan Urban Long-Term Research Areas (ULTRA), Centers for Excellence in Science and Technology (CREST), and the USGS's Water, Energy and Biogeochemical Budgets (WEBB) programs. All LUQ publications are in *italics* and the 10 most significant publications from LUQ V are also underlined.

Three sets of interrelated conclusions from our long-term studies (Fig. 1.1) guide our research in LUQ VI:

1. Patterns in the distribution of species and rates of biogeochemical cycling are strongly influenced by climate, even though ecosystems in the LEF experience uniformly warm temperatures with relatively little seasonality compared to extra-tropical ecosystems (*Barone et al. 2008, Wood & Silver 2012, González et al. 2013, O'Connell et al. 2018*). Long-term data show warming temperatures and declining rainfall in the LEF, trends that are supported by modeling results (*Scatena 1998, Schaefer 2003, van der Molen 2010, González et al. 2013*). Ongoing measurements in benchmark sites (Fig. 1.1a,c) and work along a climate gradient (Fig. 1.1e) have identified tight linkages among climate, biota, and ecosystem processes.

2. The disturbance regime exerts strong, long-term effects on tropical forest biota and biogeochemical cycling. In the LEF, the occurrence, return interval, and the interaction among hurricanes and droughts have lasting effects on plants (Fig. 1.1b), animals (Fig. 1.1f), and carbon and nutrient cycling (Fig. 1.1d) and are contingent upon the initial conditions of the environment (*Waide & Lugo 1992, Walker & Willig 1999, Beard et al. 2005*). Canopy opening is the dominant factor driving biotic response to hurricane disturbance (*Shiels et al. 2015*), while organic matter deposition drives the biogeochemical response over the long-term (*Gutiérrez del Arroyo & Silver 2018*). Land-use can have long-term effects on the biota and biogeochemistry that persist over multiple hurricanes (*Uriarte et al. 2009*). Drought is an important, but poorly understood factor acting both as a press (through climate change; *Wood & Silver 2012, O'Connell et al. 2018*) and a pulse (via periodic intrusions of Sahara dust clouds; *Mote et al. 2017, Uriarte et al. 2018*). Models and data (*Neelin et al. 2006, Knutson 2010, Kang & Elsner 2015, Khalyani et al. 2016*) portend more frequent intense hurricanes and more severe droughts over the next century.

3. The cumulative effects of increasing frequency of intense hurricanes, more frequent droughts, and climate change are likely to result in fundamental shifts in population, community, and ecosystem characteristics, akin to a state change. A model capturing the interaction of hurricanes and past land use predicts a future with a new combination of primary and secondary tree species differing significantly from previous community structure (*Uriarte et al. 2009*). Droughts cause reversible shifts in community composition in streams, a result observed in other limnetic systems (e.g., *Scheffer & Carpenter 2003*). In uplands, drought tends to increase carbon (C) losses via soil respiration, and strongly decreases phosphorus (P), a limiting nutrient, through unprecedented changes in redox conditions across the landscape (*Wood & Silver 2012, O'Connell et al. 2018*). Finally, modeling projections under a future warming and drying climate scenario predict large shifts in forest community composition and suggest

that declining precipitation may drive net forest ecosystem productivity to zero within two decades at our site (*Feng et al. 2018*).

1.1 Conceptual Framework for LUQ VI

Building on our long-term research, our conceptual framework explores how climate and disturbance drivers at global and local scales result in complex and interacting effects on plants, animals, and biogeochemistry in forest and stream ecosystems (Fig. 1.2). Our long-term data provide the context for historical response to change; our current and future data and models allow us to explore how interacting disturbances, coupled with disturbance legacies (Fig. 1.3), may push ecosystems to new states with no prior analog. We aim to improve the mechanistic understanding of change in ecosystems by studying the complex interactions among disturbances (i.e. multiple hurricanes, droughts, and their combination) and legacy conditions. We use long-term observations, experiments, and modeling to improve our mechanistic understanding of change and anticipate future possible scenarios for tropical forest ecosystems.

Changes in disturbance regimes (i.e. new patterns in the frequency, intensity, or combination of disturbances) can lead to the development of ecosystem states with no previous analog (Johnstone et al. 2016). We define ‘no-analog ecosystems’ as those that differ in important defining characteristics (i.e., combinations of dominant species or abundant life forms, C and nutrient stocks, ecosystem stoichiometry) from historically prevalent ones (Blois et al. 2013). No-analog ecosystems can arise when a mismatch exists between the contemporary disturbance regime and species traits or “information legacies” that evolved in response to a historical regime (Johnstone et al. 2016). Such a deviation from an historical disturbance regime may produce a bifurcation, or cusp (Scheffer & Carpenter 2003), leading to a shift in ecosystem states during the response to disturbance. The high species diversity and net primary productivity of tropical forests may impart resistance to shifts in ecosystem states, but the increased probability of multiple interacting stressors (Folke et al. 2004) could trigger state change in these ecosystems. The LEF faces unprecedented changes in hurricane and drought frequency that could challenge ecosystems in critical ways.

Our long-term research and synthesis activities provide a process-based interpretation of the ecological and biogeochemical mechanisms underlying ecosystem and community dynamics following disturbance, and of the importance of antecedent events in shaping such dynamics (e.g., *Zimmerman et al. 1994*, *Reagan et al. 1996*, *Covich et al. 1999*, *Lugo et al. 2000*, *Uriarte et al. 2009*, *Crowl et al. 2012*, *Lodge et al. 1994, 2014*, *McDowell et al. 2013, 2014*; Fig. 1.2). The high frequency of disturbance in our system (*Lugo & Scatena 1996*) allows us to contribute to successional theory by characterizing the long-term trajectory of ecosystem responses to a range of disturbance events. We have also identified specific mechanisms by which disturbance creates ecological legacies - post-disturbance dynamics of biotic and abiotic ecosystem components and their interactions that persist long past the disturbance itself (*Walker & Willig 1999*, *Johnson & Miyanishi 2007*, *Pickett et al. 2011*). Our forested ecosystems are, in many ways, in continuous flux as a result of hurricane disturbance and drought (*Lugo et al. 2000*, *Beard et al. 2005*, *Brokaw et al. 2012*) and provide a robust testing ground for temporal ecology and disturbance-mediated successional theory, a topic that has acquired further urgency in a rapidly changing world (*Kareiva et al. 2007*, *Prach & Walker 2011*, *Wolkovich et al. 2014*).

The high rate of disturbance at our site provides an excellent template to test hypotheses related to state change in ecosystems. Hurricane Maria, an especially strong (Category 4) storm, is the fourth major hurricane to directly strike our site in 30 years, a significant departure from the 60-year return interval for major storms (*Scatena & Larsen 1991*, *Boose et al. 2004*) that prevailed before LUQ began. The intensity and frequency of these storms agree with predictions of climate change models, and thus present a rich opportunity to refine our understanding of wind disturbance in forested ecosystems in the context of a changing climate.

Successional theory (Glenn-Lewin et al. 1992, Walker et al. 2007, Pickett et al. 2011) provides a framework for examining the principles of disturbance and response. Succession is a manifestation of temporal ecology (*Walker & Wardle 2014*), the idea that ecological patterns and processes are rarely static (Chave 2013). Johnstone et al. (2016) used the term “ecological memory” to encompass both material and information legacies existing in an ecosystem as a result of past ecological and evolutionary dynamics. Material legacies are the physical manifestations of previous disturbance (e.g., coarse woody

debris inputs), whereas information legacies represent organismal traits that have evolved in response to the historical disturbance regime (e.g., sprouting ability). Ecological memory encapsulates many concepts related to temporal ecology such as priority effects, biological legacies, antecedent effects, lag effects, time delays, historical effects, contingency and buffering capacity (e.g., Bengtsson et al. 2003, Ogle & Reynolds 2004, Golinski et al. 2008, Schaefer 2009, Walker et al. 2010, Waide & Willig 2012). Moreover, current usage of the concept (Johnstone et al. 2016) provides mechanistic ties to ideas of ecosystem resistance, resilience, and stability, and thus links our previous research (Brokaw et al. 2012) to the concepts of ecosystem state changes that we address in this proposal.

1.2 Research Goals for LUQ VI

We propose to study the separate and combined effects of the long-term trend of increasing hurricanes and droughts on tropical forest ecology. Climate change is driving an increase in the frequency of intense storms as well as more frequent droughts in the Caribbean region. These changes in the disturbance regime, coupled with effects of past disturbance and land use, are predicted to lead to the development of new ecosystem characteristics with no previous analog. Our conceptual model (Figs. 1.1, 1.2) links proposed research into the impacts of increasing disturbance frequency with our long-term data records, on-going measurements and experiments, and models. Our experiments allow us to test hypotheses about the key mechanisms driving the observed patterns, and facilitate the interpretation of long-term patterns, as well as help to parameterize our forward-looking models that enhance predictive understanding of the ecosystems we study.

Our proposed research addresses three primary questions:

Question 1. How will increased frequency of intense wind storms shape the structure and function of tropical forests now and into the future? Wind storms are an important component of the disturbance regime in almost all forested ecosystems (Everham & Brokaw 1996, Lugo 2008). Our long-term data suggest that the effects of hurricanes are contingent on the initial state of the ecosystem and the extant material legacies of past disturbances (i.e., canopy openness, debris deposition, soil redox). Species traits have evolved in response to hurricanes (Zimmerman et al. 1994, Griffith et al. 2008, Uriarte et al. 2012), and represent an information legacy of past disturbance. Climate models predict that the frequency and intensity of hurricane disturbance are changing globally (Knutson et al. 2010, Villarini & Vecchi 2013). Models based on our long-term data predict that more frequent hurricanes will lead to changes in species composition (Uriarte et al. 2009), and alterations in biogeochemical dynamics and productivity in terrestrial and aquatic ecosystems (Zimmerman et al. 1995, McDowell et al. 2013, 2014).

Question 2. In the context of frequent intense hurricane disturbance, how do severe droughts and climate drying affect 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 (Khalyani et al. 2016). Our models and empirical data suggest that rainfall is becoming more variable in the Luquillo Mountains (Scatena 1998, Schaefer 2003, van der Molen 2010, González et al. 2014). 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 precipitation changes is more rapid than previously believed (Khalyani et al. 2016). A major question is how the biota and biogeochemistry in historically wet rainforests will respond, over short and long time scales, to decreased precipitation and increased seasonality, both of which are no-analog conditions in these forests.

Question 3. How do large-scale factors such as climate change interact with hurricanes and drought to shape tropical forest ecosystems of the future? Understanding long-term trends in climate, and the relationships among climate, ecosystems, and disturbance is essential to more accurately predict future conditions. Long-term trends in climate will lead to progressive changes in biotic structure and biogeochemical dynamics (Smith et al. 2009), and the rate of change will be exacerbated by more frequent disturbances in forest and stream communities that feed back to the atmosphere (Sanford et al. 1991, O'Brien et al. 1992, Silver 1998, Erickson & Ayala 2004). The combined effects of changes in climate and disturbance regimes may result in tropical forest ecosystems characterized by community compositions with no prior analog, and altered biogeochemistry, productivity, and population and community 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 the relevant 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 to facilitate the development of models applicable to Puerto Rico, the Caribbean, and tropical forest ecosystems globally.

2.0 RESULTS FROM PRIOR SUPPORT

The LEF is distinguished by one of the longest continuous research histories in the tropics (Sastre & Santiago 1996), which has helped shape fundamental understanding of tropical forest structure and function (Fig. 2.1). Disturbance and response has been the dominant theme of research activities in the LEF. Early research by USDA Forest Service scientists experimented with management strategies and reforestation of former agricultural lands (Wadsworth 1997). In the 1960s and 1970s, the Atomic Energy Commission sponsored research on the effects of gamma radiation on tropical ecology. This effort yielded one of the most complete analyses of tropical forest metabolism, nutrient cycling, energy flows, leaf fall, and population and trophic dynamics (Odum & Pigeon 1970), including the assembly of a comprehensive food web (*Reagan & Waide 1996*). Research on hurricane disturbance began in the 1930's (Stone 1940, Wadsworth 1949) and continued following storms in 1956 (Wadsworth 1959), 1989 (*Walker et al. 1991*), 1998 (*Heartsill-Scalley et al. 2007*), and 2017.

The trajectory of our long-term research has remained focused on disturbance themes since LUQ joined the LTER network as the only tropical site in 1988 (Fig. 2.2). Our research has addressed how disturbance shapes the climatic, biotic, and biogeochemical dynamics of tropical forests. We determined how disturbance responses are mediated by both initial conditions and particular characteristics of the disturbance (*Covich et al. 1991, 1996, Walker & Willig 1999, Shiels & González 2014*). In LTER III we added climate and climate change as a focal area of our research, both as a driver of disturbance and a template upon which to evaluate background conditions in forest ecosystems (*Wang et al. 2002a, b*). This led to an expansion of our research along the elevation gradient as a climate change proxy, as well as providing a wider range of climate, biotic, and biogeochemical conditions for our field and modeling efforts (*González et al. 2013*). Our long-term data and models show decreasing rainfall (including the 1994 and 2015 droughts) and warmer temperatures in the Luquillo Mountains (*Scatena 1998, van der Molen 2010, Van Beusekom et al. 2015*). In LTER IV, we began to consider the interactions between disturbance regime and climate change (*Barone et al. 2008, González et al. 2013*).

Below we summarize our recent activities. Products from the last 6 years of LUQ include 188 peer-reviewed publications, 7 books and special features, 41 book chapters, and 10 dissertations and theses. LUQ has 154 datasets online, 33 of which are ongoing datasets.

2.1 Luquillo LTER V

During LUQ V (2012 – 2018), we examined how droughts and hurricanes affect the structure and function of tropical forest ecosystems. Our research, built upon our long-term data, focused on three themes: 1) the impacts of repeated hurricane disturbance on biota and biogeochemistry; 2) precipitation variability in space and time as well as effects on the diversity and distribution of plants, animals, and biogeochemical cycling; and 3) regional scale climate change influences on forest composition, the quantity and quality of water, and aquatic food webs.

Hurricane Disturbance – Hurricanes affect nearly every continent in the world and are among the most intense weather disturbances in forest ecosystems (*Everham & Brokaw 1996, Scatena et al. 2012*). Models predict an increase in the frequency of severe storms in the Caribbean and other regions (Frazz and Elsner 2013, Emanuel 2017). Our long-term research on the impacts of Hurricanes Hugo and Georges provides invaluable historical data to quantify the effects of a changing disturbance regime. Our data show that, historically, 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*). Other factors, such as forest structure, stream-water exports of coarse particulate matter, and abundances of some plants and animals recovered slowly or never fully recovered their pre-Hugo values (*Heartsill-Scalley 2010, 2012, Willig et al. 2011*). Comparisons of Hurricanes Hugo and Georges showed differences in their effects on both terrestrial (*Willig et al. 2012, Schowalter et al. 2017*) and aquatic ecosystems (*Crowl et al. 2012*). Hurricane Georges (1998) resulted in much less structural and compositional change, largely because the branch

structure of the forest had not fully recovered from Hurricane Hugo, reducing the impact of the second storm on the forest canopy and the amount of woody debris generated. We are now assessing the damage and initial responses from Hurricane Maria (2017) on biotic and biogeochemical dynamics.

Data from Hurricanes Hugo and Georges 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*). The results prompted us to develop a long-term, factorial manipulation experiment (the Canopy Trimming Experiment – CTE) 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 (*Shiels et al. 2015*), favoring pioneer trees, reducing the abundance and diversity of key animal groups, reducing decomposition rates via inhibition of lignin-degrading fungi, and increasing nitrate export in soil water. Debris deposition was an important source of C and nutrients to soils (*Gutiérrez del Arroyo & Silver 2018*), and contributed to a slight increase in tree basal area growth (*Shiels et al. 2010*). A second set of experimental hurricane treatments was completed in late 2014 (CTE II). The design was altered to include only two treatments, control vs. trim+debris (or hurricane simulation), following a strategic decision to focus our efforts on the effects of once-a-decade hurricane disturbance on forest ecosystem dynamics. During CTEII, a large flush of labile C and nutrients leached into soil from the deposited litter within the first three weeks following the experimental trim. Soil microbial biomass increased quickly, and microbial communities in both litter and soil shifted away from lignin-degrading basidiomycete fungi towards microfungi that degrade cellulose and hemicellulose. Lysimeters, which provide an integrated measure of the response of forest floor processes over time by collecting soil water from 30 cm depth, closely mimicked the response of stream chemistry to Hurricanes Hugo and Georges that was described by *McDowell et al. (2013)*. Hurricane simulation caused a peak in nitrate concentrations within a year after both experimental treatments, but the second trim showed lower soil water concentrations (*McDowell & Liptzin 2014, Fig. 2.3*), just as Hurricane Georges resulted in lower stream water nitrate concentrations than the earlier Hugo. These results demonstrate the strong connection between forest and stream in this rainforest system, as well as the effectiveness of our Canopy Trimming Experiment as an analog for hurricane disturbance.

At the end of LUQ V, the LEF was struck by two hurricanes, Irma and Maria. Irma (September 7, 2017) passed to the north and had mild to moderate impacts to the site. Hurricane Maria (September 20), with strong, category 4 winds (154 mph or 69 ms⁻¹ at landfall), passed near the site and caused widespread defoliation and significant alteration of forest and stream structure (Fig. 2.4). Our on-going long-term measurements allowed us to capture the immediate impacts of both storms. Two NSF-RAPID projects are underway using intensive measurements to determine the effects of the hurricanes on vegetation and biogeochemical cycling during the first year following the event.

Drought – In LUQ IV, we used small-scale shelters to begin to determine the impacts of drying and drought on microbial dynamics and biogeochemical cycling (*Wood & Silver 2012, Bouskill et al. 2013*). During LUQ V our long-term monitoring captured the impact of the intense 2015 drought, a year with only 50% of long-term average rainfall. The seasonal pattern of rainfall was similar to preliminary climate model predictions for end of century warming trends (*Mote et al. 2017; Fig 2.5*).

In a modeling study that was parameterized with our long-term forest productivity and climate data including 2015, *Feng et al. (2018)* showed that predicted drought and temperature scenarios for the Caribbean (*Neelin et al. 2006*) would cause forest NEP to decrease to zero by 2036 in mid-elevation *tabonuco* forest. The model predicted that this would signal a shift for the LEF from a C sink to a C source (Fig. 2.6). Strong effects of the 2015 drought on species-specific patterns of seedling (but not tree) mortality were recorded (*Uriarte et al. 2018*) that may portend alteration of community composition in the future. Moreover, African dust inputs associated with the drought reduced irradiance levels to the forest floor, combining with reduced precipitation to affect seedling mortality patterns (*Uriarte et al. 2018*).

An intensive study using a continuous sensor array along a hillslope revealed that drought significantly increased soil O₂ availability, lowered soil P availability, and increased soil C emissions (*O'Connell et al. 2018*). The recent drought, together with our previous work, has shown that drought also strongly alters microbial diversity and community structure (*Bouskill et al. 2013, 2016a,b*), and that effects vary significantly with topography (*Wood & Silver 2012, O'Connell et al. 2018*). The 2015 drought increased

litterfall into streams (Fig. 2.7) and drove a shift in the consumer community to include increased insect abundance (Fig. 2.8) with a concomitant loss of algal biomass.

Large-Scale Climate Drivers Impacting the LEF – Understanding drivers of precipitation is critical for determining the susceptibility of the biota and biogeochemical dynamics to droughts. During LTER V, we studied how large-scale climate drivers influence precipitation variability at LUQ (*Van Beusekom et al. 2017, Murphy et al. 2017, Mote et al. 2017*). Utilizing historical precipitation records and regional analyses, *Ramseyer & Mote (2016, 2017)* showed that high wind shear environments are associated with the driest regimes in eastern Puerto Rico, indicating these variables are the most useful for downscaling studies of local climate. Their findings showed that the early rainy season (April – July) is responsible for ~60% of the inter-annual variability in rainfall in eastern Puerto Rico and is most susceptible to factors causing drought. Building on this approach, they showed that the 2015 drought was likely caused by intrusions of hot, dry, dust-laden air arriving from Africa (*Mote et al. 2017*) and not the ENSO event that was associated with drought elsewhere in the world that same year. These data are essential for modeling future forest and stream communities and their biogeochemical dynamics.

We also explored long-term changes (1975 – 2016) in cloud base height, a critical attribute of the elevation gradient in the Luquillo Mountains potentially linked to plant and animal metacommunity structure (*Willig et al. 2013*) and plant growth rates (*van der Molen et al. 2010, González et al. 2013*). Shifts in cloud base height were associated with large-scale global changes, but unrelated to any local anthropogenic effects, i.e., forest cover, as we expected (*Van Beusekom et al. 2017, Mote et al. 2017*; Fig. 2.9). Results, however, suggest that the cloud forest ecosystem may be more vulnerable to wet season drought periods than previously assumed (*Van Beusekom et al. 2017*).

2.2 Cross Site Activities, Supplemental Funding, and Broader Impacts

During LUQ V, LUQ scientists participated in a number of LTER working groups, including Decomposition, Soil Organic Matter, and Stream Elemental Cycling. Cross-network collaborations were 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 participate in TeaComposition, a global litter decomposition study (*Didion et al. 2016*). LUQ and Florida Coastal Everglades LTER scientists are collaborating in editing a special issue of *Ecosphere* called "Resistance, Resilience, and Vulnerability to High Energy Storms: A Global Perspective" that involves cross-site comparisons with coastal Australia, Dominican Republic, Florida, Guadalupe and Dominica, Louisiana, Mexico, Puerto Rico, and Taiwan. 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 2016*). Additionally, we have initiated a collection of in-depth analyses of the challenges and accomplishments of long-term ecological research (*Waide & Kingsland*, in preparation). The latter two activities constitute part of our **broader impacts**.

We used **supplemental funds** during LUQ V (total \$105,495) to purchase equipment including a -80°C freezer placed at Sabana Field Research Station to support microbial studies and field and laboratory equipment (e.g., sensors, drying oven, pH and conductivity meters). Supplemental funds received after Hurricane Maria are being used to replace damaged equipment (meteorology sensors, data loggers, and computers), to purchase diesel for the field station generator, and to support investigator and student travel.

As part of our **broader impacts**, 48 graduate students and 76 undergraduate students participated in LUQ V. Our Schoolyard LTER program reached 47 teachers and 410 Hispanic students in Puerto Rican schools. LUQ received a \$1,108,530 grant from the U.S. Dept. of Education for an evaluation of how *Journey to El Yunque* affects student motivation and learning. With these leveraged funds, Luquillo reached 14 middle school teachers and 1258 middle schools students in the US mainland and Puerto Rico. Almost half of these students were Hispanic (46%) and 14% were African American. Since 2012, an REU program based at El Verde Field Station, and strongly connected to LUQ, has involved 48 students,

73% of whom are minorities. The REU program has produced 12 publications, 10 with the student as first author. LUQ field projects have been supported by volunteer internships for recently graduated students seeking experience in tropical research. Since 2012, 70 students have participated (59% women and 37% underrepresented minorities), and many have gone on to pursue academic studies. With the Museum of Contemporary Art (MAC) in Santurce, Puerto Rico, LUQ organized a collective art exhibit titled "Poetic Science: *Aproximaciones artístico-científicas sobre el Yunque*" that has been shown at two locations including the National Museum of Puerto Rican Arts and Culture in Chicago (bringing record attendance to the museum). LUQ scientist Alan Covich produced a film in collaboration with Freshwaters Illustrated called "Water from the Mountain." It depicts the importance of streams for biodiversity preservation and as a source of clean water for human populations.

2.3 Response to the Mid-Term Review

We hosted a site review at LUQ in March of 2017. In the words of the NSF Program Officer, "The overriding sentiment of the review report is extremely positive ... [your program deserving credit] for a high level of productivity, good progress towards accomplishing the goals set out in your proposal, forward thinking as you consider leadership transition, and overall management of a complex program with lots of moving parts and collaborations both within and outside the LUQ LTER." We have followed the suggestions made by the review team in this proposal to (1) explain in more detail in the Introduction and elsewhere how the relevant theory informs our conceptual framework, (2) make clear in Research Approaches and workplans how the interaction of models with observations and experiments informs research planning; and (3) clarify our approach to understand the occurrence of novel or no analog ecosystem conditions. We agree with the team's recommendation to incorporate an ecophysiologicalist into the program; our progress with this is explained in Project Management.

3.0 RESEARCH APPROACHES

Long-term monitoring in LUQ takes place in focused field studies that promote collaboration among the diverse disciplines represented by our research group and enable efficient use of available resources. In light of the recent disturbance by Hurricane Maria, our goals for LUQ VI are to focus our early efforts on deciphering the short-term (current funding and Year 1 of the new funding cycle) impacts of the storm and responses of forest and stream ecosystems (Question I) and how these compare with previous severe storms (*Walker et al. 1996, Brokaw et al. 2012*). In Year 2 of funding, we will return to the emphasis established in LUQ V to determine the long-term impacts of increased drying and drought (Question 2), but now in the context of increased hurricane frequency. Meanwhile, we continue to refine our mechanistic understanding of how global and regional changes in climate (Question III) drive local changes in climate and ecosystems.

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

We are conducting a set of complementary, long-term measurements of environmental, biotic, and system properties designed to reveal the relationships between disturbance and response in the Luquillo Mountains. Two key study areas are the **Luquillo Forest Dynamics Plot** (LFDP; Fig. 3.1) and the **Bisley Experimental Watersheds** (BEW) located in *tabonuco* forest (200 – 600 m asl) on leeward and windward sides of the LEF, respectively. In the 16-ha LFDP, we have followed the dynamics of >110,000 woody plant stems ≥ 1.0 cm dbh over three decades (*Thompson et al. 2002, Hogan et al. 2016a,b*). The study of species-rich communities is facilitated by large contiguous plots like the LFDP, which allow study of the mechanisms that promote species diversity and coexistence (*Zimmerman et al. 2008, Anderson-Teixeira et al. 2015*). We perform spatially explicit censuses of trees, shrubs, seedlings (since 1999), and phenology/seed rain (since 1992) at time intervals relevant to their dynamics (*Uriarte et al. 2012*). Measurements of diameter increments of living trees using dendrometers and annual measurements of coarse woody debris (CWD) allow us to detect and project long-term climate effects (*Feng et al. 2018*; see Hypotheses 1, 2, 4, and 5) and to estimate above and belowground C storage in the plot (*Lodge et al. 2016*). Data on the spatial distribution of leaf litter can also inform expected litter inputs to streams (*Uriarte et al. 2015*; see Hypotheses 3 and 6). The abundance of key heterotrophs, including gastropods, phasmids, lizards, frogs, and birds are measured annually at forty locations in the LFDP (e.g. *Bloch et al. 2007, Willig et al. 2007, Prates et al. 2015*). The next full census of the LFDP is in Year 3 of LUQ VI (2021). We are assessing tree damage (>10 cm dbh) from Hurricane Maria and monitoring seedling recruitment via RAPID funding.

The BEW comprise three adjacent watersheds that total 26 ha (*Heartsill Scalley 2017*). These include two experimental (6.3 and 6.7 ha) and one control (13 ha) watershed. Tree and shrub species are monitored in 90 permanent, 10 m diameter plots on a 40 x 40 m grid every 5 years. Understory vegetation, total aboveground biomass, and elemental chemistry are also sampled (*Royo et al. 2011*). Climate stations (rainfall, temperature, total IR, relative humidity, wind speed and direction) record hourly and daily data. Throughfall is measured weekly. Stream coarse particulate organic matter export and litterfall are measured every two weeks (*Heartsill-Scalley et al. 2007, 2010, 2012*).

Stream Monitoring is conducted in three streams of the BEW and in three streams in the El Verde Research Area: Quebradas Sonadora, Toronja, and 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 monitor decapod shrimps weekly (since 1988). In two BEW streams and the Q. Prieta and Toronja, we also monitor decapod shrimp biannually in pools (since 1988). Aquatic insects, algal standing crop (chlorophyll *a*), organic (AFDM) and inorganic deposition are measured biannually in pools and riffles of the Q. Prieta and one BEW stream (since 2009 for insects and 2003 for algae). The upper section of Prieta is where the Stream Flow Reduction Experiment is located (see below).

The **Canopy Trimming Experiment (CTE)** was initiated in 2002 in the El Verde Research Area. The first trimming treatments were designed to separate canopy opening and debris deposition, the two principal effects of hurricane disturbance to our forests (*Zimmerman et al. 1994, Shiels & González 2014*). This long-term experiment has allowed us to separate the role of microclimate, detrital inputs, and different functional groups of decomposers on detrital processing and ecosystem resilience after canopy disturbance (*Shiels et al. 2015*). Through once-a-decade repeated canopy manipulations, the CTE will also allow us to assess the effects of a projected increased frequency of intense hurricanes (Knutson et al. 2010) on forest composition, soil C storage, nutrient dynamics (*Sanford et al. 1991, Gutiérrez del Arroyo & Silver 2018*), population dynamics, and trophic structure (see Hypotheses 1 and 2). Each treatment covers a 30 x 30 m area with an inner 20 x 20 m measurement plot. The first experiment consisted of four treatments in each of three blocks. and included: 1) canopy trimmed, with debris

Table 3.1. Continuing measurements in the CTE and scientists charged with their collection.

Abiotic	Frequency	Lead(s)
Temp (air and soil)	Hourly	Ramírez/González
Soil & litter moisture	Bi-weekly-annually	Ramírez/González
Canopy openness	Quarterly	Zimmerman
Throughfall	Biweekly	Ramírez
Biotic		
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/Presley
Ecosystem Processes		
Litterfall mass & chemistry	Biweekly	Ramírez
Tree diameter increments	Annually	Zimmerman
Litter decomposition rates	6 mos post-trim	Cantrell/González
Soil nutrients (total & avail)	Quarterly	Lodge/González
Soil carbon pools and fluxes	Annually/periodically	Silver
Soil solution chemistry	Weekly - quarterly	McDowell

addition, changing microclimate, forest floor mass, and nutrient content, 2) canopy trimmed, without debris addition, 3) canopy not trimmed, but debris added, changing forest floor mass and nutrient content, 4) untreated control. To study an increased frequency of intense hurricanes, treatments 1 and 4 (hurricane and control) will be repeated every 10 years for at least 50 years duration. The first of the repeated disturbances, the second canopy trimming treatment, took place in late 2014; measurements are continuing (Table 1). In LUQ VI we plan to repeat these treatments in 2024.

The **Throughfall Exclusion Experiment (TEE)** is taking place in two stages. Prior to Hurricanes Irma and Maria, we deployed small (3 x 5 m) throughfall exclosures to determine the impact of multiple short-term droughts on soil biogeochemistry, as well as on microbes and litter organisms. These small clear plastic roofs significantly reduced soil moisture without significantly affecting other environmental conditions (i.e., light and temperature; *Wood & Silver 2012*, *Bouskill et al. 2013*). Replicate shelters were placed on ridges thus eliminating any upslope inputs and paired with untreated controls. Litterfall accumulating on roofs was removed weekly and placed on the soil surface underneath. Throughfall amount and chemistry were measured according to *Wood & Silver (2012)* allowing us to determine both water and nutrient removal as a result of simulated drought. We used 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 O₂ sensors (Apogee Instruments, Logan UT) were installed at 2 depths. Results from this phase of the study will provide us with a baseline measure of drought under closed canopy conditions. After Hurricane Maria, shelters were re-deployed within 3 weeks to study the effect of drought in the context of the recent hurricane disturbance (see Hypothesis 5).

In Year 2, we will start a controlled experiment using larger throughfall exclosures to study the mechanistic drivers of drought response (see Hypotheses 4 and 5). Larger exclosures are a necessary next step to determine the effects of drought on plants and animals. Throughfall exclosures will exclude rainfall in replicate 30 x 30 m plots and follow the protocols described by the International Drought Experiment (IDE) consortium, thus leveraging the experience and comparative results of other sites in the network. Drought will be imposed using understory troughs that passively remove throughfall by a constant, site-specific percentage (Hanson 2000, Pangle et al. 2012) based on ground area covered. The amount of rainfall reduction will be informed by ongoing climate downscaling studies. We will contrast the drought treatment with ambient unsheltered controls and each will be replicated 3 times. Continuous to quarterly biogeochemical measurements and annual censuses of selected populations and communities of consumers (e.g., gastropods, phasmids, and frogs) will be executed in four 3-m radius plots within each plot, using established protocols (*Willig et al. 2014*, *O'Connell et al. 2018*).

We are establishing a **Stream Flow Reduction Experiment (StreamFRE)** in two 150-m long stretches of adjacent tributaries of the Q. Prieta (Hypothesis 6). We will take advantage of a steep natural rock barrier 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). An un-manipulated arm of the stream with similar riparian vegetation, slope, width (1-3 m), biota, and chemistry will serve as a reference reach. We will use Randomized Intervention Analysis (RIA, Carpenter et al. 1989), a design well suited to the analysis of un-replicated whole-ecosystem manipulations. 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 pre-manipulation data (2016-19) before the beginning of the reduced-flow manipulation; currently we intend to begin manipulations of stream flow in Year 2 of LUQ VI. This schedule will allow us time to continue tracking the short-term impacts of Hurricane Maria on these reaches. Mapped and identified trees in the 1 ha area around the streams will allow estimation of species-specific litter inputs during experimental studies (*Uriarte et al. 2016*). Trimming of the canopy in part of the reference reach is planned for 2024 to coincide with the next planned trim of the CTE to study the separate and combined effects of droughts and hurricanes (Hypotheses 3 and 6).

3.2. Long-term Measurements of the Elevation Gradient

Rising to 1075 m in elevation, the Luquillo Mountains present a gradient of climate and vegetation change that extends through five life zones from subtropical moist forest to lower montane rain forest (Ewel & Whitmore 1973). Forest communities extend along the gradient from mid-elevation (200-600 m asl)

tabonuco forest through *palo colorado* forest (600-900 m) to elfin woodland (900-1075 m; Fig. 2.2). Palm forest, an edaphic formation, occurs at all elevations. We will collect long-term (80 yr) data on changes in the distribution of organisms and process rates along this gradient to examine the integrated effects of warming, drying, and more frequent disturbance over the range of biotic and abiotic conditions (Hypotheses 1 and 4). We measure changes in vegetation structure and composition every six years in three series of **Long-Term Elevation Plots** (LTEP) placed at 50 m intervals of elevation in three watersheds (Mameyes, Icacos, and Sonadora). In the Sonadora watershed, we compare upland forest types to adjacent palm forest to separate the effects of forest community composition and the abiotic environment (Willig *et al.* 2013, Table 3.2). We also monitor climate, rainfall chemistry, diameter increment, and litterfall in the Sonadora watershed.

Table 3.2. 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>Climatic characteristics (continuous)</p> <p>Meteorology and micro-meteorology along mixed forest and palm forest transects in the Sonadora Watershed. (Ramírez)</p> <p>Rainfall, air temperature, and soil temperature. (González/Silver)</p> <p>Biotic communities (every 6 y)</p> <p>Trees (adults and seedlings) and ferns along the Sonadora, Mameyes, and Icacos Watershed transects (Zimmerman/Heartsill-Scalley)</p> <p>Gastropods and phasmids in the Sonadora Watershed (Willig)</p> <p>Litter invertebrates in the Sonadora Watershed (Yee)</p> <p>Canopy invertebrates in the Sonadora watershed (Schowalter)</p> <p>Stream insects along an elevational gradient in the Sonadora Watershed (Ramírez)</p> <p>Stream decapods in the Sonadora watershed (Crowl/Covich)</p> <p>Birds, reptiles, and amphibians in the Sonadora watershed (Waide)</p> <p>Microbes in the Sonadora Watershed (Cantrell)</p> <p>Stream algae in the Sonadora watershed (Pringle)</p> <p>Grazing and detrital trophic webs (or networks) based on <i>Prestoea acuminata</i> (Sierra Palm) in the Sonadora Watershed (Waide/Willig)</p> <p>Biogeochemical Cycling & Ecosystem Processes (Periodic)</p> <p>Production (estimated by tree growth) every 6 y (Zimmerman)</p> <p>Decomposition rates (using popsicle sticks and palm leaf litter) over 1-3 y (Silver/González)</p> <p>Nutrient (N, P, Ca) fluxes in litterfall quarterly (González/Silver)</p> <p>Soil descriptions 1 time (González/Silver)</p> <p>Litterfall every 2 weeks (González/Silver)</p> <p>Rainfall chemistry weekly (González/Silver)</p>

Soil properties and plant species composition have been measured in these plots (Barone *et al.* 2008); we have also conducted biogeochemical and decomposition experiments along the elevation gradient as part of previous LTER research (Silver *et al.* 1999, McGroddy & Silver 2000, Dubinsky *et al.* 2010, Hall & Silver 2015). We began long-term studies of changes in plant and gastropod communities in LUQ III (Willig *et al.* 2013, Willig & Presley 2016), and established baseline measurements for most of the variables in Table 3.2 last year (Fig. 3.2) before Hurricanes Irma and Maria struck in September. Funds from a RAPID award are being used to conduct post-hurricane tree damage assessments in the LTEP, and other variables will be resampled during the next year and into Year 1 of LUQ VI to capture hurricane

effects, and again in Year 5, the regularly scheduled timing for the LTEP census. We will continue to measure the variables in Table 3.2 at six-year intervals until the end of the century to examine the effects of changes in environmental drivers (see Hypotheses 1 and 4) on populations, communities, and key ecosystem characteristics.

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 and forge predictions of future change. We have adopted the model-experimental (ModEx) integration, an approach that recognizes that improved collaboration between modeling and process scientists is needed to develop, test, and implement process representations in models at all scales.

During LUQ V, we parameterized the Ecosystem Demography model (ED2; Moorcroft et al. 2001, Medvigy et al. 2009) in the LEF and it has already produced startling predictions (*Feng et al. 2018*). 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, which we are using to model and inform our understanding of biogeochemical observations and experiments. Following the ModEX philosophy, we parameterized ED2 using the Predictive Ecosystem Analyzer (LeBauer et al. 2013), an eco-informatic workflow for model analysis that, among other things, accounts for the different scales and sources of model uncertainty. In LUQ VI, we will incorporate a hurricane module into ED2 (Hypothesis 1). Our data collection efforts after Hurricane Maria together with long-term data collected in the wake of Hurricanes Hugo and Georges will provide much needed data to parameterize and evaluate the model, another example of MODEX. Once the model is fitted, we will be able to examine the joint impacts of changes in rainfall and hurricanes on C and water fluxes at the whole ecosystem level and to identify what aspects of forest responses to hurricanes account for the largest uncertainty (Hypothesis 4).

To assess the effects of hurricanes and droughts on ecosystem C dynamics and biogeochemical cycling, we are using the daily time-step DayCent biogeochemical model (Del Grosso et al. 2005). Earlier model results using the related Century model predicted that a 60-y hurricane return would increase soil C storage in the LEF (*Sanford et al. 1991*). We also used the model to understand controls on C dynamics across catenas (*Johnson et al. 2011*). In LUQ VI, we will explore the separate and combined effects of hurricanes and droughts, and increases in the return interval of both (Hypotheses 2 and 5). We will also explore impacts of changes in plant community composition through changes in litter quality. Results will be compared with ED2 output as described above.

During LUQ V, we initiated development of statistical downscaling of global circulation models to understand global climate variation as a regional driver of change (*Van Beusekom et al. 2017, Murphy et al. 2017, Mote et al. 2017*). We identified the variables that are the most useful for downscaling studies of local climate, finding that the early rainy season (April – July) is responsible for much of the inter-annual variability in precipitation and is most susceptible to factors causing drought, particularly Saharan dust (*Mote et al. 2017*). During LUQ VI, modeling experiments will refine our understanding of the relative role of the changes in global circulation changes due to global warming, impacts of Saharan dust inputs, and effects of defoliation from major wind disturbance events on the hydroclimate of Puerto Rico (see Hypotheses 7 and 8).

4.0 PROPOSED RESEARCH

4.1 Question 1: How will increased frequency of intense wind storms shape the structure and function of tropical forests now and into the future?

Climate Models predict an increase in the frequency of hurricane-strength, catastrophic storms in the Caribbean region with climate change (Neelin et al. 2006, Khalyani et al. 2016, Knutson 2010), which is likely to have strong effects on forest structure and composition (*Uriarte et al. 2009*). How changes in the disturbance regime will affect biota and biogeochemical cycling is not well understood but is critical for determining the vulnerability of species and ecosystems to climate change, as well as predicting potential feedbacks from these disturbances to the global C cycle.

Our hypotheses address the real possibility of state change in biotic communities with increased hurricane frequency, and interactions with, and implications for, biogeochemical cycling and terrestrial-

aquatic linkages. More frequent canopy opening in upland and stream environments may shift plant and animal assemblages towards a dominance of early successional species (Doyle 1981, Uriarte et al. 2009, Crowl et al. 2012, Zimmerman et al. 2014). However, our long-term data suggest that repeated disturbance can also favor some later successional species, particularly those with traits that confer resistance to disturbance (Zimmerman et al. 1994, Uriarte et al. 2012, Griffiths et al. 2008). Thus, as hurricanes become more common, new combinations of species are likely to co-occur in the LEF, with effects that cascade across trophic levels and to soil C and nutrient dynamics. Hurricane response is also likely to be dictated in part by the initial conditions at the time of disturbance (Waide and Willig 2012). These legacy effects become particularly important when an increase in disturbance frequency leads to ecosystems that are constantly in a state of response to the last event. Disturbance legacies not only affect community dynamics, but also impact biogeochemical cycling via patterns in C and nutrient deposition, transport, decomposition, and storage.

Studying hurricanes is inherently messy. Natural, landscape-scale, catastrophic disturbances are difficult to control for and replicate in space and time. However, our long-term data and manipulative experiments uniquely position LUQ to determine the potential effects of repeated hurricane disturbance on the composition and structure of biotic communities, biogeochemical dynamics, and stream ecosystem responses. We use a combination of models, long-term measurements and experiments, including a new stream manipulation experiment to test the hypotheses. The two CTE manipulations completed prior to Hurricane Maria and the new StreamFRE manipulation provide an unprecedented opportunity to study the effects of repeated disturbance.

Hypothesis 1. *An increased frequency of severe storms may favor the development of biotic communities with no prior analog. The composition of these communities will result from the interplay of early successional species that are able to take advantage of a more open canopy structure and late successional species that are particularly resistant to hurricanes. The new intermingling of species groups will cascade through the food web as consumers and microbial heterotrophs respond to changes in resource quantity and quality. (Uriarte, Willig, González, Lodge, Cantrell, Shiels, Zimmerman, Waide)*

Background – Rare, large-scale disturbance events are generally assumed to favor dominance by early successional species, and initiate a long-term process of successional change in species composition (Willig & Walker 1999, Lugo et al. 2000, Zimmerman et al. 2014). However, an increase in hurricane frequency, such as is occurring in the LEF, is likely to lead to multiple interacting legacy effects on forest structure and community composition. A more open canopy structure could facilitate recruitment by shade intolerant, early-successional species as mentioned above (Doyle 1981, Uriarte et al. 2018), perhaps including early successional species from lower elevations, as the prevailing disturbance regime becomes mismatched with species' trait distributions (Uriarte et al. 2012, Lasky et al. 2015). Evidence of a shift to dominance of early successional species has already been found in community responses to Hurricanes Hugo and Georges in the LFDP (Zimmerman et al. 1994, 2010) and the BEW (Heartsill-Scalley et al. 2010), as well in the first set of experimental treatments in the CTE (Shiels et al. 2010). However, a modeling study (based on spatially-explicit species interactions in the LFDP; Uriarte et al. 2009) indicated that late successional species like the palm, *Prestoea montana*, may benefit from elevated frequency of intense storms because of low vulnerability to damage. The persistence of these hurricane-resistant species may lead to the development of shorter statured forests, much like those in the cyclone-prone areas of the Western Pacific (e.g., Lin et al. 2011), but that have no historical analog in the Caribbean.

The potential changes in vegetation composition and structure described above constitute material legacies of hurricane disturbance that in turn affect the composition of consumers and microbial heterotrophs (e.g., Cantrell et al. 2014, Willig et al. 2014), and have direct and indirect influences on soil (Hypothesis 2) and stream ecosystems (Hypothesis 3). Early successional species are predicted to be especially susceptible to the effects of drought (see Question 2), thus their status in the future forests will be dependent on the ability to withstand other types of disturbance (Uriarte et al. 2016).

The combination of the CTE and Hurricane Maria allow us to experimentally test for the development of communities and material legacy effects. Canopy structure was still recovering and early successional species were still colonizing as a result of the 2014 trim when Hurricane Maria struck in 2017. Preliminary results suggest that the forest plots that were least impacted following Hurricane Maria are the trimmed plots in the CTE. We measured differential responses of invertebrate species following Hurricanes Hugo

and Georges (e.g., Bloch & Willig 2006, Willig et al. 2010), perhaps because of differences in material legacies after the two storms, as well as cross-scale interactions (e.g., fine-scale demographics interacting with landscape configuration; Willig et al. 2007). The second trim in the CTE and data collected after Hurricane Maria will facilitate an assessment of the legacies of previous disturbances on population and community level responses to subsequent disturbances.

Work Plan – We will address this hypothesis using experimental, observational, and modeling approaches. In the fall of 2014, we conducted a second experimental trim in the CTE, changing the experimental design to two treatments, a hurricane-like treatment (simultaneous canopy removal and debris deposition) and an unmanipulated control or reference treatment. Following Hurricane Maria, we continue to measure recruitment and mortality of seedlings, ferns, and trees ≥ 1 cm DBH on an annual basis in all the original CTE treatments. In addition, we record microclimate and measure forest floor litter mass, and soil chemical and physical properties (Table 1). For consumers, we continue to focus on gastropods and phasmids, as well as herptiles. These have been followed quarterly to annually since the latest (second) trim; we will conduct annual censuses hereafter. Abundance data will be augmented by studies of stable isotope composition of the source of C in diets of common herptiles. For microbes, we sample bacteria and fungi using the methods for Hypotheses 2 and 5.

The fifth census of all trees on the LFDP was conducted prior to Hurricane Maria in 2016. These data, together with damage data collected via by a RAPID award (NSF DEB RAPID: 1801315), annual seed and seedling censuses, and the next tree census of the LFDP in 2021 will inform development of the Ecosystem Demography model (ED2). We will use ED2 to predict changes in terrestrial plant C pools and the prevalence of early and late successional species over multiple decades under increased frequency of major hurricanes, and evaluate the predictions of the model using long-term data from the LFDP and CTE. We will also use this information to develop modeling of riparian zone plant dynamics under the same scenarios (Hypothesis 3). We will evaluate patterns in species change within and across taxa and compare them with our long-term data and potential environmental drivers as a test of Hypothesis 1.

Hypothesis 2a. *In the short-term, high rates of debris deposition associated with hurricane disturbance facilitate rates of C and nutrient translocation through the soil profile that exceed rates of decomposition, leading to C and nutrient accumulation in subsoils. (McDowell, Silver, González, Cantrell, Lodge)*

Hypothesis 2b. *Over the long-term, repeated hurricane disturbance depletes soil C stocks because of decreased C protection in subsoils, the decrease in woody litter production, and an increase in the proportion of easily degradable litter. (Silver, González, Lodge, Cantrell, McDowell).*

Background – Hurricanes deposit massive amounts of litter and woody debris on the soil surface, often equivalent to an entire annual litterfall cycle, creating a large material legacy (Lodge et al. 1991, 2016). Most of this material is assumed to decompose rapidly to CO₂ and be lost from the ecosystem. Fine litter disappeared from the surface within two years following Hurricane Georges (Ostertag et al. 2003) but the actual fate of C and nutrients following hurricanes (i.e. the actual amount retained in the subsoil versus lost) is poorly understood. Humid tropical forest soils are often deep, extending many meters below the surface (Nepstad et al. 1994, Hall et al. 2016). A decade after the first CTE treatments, C, nitrogen (N), and P had accumulated within the top 60-90 cm in the debris treatment, with a similar, but non-significant pattern in the hurricane simulation plots (Gutierrez del Arroyo & Silver 2018). Even though decomposition rates are fast in humid tropical forests (Parton et al. 2007, Cusack et al. 2010), we hypothesize that large debris deposition events result in downward translocation of C and nutrients at rates that exceed litter decomposition at the soil surface, creating a long-term material legacy with consequences for the structure of soils and microbial communities.

The fate of soil C under a scenario of increased hurricane frequency is unclear. Canopy opening following hurricanes often leads to a drier and more aerated litter layer (Lodge et al. 2014). Simultaneously, we expect wetter, low redox conditions in surface and subsoils (>50 cm depth) as a result of insulation by the increased litter layer and decreased plant water uptake. These environmental changes coupled with massive litter inputs will likely change overall soil microbial community composition, as well as community activity. Carbon stored in the subsurface is often assumed to be chemically and physically protected from microbial attack and catabolism. Indeed, subsoil C in an Amazonian tropical forests not impacted by hurricanes was much older than C in the top 10 to 15 cm of mineral soil (Trumbore 2000). Much of this deep C in soils is thought to be associated with Fe and Al species (Hall et al. 2016, Coward et al. 2017).

However, this deeper C is not necessarily protected from microbial attack. With increased hurricane frequency, more frequent low redox conditions in the subsoil could facilitate C desorption from mineral surfaces. This could stimulate microbial activity and deplete subsurface C stocks (Fontaine et al. 2007).

Almost three decades ago, *Sanford et al. (1991)*, using the Century model, predicted that repeated hurricanes at a 60-y return interval would increase soil C storage due to large inputs of coarse woody debris with slow decomposition rates. They assumed that a 60-y return interval would support sufficient forest biomass recovery in the inter-hurricane periods to maintain ecosystem C stocks. The LEF is now experiencing hurricanes every decade, six times the rate used in the *Sanford et al. (1991)* modeling study. At this rate of hurricane frequency, it is unlikely that enough woody biomass regrowth will occur between hurricanes to support on-going soil C accumulation from hurricane debris. The effects of repeated hurricane frequency on the abundance and structure of tree species (Hypothesis 1) will likely have large impacts on C and nutrient dynamics. Wood and litter from early successional species is often more easily decomposable (Eaton & Lawrence 2006), likely leading to more complete decomposition and less C accumulation in soil.

Work Plan – We will use the CTE experiment to test hypotheses 2a and 2b. These plots give us a range of disturbance frequencies. Sampling began in the CTE treatment and control plots in 2002 prior to the first hurricane simulation treatment in 2004-5, continued through the 2014 hurricane simulation treatment, and is ongoing. With Hurricane Maria in 2017, the hurricane simulation treatments have experienced three large events since 2005. The controls have been continually monitored since 2002 and have only experienced Hurricane Maria.

To test Hypothesis 2a, we will follow soil C and nutrient stocks at 10 cm depth increments to 1 m. We maintained monthly sampling after Hurricane Maria as part of a RAPID grant (NSF DEB RAPID: 1803044). We will build on the RAPID project to follow patterns in C, nutrients, and microbial community dynamics over the duration of LUQ VI. Soils will be analyzed for mineral N, total C and N, P fractions (*Gutierrez del Arroyo & Silver 2018*), and Fe and Al species (*Hall & Silver 2015*). Samples along the depth profile will be fractionated and analyzed for radiocarbon (*Marin-Spiotta et al. 2008*) twice annually. Soil C stocks and fractions, radiocarbon ages (as an indication of the age of organic matter), and estimated turnover times will be compared with soil Fe and Al species along the depth profile. Radiocarbon data will be collected as part of an on-going collaboration between W. Silver and Lawrence Livermore National Lab. Lysimeters are installed in all plots and will be sampled for C, N, P, Fe and Al species at least monthly. The detection of rapid downward movement of dissolved and/or particulate species (determined via soil fractionation) will provide support for the hypothesis.

We will use both field and modeling studies to test hypothesis 2b. We will measure soil C and nutrient stocks and the ^{14}C of soil C fractions as mentioned above. Differences between controls and hurricane simulation treatments over time will indicate an impact of repeated storms on these factors throughout the soil profile. We will use the DayCent biogeochemical model to explore the effects of different hurricane return intervals on above- and belowground NPP, soil C dynamics, and the quantity and quality of litter inputs and decomposition rates. We predict that the model will show decreasing soil C storage with an increase in hurricane frequency. It is unclear, however, how quickly this decrease will occur, and when (or if) a new steady state condition will be established. We will explore the potential effects of changes in plant community composition (Hypothesis 1) through impacts on litter quality and associate C and nutrient dynamics. We will compare outputs from the DayCent model with the results of the ED2 modeling exercise to determine the consistency of predictions for plant and soil dynamics. Additional modeling will allow us to integrate the results of the ED2 model into DayCent for NPP and plant C stocks.

Microbial community dynamics and enzyme activities have been intensively sampled in the CTE plots following Hurricane Maria. We continue to use the CTE experiment to explore changes in microbial community dynamics associated with disturbance. Soils and litter will be sampled for microbial enzyme activity, bacterial, fungal and faunal community composition and biomass, and community-scale gene expression (metatranscriptomics) and metabolites (FTICR-MS). The suite of enzymes measured for the CTE study include hydrolytic enzymes: β -1,4-glucosidase (cellobiose to glucose); Cellobiohydrolases (cellulose to cellobiose); N-acetyl-D-glucosaminidase (degrades chitin); and Xylanase (polysaccharides to xylose) as indices of the activity of enzymes involved in soil C cycling. Acid phosphatase, as well as N-acetylglucosaminidase are being measured to characterize N and P activity. Microbial biomass will also

be measured by chloroform fumigation and direct extraction. Taken together, these field data and modeling activities will allow us to determine patterns of soil C and nutrient storage and loss with an increase in hurricane frequency, as well as begin to discern drivers as a test of Hypothesis 2b.

Hypothesis 3. *Increased frequency of intense hurricanes will result in a long-term shift from predominantly detritus-based to algal-based headwater stream ecosystems, due to the increases in light and stream nutrient concentrations that result from increased canopy openness with more frequent hurricanes.*

Background – Low order headwater streams in the LEF are detritus-based ecosystems surrounded by dense riparian vegetation. Canopy cover during undisturbed periods is often over 90%, except where forest gaps result in short-duration openings (*Brokaw et al. 2012*). Twenty-five years of stream research shows that there is a strong response to hurricanes, which alter terrestrial-aquatic linkages, increase concentrations of some nutrients, and change food web dynamics (*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 decomposed rapidly (*Crowl et al. 2001, Beard et al. 2005*) or exported downstream (*Heartsill-Scalley et al. 2012*), and light levels increase due to increased canopy openness (*Brokaw et al. 2012*). Forest ecosystems surrounding streams can take up to five years to recover from hurricane disturbance (*Zimmerman et al. 1996*).

Increased frequency of intense storms is expected to shift upland and riparian vegetation towards more shade intolerant trees or other vegetation types (palms, ferns, lianas, herbs), alter the transient light regime (more frequent periods of high light due to repeated hurricane disturbance), and the baseline light regime (lower LAI with more pioneer species). These shifts bring consequent changes in the quality, quantity, and timing of leaf-litter inputs (Hypotheses 1 and 2) and downstream exports (*Heartsill-Scalley et al. 2012*). The processing of this leaf material by stream biota can result in important changes in dissolved C, N, and particulate C production and export (*Crowl et al. 2001*).

In the longer term, we expect that our relatively unproductive benthic stream communities (*Cross et al. 2008*), which are limited by light and predation under non-hurricane conditions, will switch from being detritus-based to primary producer-based ecosystems, resulting in increased primary and secondary insect production along with increased densities of decapods and fish (only one grazer species of goby present). In addition, the more frequent input of coarse woody debris and palm fronds relative to pre-hurricane conditions will result in a significant increase in debris dams, leaf-litter storage, and habitat heterogeneity (*Pyron et al. 1999, Zimmerman & Covich 2007*). This increased habitat complexity will most likely result in more spatial refugia for a diversity of species, thereby changing species dominance and trophic dynamics. Taken in aggregate, we hypothesize that the increased frequency of intense storms in the LEF will result in a fundamentally new, no-analog state characterized by increased primary productivity, higher average standing stock biomass, and tighter nutrient cycling than occurred during periods with less frequent hurricanes.

Work plan – We will test Hypothesis 3 using a three-tiered approach: (1) synthesis of our long-term stream monitoring that now captures the legacy effects of four hurricanes, (2) targeted stable isotope studies of consumers to discriminate food sources, and (3) experimental canopy manipulations to simulate increased hurricane frequency.

Our long-term monitoring of streams at El Verde and BEW is focused on major environmental characteristics and biotic components, including: water chemistry, algae, insects, shrimps, and inputs and exports of riparian litter. We will continue monitoring stream responses to Hurricane Maria. In addition, we will work on synthesizing the data to assess patterns in nutrient chemistry, coarse particulate organic matter, and algal biomass related to storm frequency. Targeted stable isotope studies of consumers and food sources will allow us to identify the trophic basis of stream food webs. We will select pools with different degrees of canopy openness associated with hurricane disturbance and monitor them over time (e.g., quarterly) to relate levels of canopy openness with the reliance on algal resources (*Pérez-Reyes et al. 2015*). For those shrimp species that are known to remain resident in a particular pool (*Xiphocaris elongata, Atya lanipes*), we will obtain the isotopic signal from adults and their eggs, as eggs are produced more rapidly than muscular tissue. We will also mark other individual shrimps to establish the length of their persistent residency in these pool-scale study units; residency exceeds 10 years in some

shrimp (Crowl *et al.* 2012). Patterns in biota and biogeochemistry across pools, coupled with our long-term data will provide an initial test of the hypothesis.

In conjunction with the next round of the CTE, we will experimentally trim riparian trees in 2024 to simulate reduced canopy cover and increased light availability associated with hurricanes as a further test of Hypothesis 3. The un-manipulated branch of Prieta will remain as a reference and data will be analyzed as described above for other StreamFRE variables. Response variables will include whole-system primary productivity and respiration, stable isotopic composition of food resources and shrimp and insect consumers, and the suite of variables that we have used over the last decade, including shrimp population dynamics, algal and insect biomass, and stream nutrient chemistry. Recent advances in measuring and modeling primary productivity in streams (continuous logging optical DO probes combined with new approaches to estimating productivity and respiration (e.g. Appling *et al.* 2018) will allow us to improve earlier estimates of primary productivity and respiration in our study streams (Ortiz *et al.* 2005; Potter *et al.* 2010) and contribute to the growing body of literature on the fundamental controls of stream primary productivity across biomes (Bernhardt *et al.* *in press*).

4.2 Question 2: In the context of frequent intense hurricane disturbance, how do severe droughts and climate drying affect biota and biogeochemical cycling?

The Caribbean region is predicted to experience both a decline in overall precipitation with climate change, and an increase in the variability of intra-annual precipitation (i.e. more distinct seasonality) relative to the long-term record (Neelin *et al.* 2008, Comarazamy & González 2011, Khalyani *et al.* 2016). Drought has historically been rare in the LEF, but three significant drying events have occurred since the start of the LUQ program: 1989, 1994, and 2015. Increasing drought frequency is likely to impact vegetation and soil biogeochemistry. At local scales, topographic heterogeneity and drainage networks generate spatial heterogeneity in soil moisture (Daws *et al.* 2002) that can also shape the fine-scale distribution of species (Harms *et al.* 2001, Englebrecht *et al.* 2007) and biogeochemical dynamics (O'Connell *et al.* 2018). Soils in the LEF are characterized by low redox conditions in the upper elevations of the LTEP, and fluctuating redox (over days to weeks) on slopes and in valleys of the mid and lower elevation forests (Silver *et al.* 1999, 2013). Individual trees of drought-sensitive species may be able to persist in moist microsites (Daws *et al.* 2002, 2008, Comita & Engelbrecht 2009). On the other hand, low and fluctuating soil redox condition can limit seedling establishment and survival, and reduce plant growth rates (Schoor and Matson 2001). The implications of more frequent droughts in historically wet forests and the impacts on ecosystem C dynamics as well as the composition and diversity of biotic communities are poorly understood.

Droughts are likely to impact terrestrial and aquatic environments in different ways. Severe droughts can lead to pulses of litterfall that may stimulate soil heterotrophs and increase C losses (Beard *et al.* 2005, Heartsill-Scalley *et al.* 2012). In streams, litter deposition and associated pulses in consumer activity may exacerbate low redox conditions and negatively feed back on stream biota. Understanding the linkages between terrestrial and aquatic response to drought will facilitate whole-ecosystem modeling.

Predicted changes in precipitation are overlain on a template of more frequent hurricanes in the LEF and the Caribbean region. How these disturbances interact is unclear, but their interaction will create conditions with no historical analog. Our hypotheses address the potential effects of increasing drought in the LEF, and explore drought effects in the context of hurricane legacies. We use a combination of observation, experiments, and modeling to ask how drought affects biotic communities that are dominated by early successional species, how the fate of hurricane-derived soil C and nutrients differ with and without droughts, and how canopy opening and debris deposition interact with drought to drive changes in stream organisms and biogeochemical cycling.

Hypothesis 4a. *Over the short-term, droughts will alter the spatial patterns of survival and growth of plants recovering from hurricane disturbance along catenas. Drought will enhance soil aeration in poorly-drained valleys and generally increase survival and growth of upland species while drying effects will favor drought-tolerant species, particularly late successional species, on well-drained ridges.* (Zimmerman, Uriarte)

Hypothesis 4b. *Over the long-term, increased climate drying and drought frequency will lead to changes in the community composition of vegetation, consumers, and microbes with no prior analogs, as drought-*

sensitive species become locally extinct or restricted to moist areas. Changes will be primarily driven by impacts of increased drought on more vulnerable early successional species that become abundant after hurricane disturbance. (Uriarte, Cantrell, Crowl, Pringle, Ramirez, Schowalter, Waide, Willig, Zimmerman)

Background – Topography is a strong driver of plant distribution and demography in forested ecosystems through effects on microclimate, edaphic conditions, and hurricane disturbance (Wadsworth & Bonnet 1951, Frangi & Lugo 1985, Franklin 1995, *Scatena & Lugo 1995, Willig et al. 2013, Uriarte et al. 2018*). Differential drought tolerance of seedlings and adult plants undergoing succession from hurricane disturbance may lead to large shifts in community composition and structure along catenas as climate dries over the longer term (Engelbrecht et al. 2007, *Muscarella et al. 2013, Feng et al. 2018*). The 2015 drought, with 50% of average annual precipitation, provided critical insight into the short-term effects of severe drought on plants at our site. Drought affected stem growth of trees on the LFDP and elsewhere, but not mortality, supporting the projected decline in NEP in drying climate scenarios simulated by *Feng et al. (2018)*. Species with less dense wood suffered a greater reduction in growth (*Schwartz et al., submitted*), meaning early successional species were less drought resistant compared to late successional ones, as predicted by theory (Engelbrecht et al. 2007). Tree growth on ridges was more impacted by drought than in valleys. Topographic position similarly was the main driver of seedling survival over a nine-year period in tabonuco forest (*Uriarte et al. 2018*). The effects of soil moisture on seedling survival were strongly influenced by conspecific density and understory light levels. Thus, interactions of species, topography, and drought are complex, justifying long-term monitoring and experiments to clarify key mechanisms and relationships (*Feng et al. 2018*).

Elevation is a strong driver of population and community structure through its effects on climate, soils, and disturbance regime. Climatic changes along elevation gradients strongly challenge species tolerances in both evolutionary and physiological contexts (Grubb 1977, Cavalier 1986), and tropical organisms (*Willig & Presley 2016*) are expected to respond more strongly to environmental changes along elevation gradients compared to temperate organisms (Janzen 1967, Rapoport 1982, Tedersoo et al. 2014, *González & Lodge 2017*). The rapid rate of change in environmental characteristics within relatively short geographic distances along elevation gradients thus can provide insight into the mechanisms that mold species distributions and community assembly (Whittaker 1960, Terborgh 1971), that can then be contrasted over time (Rowe 2007, Moritz et al. 2008) and among taxa (*Presley et al. 2012*). The 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 montane ecosystems (Grytnes & McCain 2007, McCain & Grytnes 2010, Rumpf et al. 2018).

We predict that low elevation forests may reach a critical threshold of drying before high elevation forests, because changes in cloud base levels that maintain high elevation forest have lagged behind other observed climate changes (*Holwerda et al. 2006, Scholl & Murphy 2014, Van Beusekom et al. 2017*). Recent results show that cloud base height varies seasonally and among years, but the pattern over a 42-year period did not suggest any long-term alteration that might be associated with anthropogenic climate change (*Miller et al., submitted; Fig. 2.9*). By this measure, the cloud climate of elfin forests at the summits of the Luquillo Mountains has remained relatively stable over time. However, climate drying and warming is projected to strongly impact the lower elevation *tabonuco* forest (*Feng et al. 2018*) within the next two decades. If species in *tabonuco* forest are unable to adapt to the drying environment, we are likely to see immigration of more drought-tolerant lowland species (Rumpf et al. 2018) and a reordering of species distributions along the elevational gradient. The elevation gradient represents an important model system (Garten et al. 1999) for natural (i.e. observational) experiments (Körner 2003) on the long-term effects of climate change in tropical montane ecosystems.

Work Plan – We will conduct a small-scale seedling drought experiment of 20 tree species selected based on their abundance, geographic distribution (*Thompson et al. 2002, Zimmerman et al. 2010, Uriarte & Muscarella 2016*) and life history characteristics (*Zimmerman et al. 1994, Muscarella et al. 2013*). Methods will follow those of Engelbrecht & Kursar (2003), Engelbrecht et al. (2005, 2007), and O'Brien et al. (2015). We will explore the effects of non-structural carbohydrate reserves in mediating interspecific variation in tree seedling responses to drought (O'Brien et al. 2014, 2015, Doughty et al. 2015). The relative survival rates of seedlings of different species under prolonged experimental drought conditions will open a window for further investigation of species-specific patterns of drought tolerance using the LFDP and LTEP databases. This will allow us to determine the degree to which experimental

drought tolerance explains spatial patterns of seedling and tree mortality in the field, how this relates to other measured demographic characteristics such as growth and mortality rates of saplings and adults, and how drought tolerance relates to other measured ecological traits such as photosynthetic rates, wood density, and leaf characteristics as a partial test of Hypothesis 4a. The latter, already measured for all species found in the LFDP, offers the opportunity to understand and model the long-term impacts of a changing precipitation regime on the entire tree community.

As a further test of Hypothesis 4a, we will study the impacts of drought on adult trees, consumers, and microbes by installing large throughfall exclusions following the protocols described by the International Drought Experiment (IDE) consortium. Drought will be imposed using a system of troughs in 30 x 30 m plots to passively remove throughfall by a constant, site-specific percentage based on ground area covered and validated with field measurements (Hanson 2000, Pangle et al. 2012). The amount of precipitation removed will be determined by ongoing climate downscaling studies under Hypothesis 7. We will implement an ambient precipitation treatment (unsheltered control) and a drought treatment; each will be replicated in 3 blocks. We will work in areas where catena distances are relatively short so that we can monitor experimental drought effects along the topographic gradient. We will begin pretreatment monitoring of sites in Year 2 (to establish block effects) of LUQ VI and begin imposing the drought treatments after one or two years. Our experience with the CTE indicates that the plot area and level of replication is sufficient to capture critical responses of the vegetation and key populations. We will monitor growth for all trees and gather data on physiological and hydraulic traits that determine species' drought tolerance and avoidance strategies (e.g., Santiago et al. 2018). These measurements will be focused on a subset of individuals of dominant species present in both treatment and control plots, and will span a range of tree sizes. We will measure impacts of the TEE on abundances of key consumers (frogs, gastropods, phasmids, litter invertebrates, fungi, and microbial communities) using protocols established for the CTE (Shiels & Gonzalez 2014).

Beginning in 2016, we began monitoring changes in the distribution of key biota in the LTEP every 6 years. This sampling interval will capture any important changes a drying climate may impose over the long-term (i.e., over the remainder of the century) while being logistically feasible. Because Hurricane Maria is likely to have strongly influenced the biota, we will re-survey the LTEP now through the first year of LUQ VI to capture short-term effects of the storm on structure and composition of vegetation and other key biota (Table 2). Vegetation is monitored along transects in three watersheds, but we only measure heterotroph and microbial communities in the Sonadora Watershed. Of the three watersheds, primary forest extends to the lowest elevation along the Sonadora Watershed (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. Thus, our long-term data coupled with new measurements in the LFDP and along the LTEP provide a test of Hypothesis 4b.

Hypothesis 5a. *More frequent droughts will increase soil C losses, driven largely by an increase in heterotrophic respiration. Greater soil oxygen availability during drought will also increase Fe oxidation, leading to high P sorption over the short-term. High P sorption is likely to result in lower plant growth rates over the long-term and feedback to lower autotrophic respiration and ecosystem C storage (Silver, Uriarte, Zimmerman, Cantrell, González, Lodge.)*

Hypothesis 5b. *Faster decomposition rates associated with droughts, and the lack of water to facilitate leaching limit the effects of hurricane debris deposition on soil C and nutrient translocation through the soil profile. Thus, when droughts and hurricanes coincide, less C and nutrient retention and accumulation are likely to occur compared to when hurricanes are followed by normal or high rainfall (Silver, Cantrell, González, Lodge, McDowell).*

In LUQ V we proposed that soil respiration would decline during drought due to plant and microbial water stress (Wood & Silver 2012). However, we observed increased soil respiration during the 2015 drought, similar to sites in Costa Rica (Cleveland et al. 2010), and in contrast to drier forests in the Amazon (Doughty et al. 2015). Preliminary evidence suggests that this may have been due to heterotrophic activity as opposed to higher root respiration rates (O'Connell et al. 2018). The increase was greatest on slopes and valleys, which normally experience periodic anaerobic events that may inhibit aerobic respiration (Silver et al. 1999, Hall et al. 2013). During the 2015 drought, we measured dramatic increases in soil oxygen availability on slopes and in valleys that may have stimulated microbial

decomposers. Similar results are being recorded in the first phase of the Throughfall Exclusion Experiment (TEE; Fig. 4.1). Iron oxidation occurs rapidly in well-aerated soils and can strongly bind P. Significant declines in P availability, as was observed during the 2015 drought (*O'Connell et al. 2018*), may exacerbate nutrient limitation in these typically P-limited ecosystems, and feedback on NPP. In LUQ VI, we will investigate the drivers of the soil respiration drought response using the TEE. We will focus on decomposition rates, root activity, and soil oxygen dynamics over time. Long-term observations suggest that soil microbial communities in the LEF are very sensitive to drought (*Lodge 1993, Lodge et al. 1994, Lodge & Cantrell 1995*). An extended experimental drought in the LEF decreased soil microbial diversity by 40%, and led to large changes in microbial community composition, functional potential and enzyme expression (*Bouskill et al. 2013, Bouskill et al. 2016a,b*). Recent work suggests that microbial respiration per unit biomass may also increase during droughts in wet tropical forests (Waring & Hawkes 2015). This could further stimulate soil C losses. We predict that shifts in microbial community structure with drought (*sensu Fuchslueger et al. 2014*), coupled with periodic severe P shortage due to Fe-P bonding during droughts could have significant implications for long-term C storage and C turnover in the LEF.

We hypothesize that drought conditions following a hurricane will alter patterns in C and nutrient distribution through the soil profile due to decreased leaching, and higher decomposition rates. We observed C and nutrient accumulation in the subsoil over the first decade of the CTE experiment following debris deposition (*Gutiérrez del Arroyo & Silver 2018*). In Hypothesis 2, we pose that this results from faster downward transport relative to microbial decomposition. We expect that drought following hurricanes will limit the ability of material to move through the profile due to lack of downward leaching. We also predict that faster decomposition rates in well-aerated surface-soils decrease the mass of material availability of translocation to deeper depths.

Workplan – Our goals with Hypothesis 5 are to explore the effects of drought in context of short-term hurricane effects, as well as examine drought impacts with a longer-term perspective. We will use the large exclosures (Hypothesis 4) to study the effects of drought on soil moisture, temperature, and oxygen through the depth profile (10, 30, and 60 cm depth) along the catena. We will install small replicate trench plots (*Silver and Vogt 1993, Silver et al. 2000*) to determine the effects of drought on autotrophic (defined as roots and immediate rhizosphere) versus heterotrophic respiration. Continuous soil CO₂ emissions will be measured in addition to soil Fe, P, oxygen, temperature, and moisture to test Hypothesis 5a.

To test Hypothesis 5b, we will use the smaller (3 x 5 m) throughfall exclusion shelters installed in early 2017 prior to Hurricane Maria. We imposed a 6-month partial drought with the shelters and measured soil C, N (total and mineral), P (organic and inorganic), Fe and Al species, soil invertebrate and microbial community composition, litter decomposition, and soil moisture, temperature, and oxygen at two depths (Fig. 4.1). The shelters were secured during Hurricane Maria and the experiment was quickly reestablished after the storm (within 3 weeks). Hurricane debris was quantified in all treatment and control plots and the shelters were replaced. We will now use these plots to test hypothesis 5b by following patterns in decomposition, soil C and nutrients, and decomposer communities over time. We will continue the same suite of measurements that were begun in 2016 but at three depth increments (0-10, 10-30, and 30-60 cm). Fine live and dead root biomass three times per year (*Silver & Vogt 1993*).

Decomposition will be measured in both large and small exclosures and associated controls 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 & Seastedt 2001, Richardson et al. 2010, González et al. 2014*). To sample gastropods and frogs, we will use modifications of the protocol for nocturnal sampling of these species employed in the CTE and 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 components of 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), total bacteria/archaea (Fierer et al. 2005) and fungi.

We will use DayCent to explore the separate and combined effects of droughts and hurricanes (See Hypothesis 2 for hurricane modeling). Model runs will allow us to vary the length and intensity of drought and alter the drought-hurricane interaction. We will use these model runs to determine a range of potential impacts and determine biogeochemical sensitivities to hurricanes and droughts over time.

Hypothesis 6. *Drought conditions cause large pulsed inputs of low-quality detritus and increase algal productivity due to canopy opening, which will magnify the effects of instream biotic control on ecosystem processes such as primary productivity and decomposition by insects, shrimp, and microbes; this contrasts with non-drought periods, when high discharge events associated with storms frequently reset the system and disrupt biotic control.*

Background – In the short term, drought stress on riparian vegetation increases leaf litterfall and decreases shade over the stream, so stream channels receive higher amounts of detritus and light than during non-drought periods. Droughts also lack the high flows that scour and export material downstream. Pulsed leaf-litter inputs become concentrated in increasingly shallow pools along with invertebrate consumers (dominant groups: shrimps, crabs, and aquatic insects), resulting in increased leaf consumption, stronger predator-prey interactions, and alteration of in-stream nutrient cycling. At the same time, high solar radiation enhances primary production, in particular in shallow habitats that are inaccessible to large body-size decapods. These interactions create large daily fluctuations in dissolved oxygen, which result in adverse nocturnal conditions for stream biota.

Our previous work across a range of flow conditions shows that biotic interactions increase at low flow. Shrimps significantly reduce algal standing crop and the accumulation of fine benthic organic matter between high-discharge events (Pringle & Blake 1994, March et al. 2002). Riparian leaf litter inputs are rapidly processed by microbes and stream invertebrates (Wright & Covich 2005a, 2005b, Crowl et al. 2006, Bobeldyk & Ramírez 2007, Rincón & Covich 2014) with resulting increased C storage (accumulation of consumer biomass and low-quality litter), and altered detritivore growth rates (Pérez-Reyes et al. 2015). Small-scale manipulations have also demonstrated that nutrient cycling is affected by consumers (Crowl et al. 2001, Benstead et al. 2010). The presence of abundant shrimp results in a decrease in the quantity and increase in the quality (> C/N ratio) of algal biofilms and benthic organic matter (Pringle et al. 1999). Shrimp assemblage composition can also affect leaf decomposition rates (Crowl et al. 2001, March et al. 2001).

The reciprocal exchange between streams and riparian ecosystems (i.e., inputs of leaf-litter, woody materials, and insects) is likely to shift during drought. These bi-directional exchanges of 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 greater leaf-litter inputs serve to increase detrital resources for stream consumers, decreased discharge reduces the amount of available stream habitat and enhances biotic interactions. We thus predict decreases in the transfer of energy to the riparian forest through aquatic insect emergence 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 consumers. The emergence of aquatic insects from the streams is a major subsidy to terrestrial predators (Kelly et al. 2015). Stable isotope analyses demonstrated that the $\delta^{13}\text{C}$ signatures of aquatic insects consumed by spiders are distinct from that of their terrestrial insect prey in the LEF (Kelly et al. 2015).

Over the longer term (e.g. decades) the increased frequency of droughts induced by climate change is expected to result in changes in plant community structure (Hypothesis 4), including displacement of riparian tree species. The associated changes in light regime, litterfall, and nutrient and C dynamics (Hypothesis 5) will result in major shifts in the dominance of consumer species 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 the community and ecosystem level.

Work plan: We will test Hypothesis 6 using a whole-stream manipulation (Stream Flow Reduction Experiment, StreamFRE) designed to reduce stream flow (Section 3.1). Stream chemistry, food webs,

and rates of ecosystem processes will be evaluated in two adjacent streams: one experimentally manipulated and a reference. This whole-ecosystem experiment is designed to generate paired time series data from both streams before and after the manipulation, which will be analyzed using Randomized Intervention Analysis (Carpenter et al. 1989, Wallace et al. 1997). The work plan will be implemented in 2020, after we have established the effects of Hurricane Maria on our study stream, the Q. Prieta. Once we have a proof of concept for stream de-watering, we will conduct manipulations starting in April and continue them through July, the month when the effects of long-term climate change are predicted to be greatest (see following Question).

All measurements will be conducted simultaneously in both streams. At the reach scale, we will quantify effects on stream chemistry, ecosystem metabolism and the production of greenhouse gases by measuring DO (continuously) and greenhouse gases (weekly grab samples) at the bottom of the reference and experimental reaches (*Potter et al. 2010*, *Schade et al. 2016*). Within each 150 m reach, nine pools and inter-connecting riffles have been established as study sites to further characterize the biotic response to drought. Microbial and algal biomass are measured by sampling benthic biofilms along the experimental reach, using a modified Loeb sampler according to methods of *Pringle (1996)*. Primary production will be measured using stream-side metabolism chambers. Aquatic insect composition, abundance, and biomass are measured monthly by sampling riffles (using a Surber sampler) and pools (using a core sampler). Aquatic insect secondary production will be estimated monthly using the instantaneous growth method (*Benke et al. 1999*), with growth rates for major taxa determined *in situ* in growth chambers. Functional roles of aquatic insects will be evaluated based on functional feeding group categories (*Merritt et al. 2008*, *Ramirez and Gutiérrez-Fonseca 2014*). Four emergence traps are used to quantify insect emergence and isotope studies will be used to elucidate food web pathways of this subsidy (e.g., consumption by spiders, herptiles) in the riparian forest (*Kelly et al. 2015*). Shrimp and crab populations are being sampled in pools using modified baited 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*).

We will also monitor canopy cover over the streams and riparian vegetation. Leaf litter inputs, export, and standing crops will be measured every two weeks using litter baskets and by sampling the stream bottom. Leaf palm quantity and biomass in the streams will be assessed monthly. Once every year, we will conduct an experimental manipulation of consumer effects on basal resources. At three of the study pools in each stream, we will set up an electric exclusion and control to assess the effects of shrimps on insects, algae, benthic organic matter, and leaf litter decomposition. We will follow the same methods as used in previous studies in LUQ (*March et al. 2001*, *Ramírez & Hernandez-Cruz 2004*).

4.3 Question III: How do large-scale factors such as climate change interact with hurricanes and drought to shape tropical forest ecosystems of the future?

Changes in global climate and hurricane frequency are the ultimate drivers that will determine changes in structure and function of forest ecosystems in the LEF over the next century. The response of the biota and biogeochemical dynamics to this new environment will be contingent on conditions created by legacies of prior disturbances, including land use. In the previous sections we have explained how our research illuminates the possibility of biotic communities and biogeochemical dynamics with no prior analog resulting from a changing frequency of hurricanes and drought frequency.

During LUQ V, we began developing a downscaling approach to link predictions of future climate from global climate models (GCMs) to climate at spatial scales that are ecologically relevant to the forest ecosystems of the Luquillo Mountains (*Ramseyer & Mote 2017*). This approach has been enabled by the existence of multiple long-term records of climate in and around the Luquillo Mountains. The drought of 2015 refined our understanding of the role of Sahara dust in influencing precipitation patterns (*Mote et al. 2017*). During LUQ VI we will complete the climate downscaling studies and use the results of these analyses to inform simulations of the ED2 and DayCent models that will assess the future structure of forests and dynamics of C and biogeochemistry in the LEF. The impact of Hurricane Maria coupled with detailed LIDAR data before and after the storm will increase predictive understanding of the landscape controls of hurricane damage and feedbacks to climate. Over the next 6 years, we will continue the refinement of models related to future trends and variability of climate in the LEF, applying that knowledge to the development of detailed predictions of forest behavior through the end of the century.

Hypothesis 7. *A greenhouse gas-enhanced climate will drive changes at the global-to-regional scales, resulting in unique climate regimes that catalyze ecological change. The combined effects of greenhouse-enhanced climate change, impacts of Saharan dust transport, and defoliation from major hurricanes will have a greater impact on rainfall than currently projected by climate models and will result in more extreme seasonal and interannual variability in rainfall and soil moisture. (Mote, Waide, Zimmerman)*

Background - Greenhouse-enhanced climate change is expected to yield a 20-50% reduction in rainfall over the eastern Caribbean during the Early Rainfall Season (ERS, Apr-Jul) (e.g., Karmalkar et al. 2013). Our ongoing work has identified that high wind shear environments are associated with the driest regimes in eastern Puerto Rico (Ramseyer & Mote 2017). Future increases in wind shear are expected in a greenhouse-enhanced climate (e.g., Rauscher et al. 2008, Cook & Vizzy 2010, Taylor et al. 2011, 2012), and this change will disproportionately affect rainfall during the ERS when lower shear environments have occurred climatologically.

Other findings indicate that the ERS is responsible for ~60% of the inter-annual variability in rainfall in eastern Puerto Rico. Furthermore, the warm, dry, dust-laden Saharan Air Layer was recently found to play a key role in inhibiting ERS rainfall (Mote et al. 2017). Although projections developed from climate models indicate a slight downward trend in dust emission and transport as greenhouse gas concentrations increase over the 21st Century (Evan et al. 2016), African dust will continue to play a significant role in affecting the climate of the eastern Caribbean, particularly through the seasonal timing of the dust releases as was the case in 2015 (Mote et al. 2017).

Additionally, landscape-scale changes in land cover, particularly widespread defoliation associated with major hurricanes, can result in a decrease in evapotranspiration and an increase in the sensible heat flux (O'halloran et al. 2012). Hydrologic changes after Hurricane Hugo were observed on the island that included an increase in the height of the orographic cloud layer and a three-month dry period. In addition to the primary ecological consequences caused by the Hurricane Hugo's winds and slope failures, secondary consequences associated with the subsequent dry period were detected in animal populations (Woolbright 1991) and fine root mortality (Parrotta and Lodge 1991). Further, modeling experiments have shown that circulations caused by variations in sensible heat flux distribution can drive regional precipitation patterns (Hu et al. 2017).

Satellite imagery after Hurricane Maria and temperature observations from the El Verde Field Station (Fig. 4.2) provide evidence in support of decreased cloud cover in the lower to mid elevations of the LEF. Although rapid regrowth can occur, the climatic feedbacks of defoliation from the hurricane may continue in the subsequent dry season and ERS. Recent evidence suggests an increase in more intense storms like Hurricane Maria in a warming climate (Kang & Elsner 2015) in the mid to late 21st Century.

Workplan - We propose a unique modeling effort to examine the superposition of climatic disturbances from global circulation changes due to greenhouse-enhanced warming, regional changes in the tropical Atlantic due to Saharan dust, and landscape-scale change due to defoliation from major wind disturbance events. Modeling experiments will evaluate the relative contributions of these disturbance mechanisms to changes in Puerto Rico hydroclimate (temperature, precipitation, soil moisture, and evapotranspiration). The proposed study will rely on dynamically downscaled regional climate projections from the Weather Research and Forecasting (WRF) model, including a fully coupled Land Surface Model. WRF has a rich precedent in regional climate modeling research and is routinely applied to test hypothetical effects of land-cover modifications. WRF is initialized using a static land-surface model based on a 20-category MODIS-based land cover classification as well as remotely sensed climatological averages of land-surface radiative and vegetative properties. However, the model's default land surface characteristics can be changed to test the consequences of user-defined landscape modifications on regional climate. WRF-Chem is the WRF model coupled with atmospheric chemistry. The model simulates the emission, transport, mixing, and chemical transformation of trace gases and aerosols simultaneously with the meteorology. This model is used for investigation of regional-scale air quality, field program analysis, and cloud-scale interactions between clouds and chemistry. Furthermore, it has been used to assess the uncertainty of aerosol forcing in regional climate projections (Crippa et al. 2016).

This project will use remote sensing imagery from after Hurricane Maria in Puerto Rico as a proxy for the (near) maximum defoliation and change in land surface radiative properties that can plausibly occur following a powerful hurricane interaction. Landsat-8 OLI and MODIS 8-day composites will be compared

pre- and post-Hurricane Maria in conjunction with the recently gathered post-Hurricane Maria LiDAR observations to quantify the relative reduction in albedo, green fraction, and leaf area index that was observed in Puerto Rico. These changes will then be adapted to create a post-hurricane land surface for WRF.

WRF-Chem will be initialized using boundary conditions from a 5-year historical period using ERA-Interim reanalysis. A three-domain nest structure will be implemented, so that the smallest domain can be run at a convection-allowing high resolution. The altered-land-surface runs will be compared to current-land-surface WRF runs to discern simulated changes in Puerto Rico precipitation amount and distribution resulting from the hypothetical hurricane landfall. This same sequence will then be repeated for 1-2 less severe defoliation scenarios as computational resources permit to identify the critical defoliation threshold at which persistent hydrologic consequences are manifested. The less-severe runs will be initialized with land-surface properties changes lying between the current-land-cover scenario and the (near) maximum scenario identified by the post-Hurricane Maria analysis for Puerto Rico. Additionally, altered-dust-aerosol WRF-Chem experiments will be conducted for the current and altered land-cover scenarios. These experiments will assess the relative sensitivity of seasonal rainfall in Puerto Rico to regional dust transport and land-cover, by both allowing and suppressing Saharan dust emission. Lastly, a RCP-8.5 CMIP6 GCM ensemble will be used to dynamically downscale future LEF precipitation and temperature at both mid- (2045-2049) and late 21st century (2085-2089) for the defoliated, dust-permitting scenario. This final sequence of modeling experiments will inform how GHG-enhanced global warming acts in concert with regional dust transmission and local land-cover change to modify hydroclimate in the LEF. Overall, this project will yield roughly 9 permutations of regional climate models for Puerto Rico simulating hydroclimate changes resulting from combinations of GHG-forcing, dust aerosol, and defoliation disturbance. Phase 1 will consist of extensive validation with in situ observations of meteorological and soil conditions for control simulations to permit bias adjustment of future simulations. Phase 2 will consist of sensitivity analysis using the modified land cover with a focus on effects on precipitation, temperature, soil moisture, and cloud base height and distribution. Phase 3 will consist of sensitivity analysis using the modified dust aerosol with a focus on precipitation, incident solar radiation, cloud base height and distribution. Phase 4 build upon the results of Phases 2-3 to conduct a sensitivity analysis of the additive effect of global GHG-enhanced warming, regional dust transport, and local land-cover change on LEF hydroclimate.

Hypothesis 8. *Effects of landscape defoliation and Saharan dust intrusion on local climate will alter landscape C and water dynamics. Drought driven by Saharan dust intrusion and changes in air temperature and soil moisture associated with landscape-scale defoliation will reduce forest C uptake across the LEF. (Uriarte, Mote)*

Background -- The changing hydroclimate of the LEF resulting from drought events and hurricanes should have strong effects on forest function in the future. Large-scale defoliation and biomass loss in the wake of a storm modifies vegetation water demand, respiration, albedo and surface temperature (O'halloran et al. 2012) while deposition of high amounts of litter and coarse woody debris alter soil biogeochemistry. Modeling and observational studies suggest that forests growing at high elevation or on windward slopes are more exposed to wind damage, and may experience greater mortality from storm events (Everham & Brokaw 1996, Arriaga 2000, Bellingham & Tanner 2000). The observed associations between topography and tree damage may also be mediated by soil characteristics. Trees growing in shallow soils on ridges or hilltops, on steeper slopes, or on soils with poor drainage have more restricted root growth, and as a result may be more vulnerable to wind-throw and stem break (Everham & Brokaw 1996, Arriaga 2000, Bellingham & Tanner 2000). Local topography may influence not only the forest's ability to withstand storm damage but also rates of recovery and succession (Scatena & Lugo 1995). To the degree that wind exposure is greater on slopes and at high elevations, increased storm intensity may make forests growing in these areas particularly vulnerable to damage. As drought effects on soil moisture are more marked on slopes, recurrent drought may also slow recovery.

Work plan -- Meteorological (temperature, precipitation, and solar radiation) and soil moisture output derived from WRF-Chem dust intrusion and defoliation scenarios will be used to generate meteorological drivers for the ED2 model to test this hypothesis. Modeling experiments will evaluate the relative contributions of these disturbance mechanisms to C fluxes and ecosystem dynamics in forests across LEF between two test periods: 2045-2049 and 2085-2089. An accurate assessment of initial ecosystem

state is important in short-term, annual-to-decadal scale simulations and significantly constrains model uncertainty. Remotely sensed data imaging can provide sufficiently detailed, accurate, and spatially comprehensive estimates of canopy composition and structure and this approach has been used successfully in a landscape parameterization of ED2 at Harvard Forest (Antonarakis et al. 2014). In LUQ, initial biomass and PFT composition model conditions will be derived using a series of recent (2011, 2013, 2016, 2017) airborne LiDAR data collections coupled with high resolution stereo photographs and hyperspectral information collected across the LEF using the GLiHT platform (Cook et al. 2013). Simulations will be validated using the LiDAR data collected before and after the 2015 drought and Hurricane Maria, as well as ground based tree inventories, including coarse woody debris, in several plots distributed across the LEF.

4.4 Synthesis

Despite being one of the six goals of the LTER Network, effective synthesis at site, cross-site, and network scales is difficult to achieve without strategic direction that leads to focused allocation of resources (Waide 2016). Leadership of LUQ uses the strategies of 1) an inclusive conceptual framework to define common goals, 2) frequent, focused interactions among investigators and their students to assure cross-fertilization of ideas, 3) co-location of multi-disciplinary observational studies (e.g., LFDP/BEW and Stream Monitoring; LTEP) to stimulate integration, 4) inclusive, cross-disciplinary experiments (e.g., CTE, StreamFRE, TEE) to encourage synthesis within the LUQ research team, and 5) coupled simulation models to generate new hypotheses informed by long-term data.

During LUQ VI, we will continue our custom of monthly webinars focused on synthesis themes informed by long-term data. As a new component, we will conduct these webinars as a distributed graduate seminar that focuses on a theme chosen to engage a broad cross-section of LUQ and affiliated (e.g., LCZO, NEON, ULTRA) researchers. For example, discussions of coupling and decoupling terrestrial and aquatic populations and processes or redefining resistance, resilience, and vulnerability for no-analog ecosystems might lead to an initial theme. Themes will be selected among ideas presented by investigators and students in a special discussion session at our annual meeting. A facilitator will help the group select among options, and 2-3 thematic leaders will organize the monthly webinars. LUQ will provide resources to writing teams to meet and draft synthetic manuscripts from the webinars.

We will continue to conduct cross-site and cross-network synthesis leading to integrative publications via collaborations with other LTER sites and networks (e.g., the NeSelvas (PARTNERS) RCN and the CloudNet RCN). We are an active participant in Drought-Net, a collaboration to assess the sensitivity of terrestrial ecosystems to drought. Collaboration with NASA/USFS on a LiDAR based assessment of changes in three-dimensional structure before and after a severe drought and hurricanes will allow us to make a seminal contribution to this important issue. We plan to convene a workshop involving LTER, DOE, NASA and Smithsonian scientists to incorporate this information into global assessments of tropical forest responses to a changing climate.

5. RELATED RESEARCH PROJECTS

The Luquillo Critical Zone Observatory is co-located with LUQ, sharing leadership, students, technicians, and infrastructure. We hold joint annual meetings and the collaboration has resulted in at least one unique publication (Wolf et al. 2016). 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 Technological University (Tropical Responses to Altered Climate Experiment [TRACE]). This project, mounted with funding from USDA Forest Service and the Department of Energy, is testing the response of forest plots to a temperature increase of +4° C above ambient (Cavaleri et al. 2015, Kimball et al. 2018). LUQ has collaborated with this effort so far by providing scientific input and field help. 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. They are currently collaborating with researchers at Florida International University on the impacts of sea level rise on coastal wetlands. 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

model representations of these interactions and their influences on the Earth's future climate. Finally, LUQ collaborates closely with the USDA Caribbean Climate Hub.

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, 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. During LUQ V, we revised 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. During the data jam workshop, teachers will work with LUQ data 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. During LUQ V we conducted basic research, in collaboration with an educational psychologist, on how the program affects motivation and learning. The results of this research project has been the basis to seek additional funding from NSF to significantly revise the web site materials based on new ways to support student.

Natural Resource Career Tracks – This program was recently refunded in Puerto Rico by USDA National Institute of Food and Agriculture. With annual funding of roughly \$250,000, 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. REUs funded by LTER are integrated into the site REU 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, CTE, LTER and other projects. Students are oriented to research goals and trained in field protocols, data management, and identification of tropical biota. Field trips and seminars by scientists enhance their field experiences. Working for 4-month stints, interns 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 18 graduate students currently involved in LUQ research at 14 institutions. Approximately half 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). Omar Gutiérrez del Arroyo is the current representative. 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.

FIGURES

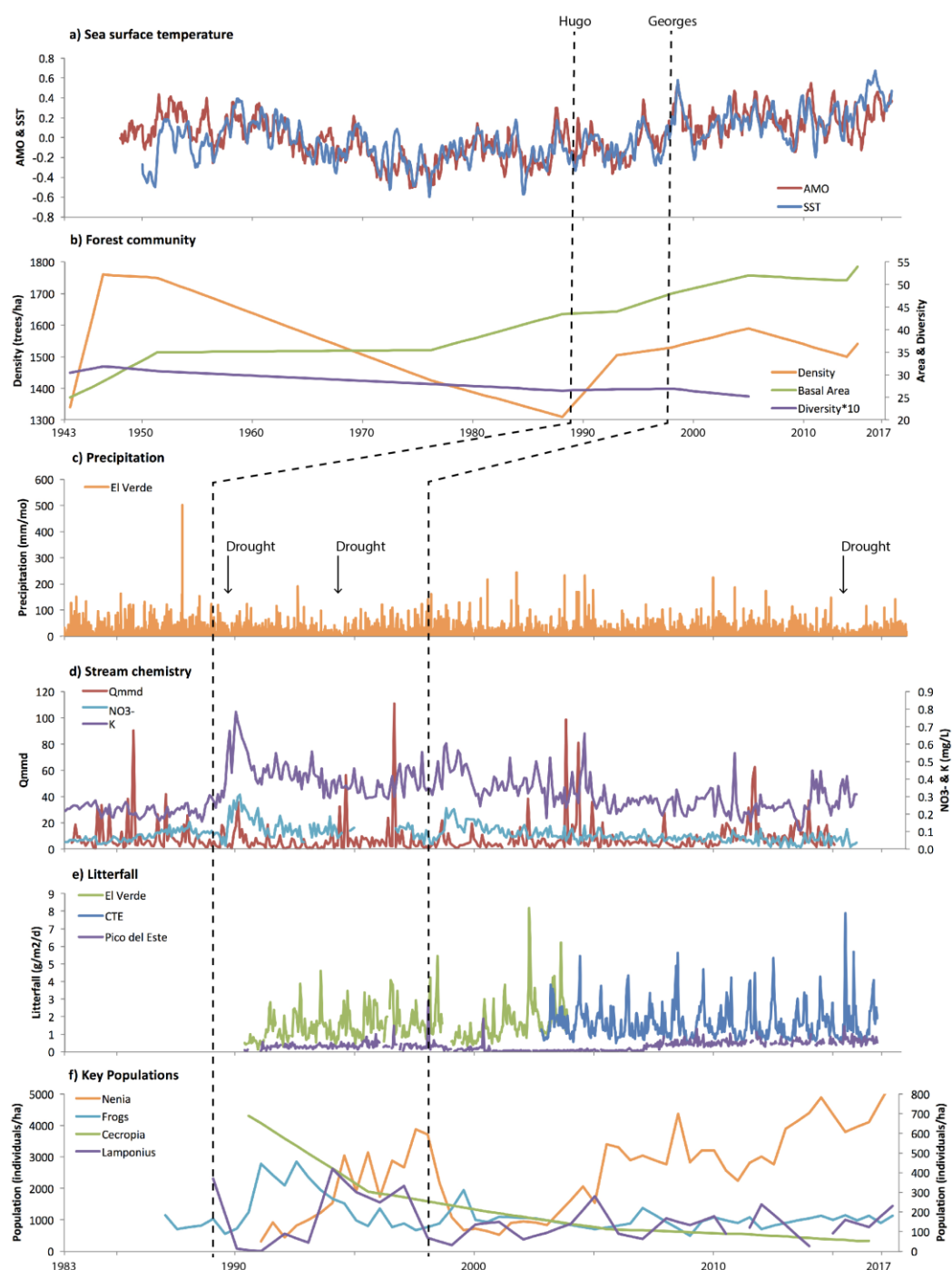


Figure 1.1. Long-term data sets collected in the LEF that contribute to LUQ research. Climate variability is strongly related (a) to the climate index Atlantic Meridional Oscillation (AMO) and sea surface temperatures (SST), which influence temperature and precipitation. Forest plots established by the Institute of Tropical Forestry in 1943 (b) show that *tabonuco* forest was recovering basal area after human and hurricane disturbance in the early 19th 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 (Heartsill-Scalley 2017). Litterfall (c) in *tabonuco* forest at El Verde Field Station collected from two data sets (“MRCE” and the CTE), compared with data from elfin

forest at Pico del Este. In the Quebrada Sonadora, (d) concentrations of NO_3^- and K^+ in stream water responded to hurricane disturbance 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 of key organisms by LUQ (e) show diverse responses to hurricane disturbance (McDowell et al. 2013). 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 (Woolbright 1991) that 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 (Bloch et al. 2007). The walking stick, *Lamponious portoricensis*, was very abundant before H. Hugo, but, surprisingly, never recovered its former abundances (Willig et al. 2011).

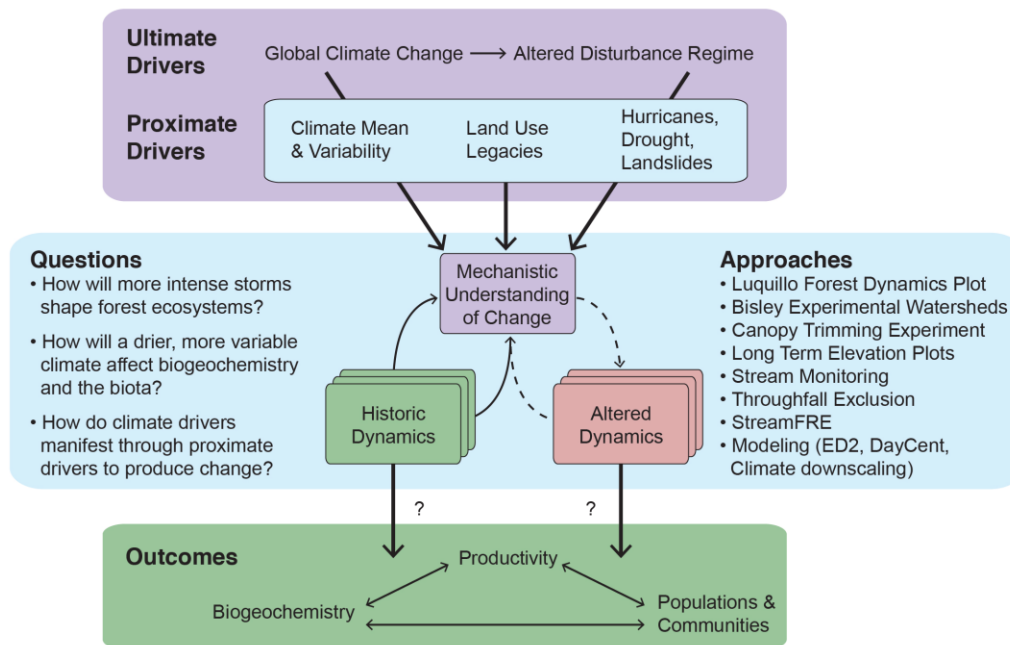


Figure 1.2. Conceptual Framework for the LUQ LTER Program. We view global climate change -- and the resulting altered disturbance regime -- operating through local climate change, legacies of land use, and disturbance frequency and intensity, as the ultimate drivers of ecosystem change. We hypothesize that such scenarios may include altered ecosystem states that differ from historical ones. Our long-term measurements of biogeochemistry, productivity, and key populations of producers and consumers will allow us to detect critical changes in ecosystem state.

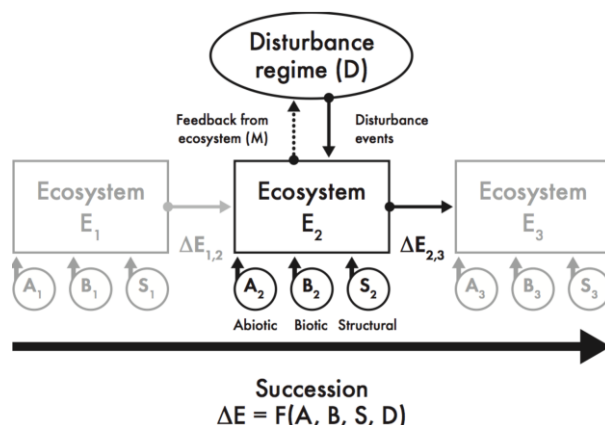


Fig. 1.3. A model linking disturbance and succession at LUQ. Abiotic, biotic, and structural environments interact with one another and the disturbance regime to determine the state of the ecosystem. Meanwhile, the state of the ecosystem can influence the disturbance regime and future ecosystem states, implying contingency or ecological memory. From Willig & Walker (1999).

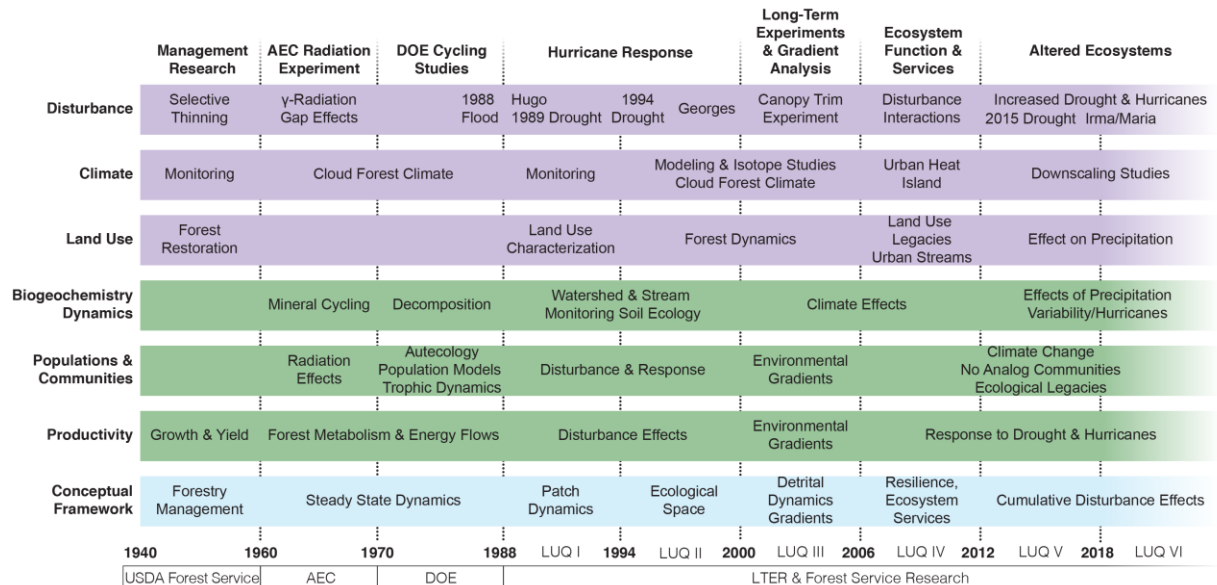


Figure 2.1. Research history in the Luquillo Experimental Forest, showing key long-term studies in relation to fundamental components of LUQ activities (horizontal bars). Disturbance and factors that modify the disturbance regime (Fig. 1.2) are color-coded purple and measured responses are green. Evolving 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 (bottom).

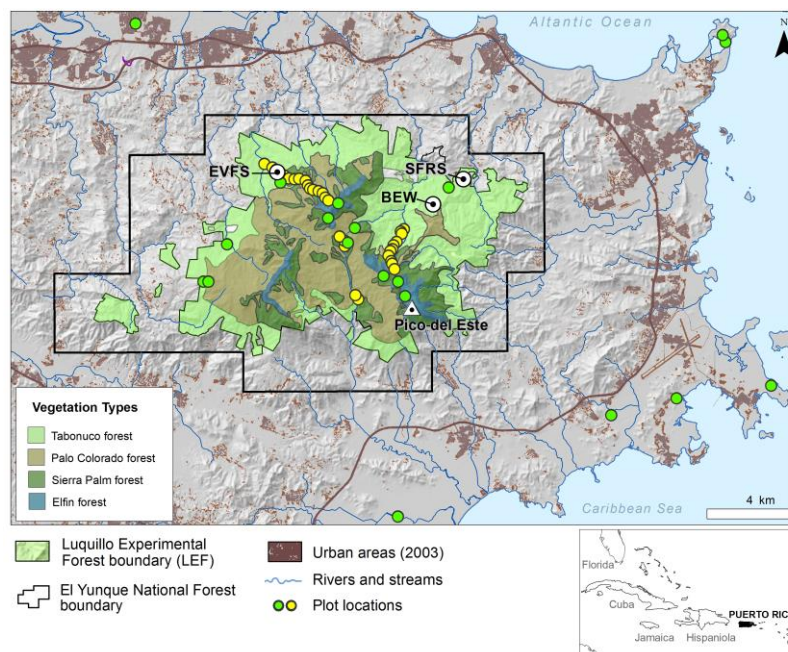


Figure 2.2. Map of the Luquillo Experimental Forest in northeastern Puerto, showing the major forest types. Key study locations in the LEF include El Verde Field Station (EVFS), Sabana Field Research Station (SFRS), Bisley Experimental Watersheds (BEW) in *tabonuco* forest (200 – 600 m elevation) and Pico del Este in elfin forest. Location of Long-Term Elevation Plots are shown in yellow, additional elevation gradient plots monitored by IITF are shown in green.

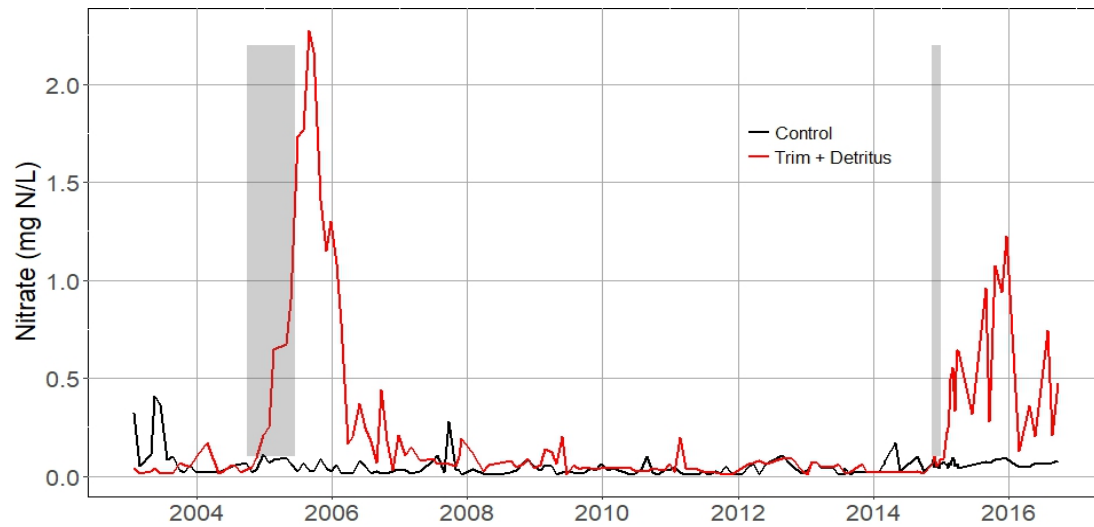


Fig. 2.3. Changes in mean concentrations of nitrate in three replicate blocks of the Canopy Trimming Experiment, contrasting control (green line) and trimmed (red line) plots where the canopy was trimmed by arborists and the detritus was placed on the ground to simulate hurricane conditions. Gray bars indicate treatment periods in 2004-5 and 2014.



Fig. 2.4. Hurricane disturbance in the LEF following the passage of Hurricane Maria. (Left) A forest scene one week post-hurricane, showing the open canopy and hurricane debris typical of most areas (J. Zimmerman photo). (Right) A debris dam on the Prieta Stream with a 1 x 1 meter quadrat for scale (Pablo Gutiérrez photo).

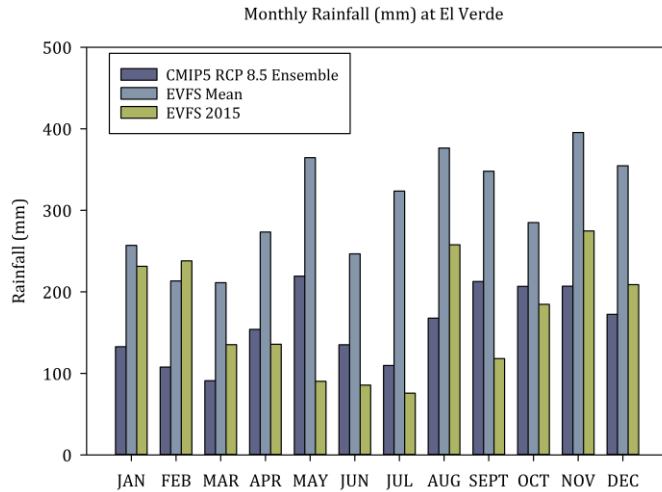


Fig. 2.5. Seasonal rainfall in CMIP5 RCP 8.5 (business as usual) scenario climate model runs for 2070-2099 (blue) compared to monthly means from El Verde Field Station (gray bars; 1975 – 2015) and the drought year of 2015 alone (green).

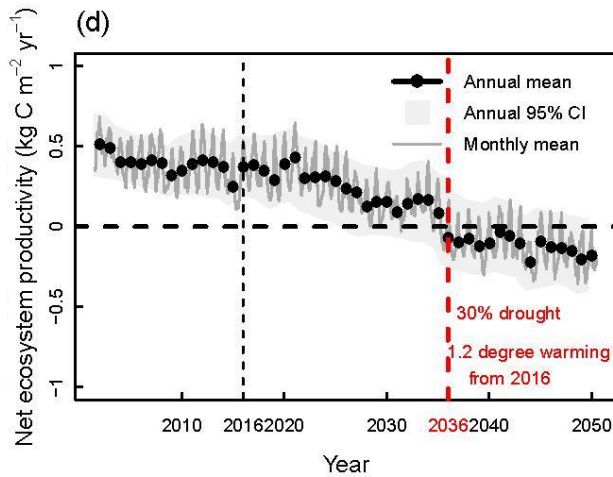


Fig. 2.6. Net ecosystem productivity (NEP) estimated from the ED2 model for *tabonuco* forest in Puerto Rico showing the impact of progressively increasing drought (to a 50% reduction in precipitation) and temperature (2 C) over time ([Feng et al. 2018](#)). Red line indicates where NEP is predicted to fall to near 0.

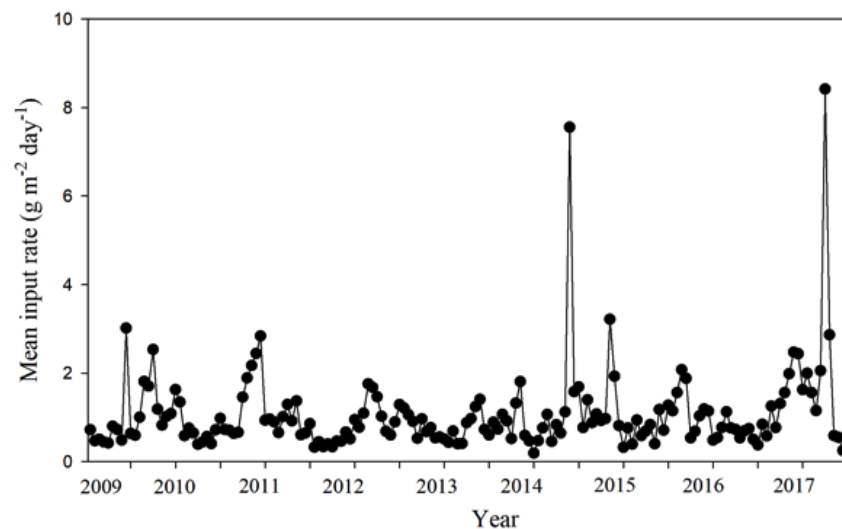


Fig. 2.7. Litterfall measured in the Prieta Stream showing the increase in litterfall during the 2015 drought and from disturbance by Hurricane Irma in 2017. Hurricane Maria destroyed the litter traps such that litterfall could not be measured. They were immediately replaced.

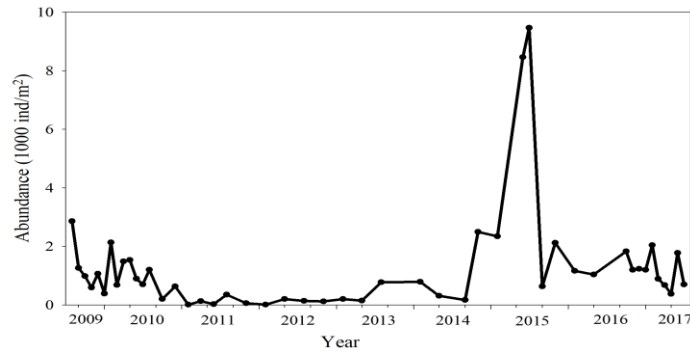


Fig. 2.8. Abundance of insects in the Prieta Stream showing the increase recorded in stream pools during the 2015 drought.

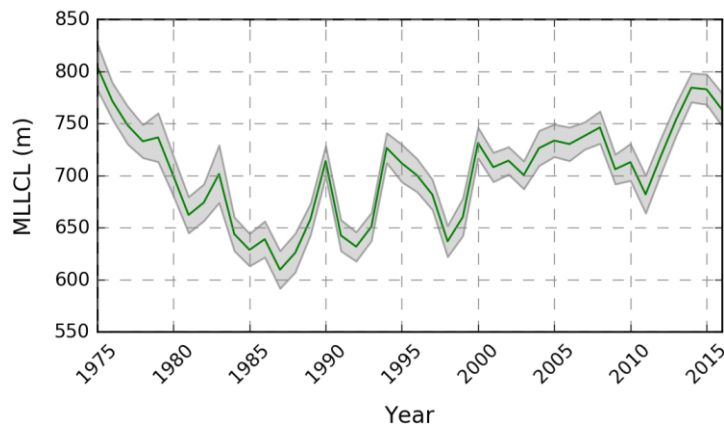


Fig. 2.9. Cloud base heights vary with time but are not currently different than they were in the 1970s (*Miller et al. submitted*). Heights were computed by calculating the mean-layer lifted condensation level (MLLCL), a meteorological characterization of the height at which a mixture of near-surface (<~1 km asl) air would cool to saturation. Mean value (green line) and 95% confidence interval (grey shading) shown.

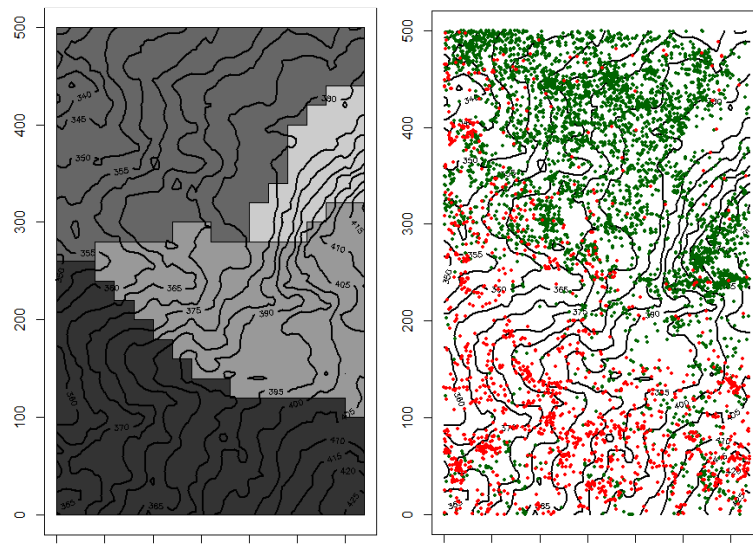


Fig. 3.1. The Luquillo Forest Dynamics Plot (LFDP): maps of (upper left) land use (LU) history (canopy cover in 1936 aerial photograph such that darkest shading represents >80% cover; remaining classes are 50 – 80%, 20 – 50%, and <20%, represented by decreasingly lighter shades of grey [*Thompson et 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 illustrate responses to > 80 vs. <80 % canopy cover (i.e., high vs. low LU intensity). Changes over time show (bottom) numbers of species in small (1-10 cm diameter at breast height [DBH] and large tree diameter classes (>10 cm dbh). Species loss from the plot was also due to loss of many shade intolerant species and the local extinction of very rare species (<1 cm dbh; *Hogan et al. 2016a,b*).

Year	No. of Items			Species Richness		
	≥1, <10 cm	≥10 cm	Total	≥1, <10 cm	≥10 cm	Total
1990	91681	11754	103435	143	94	154
1995	71320	14339	85897	137	90	145
2000	65213	15881	81094	130	89	141
2005	35390	16584	51974	121	87	130
2011	25396	17004	42400	113	90	123
2016	16605	15543	32148	115	90	126

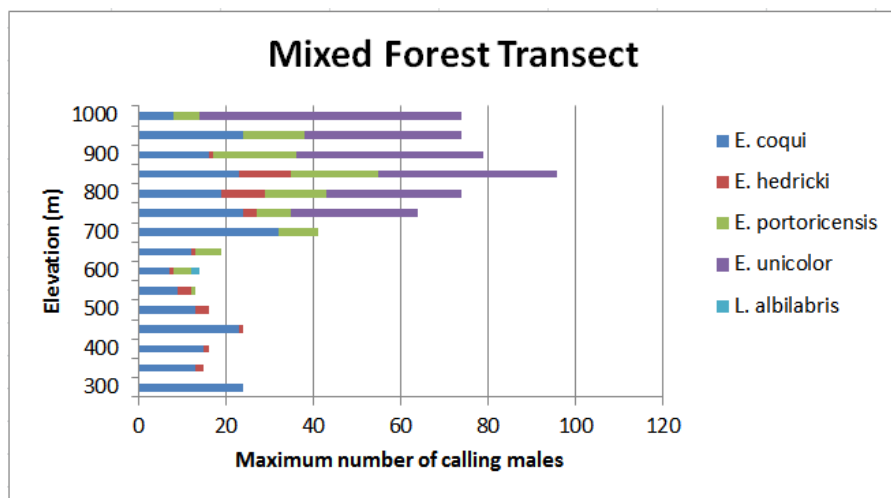


Fig. 3.2. An example of an elevation distribution we are measuring every six years. The graph shows the distribution of frog species in the genera *Elutherodactylus* and *Leptodactylus* in the Sonadora Watershed recorded in the summer of 2017 in mixed (vs. palm-dominated) forest.

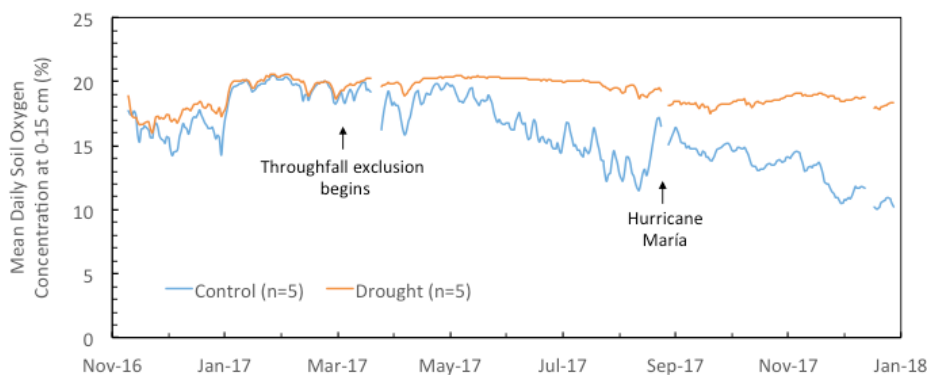


Fig. 4.1. Soil oxygen concentration over time in the throughfall exclusion experiment (TEE).

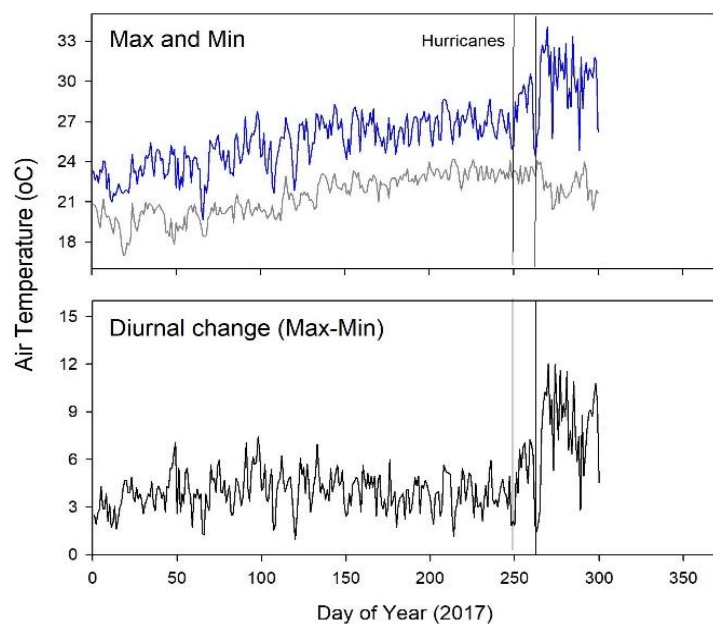


Fig. 4.2. Trace of daily maximum and minimum temperature ($^{\circ}\text{C}$) (top) and the diurnal temperature range (bottom) in the Prieta Stream during 2017. The vertical black lines mark the passages of Hurricanes Irma and Maria, respectively.

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PROJECT MANAGEMENT

A Management Committee (MC) consisting of the PI and four co-PIs undertakes project management in the Luquillo LTER program. Jess Zimmerman is the Lead PI of the LUQ. Nick Brokaw, the former Lead PI, will continue to serve as co-PI at the University of Puerto Rico. The remaining co-PIs are Grizelle González (USDA Forest Service), Whendee Silver (University of California-Berkeley) and Michael Willig (University of Connecticut). The structure of the MC was established to (1) provide administrative support at UPR where the program is managed while (2) providing input into the management of the program by collaborating institutions.

Zimmerman will continue as Lead PI through LUQ VI. Brokaw continues as co-PI, providing institutional memory from his time served. Brokaw will retire from LUQ early during the next funding cycle. To replace him, UPR continues its search for a senior person to take up the Co-PI position, but the search has been delayed during the recovery from Hurricane Maria. Our plan is to continue the search for a new Co-PI in the current year and have this person in place to be mentored to become Lead PI in LUQ VII.

Zimmerman has 26 years of experience as an administrator and researcher at UPR. He is the former Director of The Institute for Tropical Ecosystem Studies (ITES; 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. Zimmerman served as a Program Officer at the National Science Foundation from 2004-2007 before returning to UPR to become Project Director 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. Zimmerman is committed to serving a leadership role in LUQ through LUQ VI, helping with mentorship of a new Lead PI for LUQ VII and beyond.

Grizelle González represents the IITF – USDA Forest Service on the MC. She serves as Project Leader at IITF, where she has worked for 15 years. IITF and its researchers participate in the LUQ LTER by supporting research activities at Sabana Field Station (which González also leads), the Bisley Experimental Watersheds, and at Pico del Este. González is essential for coordinating this portion of the research effort and has contributed greatly to the success of LUQ by guiding and supporting synthesis efforts (e.g., González et al. 2013, Shiels and González 2014), among many other accomplishments.

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 UC-Berkeley. She has been with LUQ since 1994. She is a leader in the field of tropical biogeochemistry and has had many research grants at our site. She is also co-PI on the Luquillo CZO project, providing a critical link with this sister project.

Michael 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, selecting new hires, and making changes in administrative policy. The MC meets monthly 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 operation of the LTER award.

The MC is supported by a Science and Education Advisory Committee (SEAC) whose members are seven LTER researchers (Senior Personnel and Associate Researchers) nominated from among by the LUQ community (including Associate Researchers and graduate students) and chosen by the MC for a three-year renewable term. The Information Manager (IM), one Student Representative, and the Education Coordinator (EC) are *ex-officio* members of the SEAC, along with the Founding PIs, Robert Waide and Ariel Lugo.

Table 1. LUQ investigators and their roles in the Management Committee and the Science and Education Advisory Committee.

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>Senior Personnel</i>		
Báez, Noelia ¹	Education Coordinator	University of Puerto Rico
Cantrell, Sharon		University of Turabo
Covich, Alan ¹		University of Georgia
Crowl, Todd		Florida International University
Heartsill-Scalley, Tamara ¹		IITF, USDA Forest Service
Lodge, D. Jean	Information Manager	USDA Forest Service
McDowell, William		University of New Hampshire
McGee, Steven		Learning Partnership, Inc., Chicago
Meléndez, Eda ¹		University of Puerto Rico
Mote, Thomas		University of Georgia
Pringle, Cathy ¹		University of Georgia
Ramírez, Alonso ¹		University of Puerto Rico
Schowalter, Timothy		Louisiana State University
Shiels, Aaron ¹		Natl. Wildlife Res. Ctr. USDA
Uriarte, Maria ¹		Columbia University
Waide, Bob ¹		University of New Mexico
Wood, Tana ¹		IITF, USDA Forest Service

¹Members of the SEAC

The SEAC meets annually to review progress in achieving scientific and education goals established in the most recent proposals, exchange ideas on new research initiatives, etc. With the SEAC, the MC conducts regular reviews, at least every three years, of the contributions of each of the Senior Personnel and recommends changes to the membership of the Senior Personnel and the SEAC.

External advisors are utilized to maintain an objective perspective on the development and performance of LUQ. This group consists of three scientists not otherwise affiliated with LUQ who form an External Advisory Committee. External Advisors serve 3-year term, renewable for additional terms as determined by the MC. The External Advisory Committee members attend LUQ meetings and provide oral and written input on the progress of the program. With this proposal, the Advisory Committee will continue with Aaron Ellison of Harvard Forest, Tim Fahey of Cornell University, and John Porter of the University of Virginia.

Monthly meetings are held with the LUQ scientific community via the web or in person at UPR. The MC organizes seminars and they use this venue to keep the LUQ community informed of key information. An annual LUQ All-Scientists Meeting is held each June, consisting of a day of seminars and posters (usually held in conjunction with the Luquillo Critical Zone Observatory), a day of review of scientific progress and future planning, and one-half day of a business meeting among the SP.

Each January we have a Planning Meeting, usually attended by SP, the IM, the EC, and the graduate student representative. These meetings are usually focused on upcoming programmatic tasks such as the mid-term review, renewal proposal development, or mounting a new project within the program.

Associate Researchers are those who have research related to LUQ but who are not closely involved with the management and development of the LUQ program. The MC, with the advice of the SEAC, appoints Associate Researchers. Associates are normally appointed for the duration of the six-year funding cycle. These may be junior faculty intending to take the place as Senior Personnel in the project or seasoned researchers who have a low level of annual effort on a long-term project that contributes to LUQ's overall goals. They are supported by LUQ with travel funds, student support, or the like. Currently, they are Chris Bloch (Bridgewater State University), Qiong Gao (UPR), William Gould (IITF), Pablo Gutiérrez, Erika Marin Spiotta (University of Wisconsin), Sabastian Martinuzzi (University of Wisconsin), Olga Mayol (UPR), Bob Muscarella (Aarhus University), Jorge Ortiz (UPR), Chelse Prather (University of Dayton), Steve Presley (University of Connecticut), Joanne Sharpe (independent), Jill Thompson (CEH Edinburgh), Maria Natalia Umaña (Yale University), Shiela Ward (independent), Lawrence Walker (University of Nevada-Las Vegas), Larry Woolbright (emeritus), Joe Wunderle (IITF), and Mei Yu (UPR).

We are committed to recruiting an ecophysiological to the research group as suggested by the Mid-Term Review team. Efforts to identify this person were held up by Hurricane Maria and the aftermath. Discussions are currently proceeding and we plan to use the Annual Meeting in June to interact with several candidates. We seek a person with a history of funding ecophysiological research in the tropics who has specific knowledge of drought impacts on tropical vegetation. This person would be expected to take a leadership role in the developing of the large-scale TEE and assist the group in seeking external funds to develop an ecophysiological component to the TEE.

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

Introduction: the Luquillo Information Management System (LIMS), a product of collaboration

The LIMS, a tool for data discovery, is a product of continual collaboration between the LUQ information management staff and the LTER research community. Designed in collaboration with members of the LTER Information Management Committee, the LIMS complies with LTER Network policies and uses software that serves both as an information management system and a tool for data discovery.

Interaction with the LUQ Community. The LUQ principal investigator and information manager initiated development of LIMS in 1990 by defining a LUQ data set. A data set is one or more data tables along with their metadata, known today as a data source. A data source is data collected with a specific methodology, location, and/or time period. This initial definition was the starting point for LIMS development and was crucial in the development of metadata standards and the current IMS. Data from a specific project is organized and divided into one or several data sets depending on the methodology used to collect data.

The LUQ information manager, Eda Melendez, works closely with researchers during all phases of the Data Life Cycle (Figure 1) from planning to publication. The LUQ IM team has worked with the LUQ scientific community to develop their respective tasks for each stage of the data life cycle. This iterative development process has resulted in an IMS that serves as a tool for both data documentation and discovery.

Figure 1 LUQ's Data Life Cycle and Products



The LUQ Data Life Cycle

The primary goal of LIMS is to support science through all of the stages of the Data Life Cycle. Investigators and IM staff have complementary roles in each of these stages.

Planning. Once investigators define the scientific purpose of a project, they describe the data that will be collected and the different roles of the people involved in data collection. During this stage, the information manager develops a set of common attributes (measurements or variables) that will be present in all data collected by the project, including research site name or code, plot identification, date and any other common attributes distinctive to the project. Working with the investigators, the information manager starts developing the metadata for the project's data sets (list of people, preliminary list of attributes and protocols) in a Word document. Investigators and IM staff jointly agree on which personnel will enter field data, either technicians who collect the data or IM staff, and the parameters for doing so.

Data Structure Design. At the end of the planning stage, the IM staff designs a set or sets of data tables for data entry and completes the design of the data sheets to gather the data in the field after consulting the field technicians. Field protocols are developed by the scientists and field technicians. Data tables are properly formatted to facilitate further use in analysis and synthesis. We use only the first row for labeling the data columns, enter in each column only the set of values belonging to a single type of measurement, and do not enter summaries or statistical formulas within a column. Summaries and statistics are performed in separate spreadsheets, always conserving the integrity of the raw data gathered at the field. The information manager develops quality control procedures and documents data sources at this stage.

Data Collection, Entry, Validation, and Preservation. The IM staff provides feedback to field technicians on the quality of the data collected as they are entered into the database. Inconsistencies that appear during the data entry process can cause field technicians to go back to the field to verify the data. The processes of data collection, entry, validation and preservation are iterative until quality control (QC) standards are met. For some data, scripts and templates have been developed for data control or validation. QC procedures are also performed during the entry process using validation functions provided by entry tools (spreadsheets and data base management system software). A list of accepted values is developed, incorporated, and maintained by the IM staff for each data column whose set of values are finite in a data source (e.g., Species codes).

Data preservation is assured by performing backups online, nearline and offline during and following the data entry process using Dropbox, three USB drives and an internal 1-TB drive. One USB drive is carried home and safely kept by the data entry person and another by the information manager. The information manager's laptop and an external drive used for monthly backups hold the original data provided by the investigators (generally spreadsheets). This process includes the entire data file system on the information manager's and data entry persons computers. A copy of the server's MYSQL data base is maintained on the information manager's laptop using a web tool and backed up on the 1-TB hard drive.

The system administrator maintains a 500 GB external USB-drive with old versions of metadata and data. He administers a second Apache web server that contains a Plone CMS that is used as the online LUQ Intranet for LUQ scientists. Another mini-LAN, located in the El Verde Field Station (EVFS), comprising a Linux server with the downloaded EVFS sensor data and a standalone computer with backups of these data are also maintained by the system administrator.

Data Report and Metadata completion. Before data are made public, the owner of the data must revise and approve them. Several iterations of data report, data collection, entry, validation and preservation may take place before the data are ready for analyses and publication. During these iterations, it is possible that the field technicians have to re-visit the field for QA purposes.

Before the IM staff enters the data, the investigator receives, corrects and approves the data structure (the collection of data columns in a data file) designed by the information manager for all the project's data sets. At this stage the documentation of the data sets, which was started by the information manager during the planning stage of the experiment, is completed by the owner. This is performed using the LUQ Metadata form that contains all the metadata fields featured by LUQ.

At this stage, the data are shared only with the principal investigators of the project on the LUQ's Intranet, a private website for the LUQ scientific community and IM Staff. The metadata is made public in the website-IMS as soon as the documentation process is completed and before the data are published.

Data Analyses, Publication, Sharing and Discovery. Data integration and analysis processes are performed by the investigators for publication purposes. In addition, the LUQ IM uses relational databases to summarize and integrate data from different data sets to perform quality control processes and to answer specific data requests.

Within two years of collection, all LUQ-funded data are published in LIMS as well as in the Environmental Data Initiative's (EDI) repository, complying with the Data Management Policies of LUQ and the LTER Network. Every time data are added to a data set, or in the rare case that a change in methodology occurs, the metadata and data table are updated in LIMS and the EDI repository. LUQ data can be downloaded from the website by clicking on links embedded in the metadata of a data set.

The LIMS website displays policies, user's responsibilities, and data management templates and protocols. Additional information on the website includes a list of LUQ IM publications, presentations, some reports, a template for the data entry and conversion of the rainfall and temperature gathered at the El Verde Research Station, rules and templates to file metadata into the LIMS, and restricted websites for Scientists and Graduate Students.

Data are made discoverable online by search engines designed by the information manager. Searches on data sets can be performed by specifying a program type, a LUQ ID number, a phrase in the data abstract or title, a keyword from the LTER Controlled Vocabulary or assigned by the researcher, or by combining any set of these search elements. In addition, users may click on people's names to see their

profile, research sites to see their location, a publication to see its complete citation, and on a specific keyword to see other data sets with the same keyword. LUQ has further customized LIMS to allow users to discover data by research project, length of data record (ongoing or completed), LTER Core Area, and/or Research Sites.

Key Features of the LIMS

Integration with LTER. The information manager has collaborated with the LTER Network's IM community to develop LIMS and to ensure that it follows Network policies related to data publication and access as well as complies with the LTER Network IM best practices.

The LUQ Data Management Policy (revised and updated in 2015) establishes the obligation of the scientists to release data collected with LTER funding after two years. It is the responsibility of the LUQ information manager to assure that the data, along with their metadata, are made accessible in a timely manner on the LIMS website and the LTER Network Data Portal, which is maintained by EDI.

Following LTER IM best practices, LUQ encourages users to acknowledge the use of LUQ's data in their publications. An example of an appropriate acknowledgement for this purpose is available online. By downloading LUQ's products, users agree to notify LUQ or the project's principal investigator (PI) about any derivative work done, to acknowledge that the original data were obtained with the support of NSF, and to send LUQ copies of their publications. LUQ data are made available with a disclaimer displayed on the LUQ website which liberates LUQ from having to justify the suitability of the use of LUQ's data for any purpose and from the liability for any damage suffered by its use.

Innovation of Technical Approach. Since 2009, LUQ has used a content management system (CMS) known as DEIMS, the Drupal Ecological Information Management System. DEIMS is a customized version of Drupal for the documentation and publication of LTER data and metadata. Members of the LTER IM community from several sites, including LUQ, and sites from ILTER countries collaborate in the task of maintaining DEIMS.

DEIMS is used as the LUQ *website*-IMS and has evolved at the Network level to DEIMS 2 with LUQ's contribution being a crucial one in this process. DEIMS is used as a tool to generate Ecological Metadata Language (EML) documents that are necessary to upload data sets into the EDI repository. DEIMS uses 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, complying with LTER Network Best Practices. LUQ has further customized DEIMS to provide the community with ways to improve data discovery and access by creating special Views to search for data sets using different types of information.

Security and Stability. LUQ IM has developed reliable ways to preserve the site's data with the collaboration of the local system administrator. The recent hurricanes in Puerto Rico illustrate the security of our IMS. One month after the hurricane events in September 2017, and in the absence of power in our host University, the system administrator uploaded an up-to-date version of the LUQ website-IMS for public access in a cloud environment. Backups performed by IM the day before the hurricane and the regular backups done by the system administrator made the prompt publication of the LTER website possible. Data entry and management tasks continued right after the hurricane thanks to the existence of our regular backups.

Data collection performed by field technicians was temporarily interrupted during and after the hurricane events. We began to collect data again at different times after the hurricanes, depending on the methodology used for data gathering. Specifically, manual data collection restarted within 2 weeks of the second hurricane event. Collection of meteorological data required replacement of damaged equipment, which was completed within two months of the second storm. No information (digital data, metadata, or other files) was lost.

LUQ Information Manager's Network and Outreach activities

LTER IM Community activities. The information manager is an active member in the LTER IM community and has originated and chaired working group (WG) 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. She has been the Databits' editor twice and is currently the editor for the 2018 Databits Spring edition, for which she has invited international information managers from Taiwan, Germany, Israel, and South America to submit pieces for the first-time in the history of Databits. In 2017, she also initiated a WG to write the History of the LTER Information Managers. Four US LTER sites' information managers will be engaged in this new project.

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, 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 the University of Puerto Rico, Río Piedras Campus Integrative Graduate Education and Research Traineeship (UPR IGERT) students on three occasions.

Local administration resources. The LUQ information manager has developed several online-private data tables for the administration of the research programs managed at the Department of Environmental Sciences (DES) and the preparation of administrative workflows. In a special project with the DES Director, all available historic pre-LTER research documents were scanned and made public on a website.

Future Projects

Integrating spatial data into LIMS. Although currently downloadable from the local LUQ website, there are 19 GIS shapefiles that will be incorporated into the LUQ website-IMS which will make them publicly available in the local as well as in the Network Data Repository. For this, the information manager will explore incorporating into DEIMS elements of the metadata system developed by the BES site which manages spatial data.

Updating DEIMS. The LUQ information manager will lead the effort currently underway at the US LTER Network to upgrade the DEIMS system to the current version of DRUPAL. This involves coordinating collaborations among 6 other USA LTER sites using DEIMS and, hopefully, with the Taiwan Ecological Research Network information management staff.

Improve data discovery and access. Online searchable databases will be developed in the local website-IMS. The vegetation species database will be the first one to be developed and will serve as a pilot project for future online, searchable databases. This will be used as an aid for data discovery and synthesis.

Outreach activities. Staff in the Department of Environmental Science, University of Puerto Rico, will be trained in the use of DEIMS for data entry and information discovery and download. Qualified schoolyard data will be published in the LUQ website-IMS on a special online Catalog in the Schoolyard web pages.

Developing a DEIMS-based data entry form for the technical component of LUQ. The possibility of developing online data entry forms that could be used in the field for data gathering will be explored. DEIMS provides the tools to develop webforms that could be used to enter data in the field directly to the website without making them public right away. After going through documentation and quality assurance and control processes, these data can be made readily available to their investigator for their inspection and use and can be eventually made public in a timely manner following our Data Management Policies. Connectivity problems are the major challenge for this project. The information manager will work with the LUQ system administrator to explore ways to achieve this task.

LUQ Data Product Description

Meteorological and streamflow data. Different types of meteorological sensors are in several locations, namely, the Upper Bisley Climate Tower (USGS), the lower Bisley Climate tower, the roof of the Sabana Field station laboratory building (USFS), the El Verde Field Station (EVFS) (top of a 30m tower) and the Canopy Trimming Experiment (CTE) plots. Gauge height data from seven gauging station and historical gauge data in the LEF are reported as daily averages for some stations and as gauge height for others.

Plants, seedling and phenology data. Inventory and measurements of plants, percent cover, and phenology are performed yearly in El Verde area for the Luquillo Forest Dynamics Plot (LFDP) and the CTE Plots.

Chemistry data and water sample collection. Stream water (14 sites) and rain and throughfall (5 sites) samples are collected weekly at the Luquillo Mountain sites.

Community composition in response to disturbance data. Data are collected from different studies related to the effect of disturbance on activity, abundance, density, and spatial distribution of anoline lizards and frogs; changes in populations of birds; rates of decomposition of pre-existing litter and green hurricane litter; canopy invertebrates; litter and flower fall; germination, growth, survival, nutrient cycling, soil conditions, and trophic structure; relative abundance and diversity of microorganisms in leaf litter at different stages of decomposition; soil and leaf litter microbial community structure and composition; long-term population and community dynamics of terrestrial gastropods and walking sticks, and stream ecosystems.

Elevation Gradient data. Data are collected on the effects of elevation and litter quality and quantity on the composition and biomass of the litter invertebrate community; on composition of plant communities; changes in fungal and bacterial diversity, and abundance and composition of microbial functional groups, and on animal species and community structure.

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

LUQ IM Publications

- Chau-Chin, Lin, A. B.D. Rahman-Kassim, K. Vanderbilt, D. Henshaw, E.C. Melendez-Colom, J. Porter, K. Niiyama, T. Yagihashi, Aun S. Tan, S.S. Lu, C.W. Hsiao, L.W. Chang, and M.R. Jeng. 2011. An Ecoinformatics Application for Forest Dynamics Plot Data Management and Sharing. Taiwan Journal of Forest Science 26(4):357-369. <http://www.treesearch.fs.fed.us/pubs/42559>.
- San Gil, I., A.F. White, E.C. Melendez-Colom, and K. Vanderbilt. 2010. Case Studies Of Ecological Integrative Information Systems: The Luquillo And Sevilleta Information Management Systems. In Metadata and Semantic Research. Sánchez-Alonso, S. and Athanasiadis, I.N. Springer Berlin Heidelberg, 18-35. http://link.springer.com/chapter/10.1007%2F978-3-642-16552-8_3.
- Melendez-Colom, E.C., and K. Baker. 2002. Common Information Management Framework: In Practice. Pages 385-389 in Callaos, N., Porter, J.H. and Rishe, N. Proceedings of the 6th World Multiconference on Systemics, Cybernetics and Informatics: Volume VII Information Systems Development II, July 14-18, 2002.