Luquillo LTER 5 Renewal Proposal

Summary

Intellectual Merit: The Luquillo Long-Term Ecological Research Program (LUQ) integrates research and educational activities through a focus on two great challenges confronting society in the 21st Century: climate change and land use change. Our goal is to understand: 1) how the environment of northeast Puerto Rico is changing; 2) the consequences of such change for biodiversity, biogeochemistry, and ecosystem services; and 3) how society can manage or adapt to these changes. Earlier LUQ research (1988-2012) showed that natural ecosystems are largely resilient after episodic, pulse disturbances, such as hurricanes, landslides, floods, and droughts. Building on that work, LUQ 5 (2012-2018) focuses on the resilience and vulnerability of ecosystems and services in the environs of the Luquillo Mountains (LM) as they respond to interacting pulse and longer-term, press disturbances (changing hurricane regime, lower and more variable rainfall, warming, and rapid change in land and water use). We particularly focus on water, as an important ecosystem component and essential ecosystem product. In this context we ask: **How do long-term changes in climate and land use interact with other disturbances to affect biodiversity, biogeochemistry, and their interactions to determine ecosystem services in northeast Puerto Rico?** We address this question with continuing long-term studies along climate and land use gradients, modeling and synthesis, and, noteworthy in this cycle, long-term field experiments and a new landscape-level project that are designed to provide a mechanistic understanding of the effects of key drivers of long-term change. The overarching question leads to three focal questions.

1 **How do environmental drivers affect the multiple dimensions of biodiversity?** Biodiversity research mainly focuses on the taxonomic dimension, particularly species richness. Less studied are functional and phylogenetic biodiversity, which relate to ecosystem function and evolutionary history. We will study effects of interacting press and pulse disturbances on spatio-temporal variation in these multiple dimensions of biodiversity, and, in the new Litter Exclusion Stream Experiment, the importance of variable inputs of terrestrial detritus for stream biodiversity and water quality.

2 **How do environmental drivers affect biogeochemical pathways, responses, and rates?** We will continue to document how long-term biogeochemical dynamics (e.g., litterfall mass, stream chemistry, trace gas flux) respond to pulse and press disturbances. We will continue the Canopy Trimming Experiment (field simulation of hurricane effects) and begin a Throughfall Manipulation Experiment, which will help us understand the effects of more extreme wetting and drying events on forest biogeochemistry.

3 **How do environmental drivers affect ecosystem function and services?** The LM provide water, biodiversity, recreation, and other ecosystem services and products that are affected by changes in the hydrologic connectivity between the lowlands and the LM, and by land use in the lowlands surrounding the LM. In LUQ 5 we will study how changing connectivity affects ecosystem function and services, and in the new Landscape Project, how construction of a four-lane highway near the LM influences the functioning and services of both aquatic and terrestrial ecosystems.

Broader Impacts: Using integrated theoretical, experimental, and observational approaches, LUQ 5 will provide a comprehensive scientific framework for evaluating the management of tropical ecosystems and their services. The program will continue to train numerous graduate and undergraduate students, especially members of underrepresented groups, producing a cadre of collaborative, multidisciplinary scientists who can link population, community, and ecosystem approaches to provide a predictive understanding of environmental change. LUQ 5 will capitalize on its recent success in catalyzing major projects in Puerto Rico, such as NEON, STREON, IGERT, CZO, and ULTRA-Ex. Schoolyard LTER in LUQ 5 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.

Section 1   Results from Prior NSF Support

"Luquillo LTER 4: Understanding Change in Ecosystems of Northeast Puerto Rico"; NSF Grant DEB-0620910; Dec. 2006–Nov. 2012; $4,920,000. Supplements: $543,664.

The goal of the Luquillo Long-Term Ecological Research Program (hereafter LUQ) is to understand how disturbance affects forest and stream ecosystems, and the services they support, in a tropical landscape. In the early phases of LUQ (1988-2006), we documented the high resilience of populations, communities, and biogeochemical responses to natural, pulse disturbances in the Luquillo Mountains (LM) of northeastern Puerto Rico (Walker et al. 1991, 1996, Brokaw et al. 2012a). This work led to research in LUQ 4 (2006-2012) on responses to longer-term, press disturbances associated with climate and land use change. We also identified long-term trends in ecosystem characteristics over the 24 yr of LUQ (Peters et al. 2012) and synthesized our results in several publications (Sect. 1.4). A major achievement of LUQ 4 was leading the establishment of four non-LTER, NSF-funded network sites in Puerto Rico that complement LUQ (Sect. 1.5). Below we highlight results from LUQ 4 that motivate proposed research in LUQ 5 on how key environmental drivers – hurricanes, climate, and land use – cause long-term change in biodiversity, biogeochemistry, and their interactions. Our ultimate aim is to forecast ecosystem states and to provide insights for better managing ecosystem services in the tropics (Fig. 1). The 10 most important publications of LUQ 4 are underlined in the text.

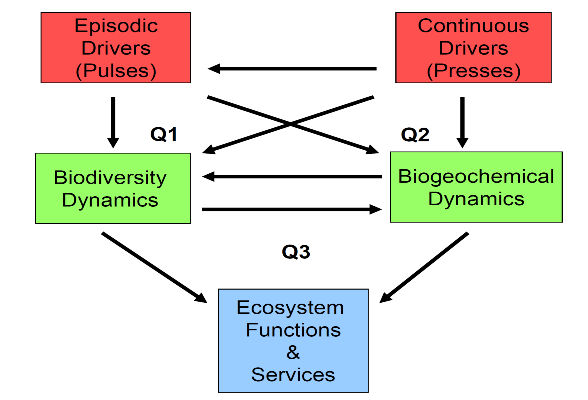

Figure 1 – Conceptual framework for LUQ. The framework arises from a set of relationships: 1) those between drivers of environmental change, including both press (e.g., climate change) and pulse (e.g., hurricane) disturbances (red boxes); 2) those between these disturbances and biodiversity or biogeochemical dynamics (green boxes), including their interactions; and 3) the effects of linked biodiversity and biogeochemical dynamics on ecosystem functions and services (blue box). The associations of the focal questions of LUQ 5 (Sect. 2.4, Fig. 7) within this conceptual framework are shown by Q1, Q2, and Q3.

1.1   RESEARCH RESULTS FROM LUQ 4 (2006-2012)

1.1.1 Hurricanes: impacts of change in regime and interaction with human disturbance

In LUQ 4 we showed that biodiversity plays a role in carbon dynamics after a field simulation of hurricane effects, and that hurricanes interact with human disturbance to affect populations and communities. Hurricanes are a dominant disturbance structuring forests in Puerto Rico (Heartsill-Scalley et al. 2007, 2010, Lugo 2008,) and elsewhere in the tropics, and stronger or more frequent hurricanes (Emanuel 2005, Knutson et al. 2010) will have significant impacts on forest structure and ecosystem services. The Canopy Trimming Experiment (CTE) decoupled the main direct effects of hurricanes (canopy loss and debris pulses) to understand the effects on biodiversity and biogeochemistry. Under opened canopy, decomposition rates slowed and soil respiration was lower because of a shift in the decomposer community from fungi to bacteria and a decline in invertebrate numbers and diversity (Rivera-Figueroa 2008, Richardson et al. 2012, Willig et al. 2012b, Silver et al. in prep.). Under intact canopy, decomposer communities changed less and decomposition and soil respiration were faster. Addition of canopy debris to the forest floor resulted in greater fungal connectivity and thus higher nutrient translocation (Lodge et al. 2008). Over the first four yr of the experiment, litter inputs (index of NPP) became decoupled from soil CO_2 efflux in disturbed plots. Canopy opening resulted in large, prolonged reductions in litterfall production, amounting to over 9 Mg C/ha over four yr (Silver et al. in prep). Soil respiration rates recovered more quickly than did litterfall, suggesting that decomposition could exceed litterfall production, leading to C losses from the ecosystem. Over the 20-yr duration of this experiment, we will examine the effect that increased frequency of simulated hurricane impacts has on ecosystem C balance due to changes in biota.

Based on our long-term data in LUQ 4 we quantified how successive hurricanes interact with human disturbance at various temporal and spatial scales to affect populations and communities (Bloch & Willig 2006, Willig et al. 2007, 2011a). For example, the population of the common tree, *Cecropia schreberiana*, was resilient after Hurricane Hugo but not after Hurricane Georges, which followed 9 yr after Hugo (Brokaw in prep.). This difference suggests that more frequent storms will cause additional declines of a species that played a major role in restoring nutrient balances after Hurricane Hugo (Scatena et al. 1996). The response of an important insect herbivore, *Lamponius portoricensis*, to hurricane-induced damage depended on microclimatic conditions and forage plants (*Piper* spp.) but also on past land use in the forest (Fig. 2, Willig et al. 2011a). Looking at multiple spatial scales, the species composition of

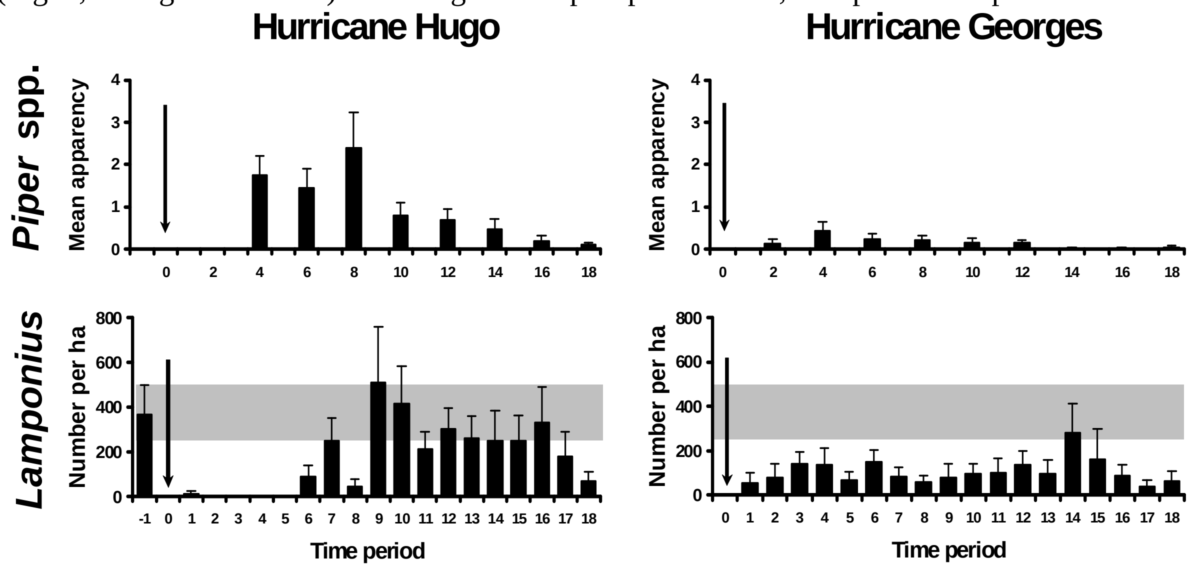

Figure 2 – Effects of repeated hurricanes on abundance of an early successional plant (*Piper* spp.) and keystone, herbivorous walking stick (*Lamponius portoricencis)*. Each time period is a 6-month interval with hurricanes at time = 0 (arrow). Vertical bars are one (*Piper*) or two (*Lamponius*) SE. Walking sticks exhibited differences in resistance and resilience to the two pulse disturbances, with a new and lower stable state for density following Hurricane Georges. (Willig et al. 2011)

canopy trees in low-elevation forest was altered greatly by intense hurricane damage in patches less than 0.1 ha but was little changed at larger scales (Heartsill-Scalley et al. 2010, Zimmerman et al. 2010). For subcanopy trees, however, there was larger-scale change after hurricanes, apparently driven by interactions with canopy species and effects of past land use.

Our studies of experimentally simulated and actual hurricane effects in LUQ 4 indicate lines of research for LUQ 5. Because the CTE revealed a potential loss of ecosystem C with increasing hurricane frequency (Sect. 2.4.2), we will conduct the second, planned canopy trimming to better understand response mechanisms. In LUQ 4, the differential effects of canopy opening on bacteria versus fungi, and the related biogeochemical responses, highlighted the crucial role of biodiversity for ecosystem function and response to change. Long-term records indicated the importance of scale and interaction of hurricanes with human disturbances on biota. Thus, we will begin integrated studies on how human and natural disturbance in terrestrial and aquatic habitats affect multiple dimensions of biodiversity (taxonomic, functional, and phylogenetic) at multiple scales over the long term (Sect. 2.4.1).

1.1.2 Climate: impacts of warming, drying, and more variable precipitation

Our work in LUQ 4 shows that climate, directly or indirectly, controls much of biotic structure and ecosystem function along an elevation gradient and that variable precipitation can have large effects on aquatic and terrestrial systems. Global climate change plus urbanization are likely to produce warmer and drier conditions and more variable precipitation in the Caribbean (van der Molen et al. 2010, Comarazamy & González 2011, Neelin et al. 2006). That trend parallels climate change (cooler-wetter to warmer-drier) from high to low elevations in the Luquillo Mountains (LM), thus providing a research gradient from which to predict responses to future climates (González et al. 2012). However, because both climate and forest type change with elevation (Barone et al. 2008), it is necessary to separate the direct effects of climate from the indirect effects of forest type on animals and ecosystem processes along the gradient. For invertebrates, we separated the effects by comparing elevation changes in population and community characteristics in plots of changing flora and unchanging flora (palm brake) with elevation. Richness of litter invertebrates (Richardson & Richardson 2012) changed little in palm plots but declined with elevation in the plots of changing flora, suggesting that differences in invertebrate communities with elevation reflect changes in the physicochemical properties of non-palm litter, not the direct effects of temperature or rainfall. In contrast, for most terrestrial gastropods (Willig et al. 2011b, 2012b), species abundances, richness, and diversity decreased with increasing elevation in both variable flora and palm plots, suggesting a dominant role for climatic effects (Willig et al. 2012b).

Drying and warming trends in the LM (van der Molen et al. 2010) will change biodiversity patterns on the elevation gradient (Laurance et al. 2011). This change may lead to extinctions of some high elevation species, as they lose the advantage of their adaptations to cool, wet habitats, and to upward shifts in the distributions of other species (Barone et al. 2008). The consequences for biogeochemistry are suggested by results of the CTE, showing connections between biota and system function, and by studies along the gradient. For example, as the microbial community shifts to domination by bacteria with increasing elevation (Cantrell et al. 2012), the development of mat-forming fungi, which speed decomposition of low-quality leaf litter (Lodge et al. 2008), decreases. Other biogeochemical changes are also expected. With soil drying we anticipate an increase in net methane and nitrous oxide consumption (Wood & Silver 2012), as soil oxygen concentrations increase and anaerobic methane and nitrous oxide production decreases (Liptzin et al. 2011). Warming will cause positive feedbacks with atmospheric CO_2, because soil CO_2 efflux appears to be sensitive to the relatively small seasonal increase in temperature in the LM (Fig. 3, Silver in prep.). The predicted increase in droughts and floods will alter stream nutrient cycling and productivity (Cross et al. 2008a, Benstead et al. 2010). The leaf litter delivered from adjacent riparian forests sustains headwater productivity, highlighting the connection between terrestrial and aquatic systems. Delivery is mediated by mat-forming, forest fungi that trap and release litter slowly and improve its nutrient content for stream organisms that depend on detrital inputs (Cross et al. 2008a, Lodge et al. 2008, Heartsill-Scalley et al. 2012). But droughts inhibit mat fungi, so that later floods deliver leaf-litter detritus in large pulses and of inferior quality, affecting both headwaters and communities downstream.

These results from LUQ 4 indicate that to detect and understand the mechanistic bases of impacts of climate change we need two approaches in LUQ 5. First, we will continue monitoring biodiversity on the elevation gradient to characterize long-term shifts in composition that affect ecosystem function. Second, we will conduct experiments on the effects of drying and variable precipitation on 1) terrestrial detrital inputs to streams and stream trophic structure and production (Sect. 2.4.1), and 2) terrestrial biogeochemistry, especially trace gas flux (Sect. 2.4.2).

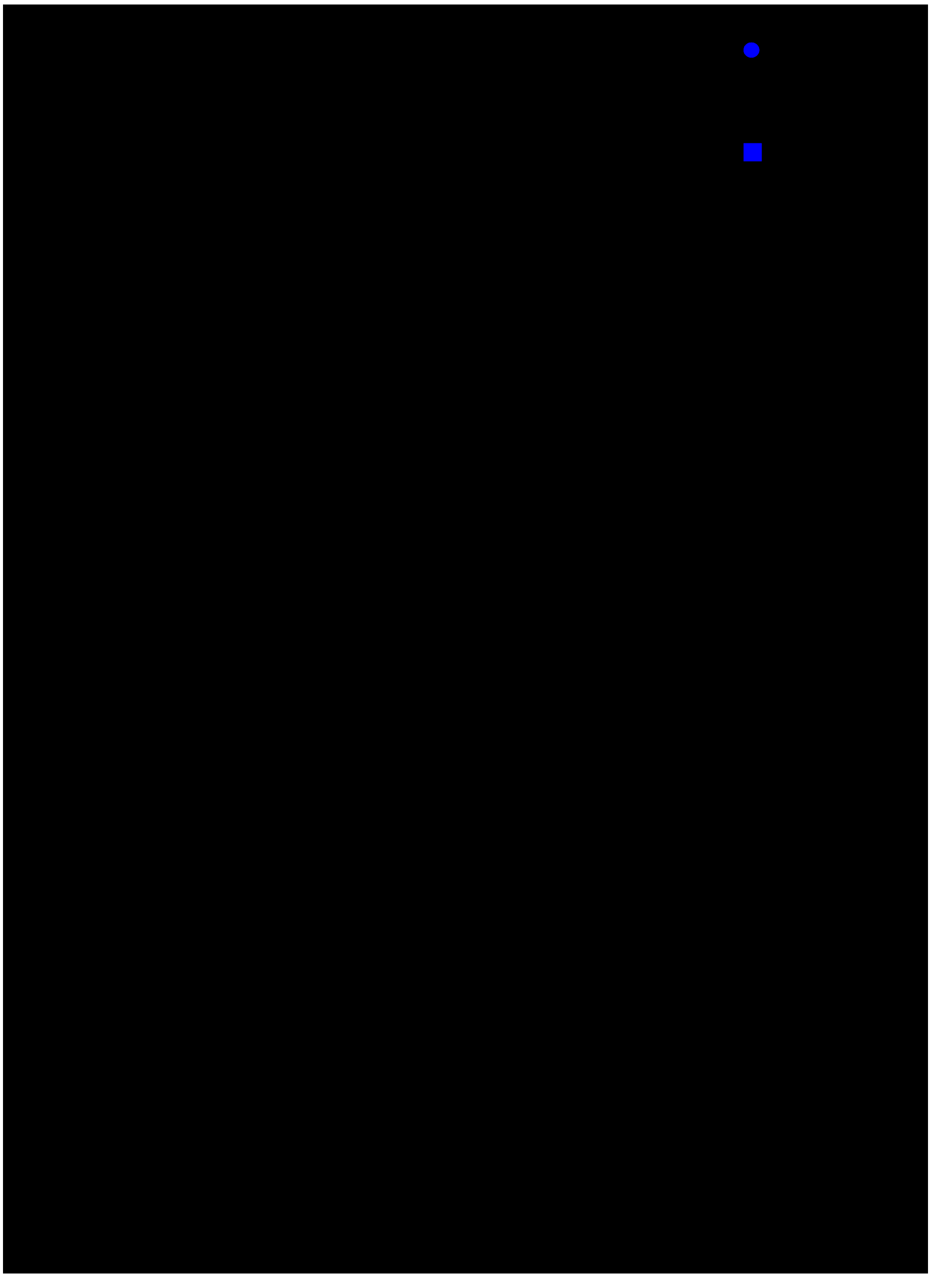

Figure 3 – Soil respiration (top) and litterfall (bottom) before, during (yellow column), and after canopy trimming and litter manipulation in the Canopy Trimming Experiment. Canopy trimming (blue rectangles, open diamonds) significantly decreased soil respiration for one year. Litterfall declined with trimming and was still significantly lower than controls almost 6 yr later.

1.1.3 Land use: impacts of land and water use

In LUQ 4 we focused on the impacts of land and water use on quantity and quality of water, and on effects of land use legacies on secondary forest. Increasing urbanization is pervasive in the tropics (UNPD 2009), including Puerto Rico (Lugo et al. 2004). Urbanization and other land and water uses have direct effects on ecosystems, and indirect effects via local climate change.

Dams and urbanization in Puerto Rico affect stream biodiversity and, consequently, biogeochemical processes in streams. Dams interrupt upstream movements of snails and shrimp that process detritus and clear benthic surfaces, helping maintain water quality (Greathouse et al. 2006b, Covich et al. 2009). Dams and water withdrawal interfere with the inter-stream connectivity of aquatic fauna that disperse from stream to stream via the ocean, which helps sustain genetic diversity of the regional stream metacommunity (Cook et al. 2008a, b, 2009). Urbanization has varied and unexpected effects on streams in Puerto Rico. Microbial and fish diversity are higher in some urban versus non-urban streams (Ramírez et al. 2009, Engman 2011, Burgos & Ramírez, in prep.). In contrast, aquatic insects are less diverse with increasing urbanization (de Jesús-Crespo & Ramírez 2011). Urban streams are solute rich, and nutrients, conductivity and dissolved organic carbon are positively related to percent urban vegetation cover (de Jesús-Crespo & Ramírez 2011). Disturbances, such as floods, play an important role in urban stream processes; detrital breakdown is more controlled by changes in flow and sediment and less by consumer activity (Engman 2011).

Due to an urban heat island effect, San Juan, Puerto Rico, is ~2 °C warmer at dawn compared to rural areas (Murphy et al. 2010). The heat island includes the city and suburbs (Fig. 4), which continue to encroach on the LM. A heat island can raise cloud levels and reduce rainfall, which may be compounded by regional drying and by forest clearing in the lowlands that affects onshore winds and reduces rainfall in the LM (van der Molen et al. 2010). While drying has the obvious effect of reducing water supply, our work in LUQ 4 shows that drying also has negative effects on stream biota (Covich et al. 2003, 2006, 2009), with consequent effects on water quality, compounded by dams that alter faunal distributions as well.

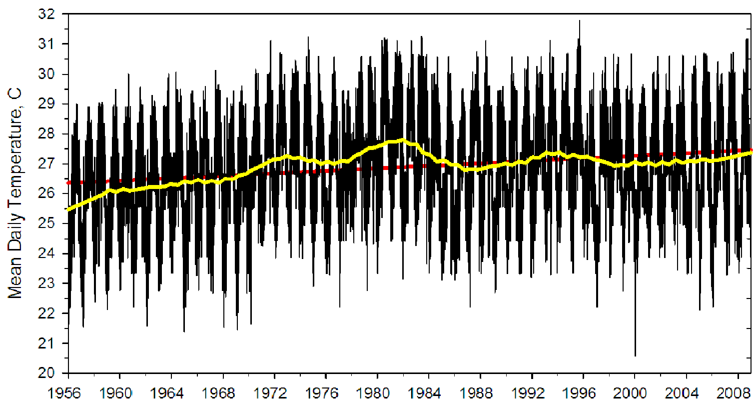

Figure 4 – Mean daily temperature at San Juan International Airport, 1956-2009. Running average (yellow) and linear regression (red) are shown. (Data from NOAA)

In LUQ 4 we also continued to study how past land use interacts with other disturbances to shape forest species composition. This is important in widespread tropical landscapes that are increasingly characterized by secondary forests (Lugo & Helmer 2004, Bloch et al. 2007, Willig et al. 2007, Uriarte et al. 2010a). Effects of past land use interacting with natural disturbance are striking in the Luquillo Forest Dynamics Plot (LFDP). Research in the 16-ha LFDP has continued for 22 yr and included identifying and mapping ~150,000 tree stems to document rates of change in species growth and survival over time. Our SORTIE-PR model explores how hurricanes, land use legacies, phylogenetic relationships, and life history traits of tree species determine forest composition and resilience (Swenson et al. 2006, 2007, Flynn et al. 2010, Kress et al. 2010). Both hurricane intensity and frequency affect forest composition, while past land use differs across the 16-ha plot and produces novel communities with distinctive dynamics (Comita et al. 2009, 2010, Uriarte et al. 2004, 2009, Canham et al. 2010, Zimmerman et al. 2010).

Our work in LUQ 4 on stream ecology, water use and urbanization indicates research directions for LUQ 5. The effects of dams and water withdrawal, coupled with effects of drying and more variable precipitation, on river connectivity and water quality, indicate the need to continue study of how interacting natural and human disturbances affect stream biodiversity, biogeochemistry and water quality (Sect. 2.4.3). The documented effects of urbanization and land use on streams and forest composition indicate the value of taking advantage of plans for highway building and urban development near El Yunque National Forest to study long-term impacts (Sect. 2.4.3).

1.2 LUQ 4 RESULTS AND LUQ 5 DIRECTIONS

Changing hurricane regime, more variable precipitation, and increased land and water use will continue to affect Puerto Rico and other parts of the tropics. Our long-term observations and results from LUQ 4 have revealed how these trends affect biodiversity, biogeochemistry, their interactions, and a critical ecosystem product – water quantity and quality. In LUQ 5 we will continue observations of biodiversity and biogeochemistry to determine long-term trends as the basis for long-term field experiments and projects designed to identify the mechanisms and consequences of the main drivers of long-term change. These efforts include the Canopy Trimming Experiment, to study how changing hurricane regime affects C balance, new field experiments on how increasing variability of precipitation affects aquatic and terrestrial systems, and a new, long-term project on the effects of a four-lane highway under construction near the LM on forests, streams, and water quality. This research will be done in a framework that comprises the cumulative and interacting effects of episodic events (pulses), typically caused by natural disturbances, and long-term disturbances (presses), typically caused by humans. Our research will incorporate local and global drivers, at multiple scales. For example, local and global influences will be incorporated into a new, landscape-level model that links changes in water quality and quantity to physical, biological and socioeconomic drivers (Uriarte et al. 2011).

1.3 RESULTS FROM SUPPLEMENTAL FUNDING

We used supplemental funds during LUQ 4 (total $543,664) for Schoolyard LTER, Research Experience for Undergraduates (REU) and Research Experience for Teachers (RET); international research; network-level activities in IM and landscape studies; and research equipment and sample analyses. The Schoolyard LTER program included workshops for students and teachers at El Verde Field Station on field data collection and computer analyses, a teaching website (Sect. 1.5), and research symposia for students and teachers. LUQ REU and RET involved nine students and three teachers (one from Puerto Rico, two from mainland US) studying stream and forest ecology. International research included two workshops on comparing results and standardizing methods for research on hurricane effects, held in Mexico and Florida. A supplement supported an LTER Network-level workshop on incorporating social science into LTER, attended by representatives from 20 LTER sites (Zimmerman et al. 2009). Using supplemental funds, LUQ participated in a cross-site LTER study of land-cover and land-use change and in Network-level IM efforts on managing sensor data, incorporating GIS into IM, and improving EML with DRUPAL. Supplemental funds also paid for meteorological, stream sampling, laboratory, and computer equipment and for sample analyses.

1.4 SYNTHESIS ACHIEVEMENTS AND PUBLICATIONS

The 24 yr of LUQ have given us a commanding perspective on tropical ecology, resulting in many synthetic works in LUQ 4. Our site synthesis book comprises chapters whose content ranges from theory to management, and that reflect our long-term research on the responses of tropical systems to a changing disturbance regime (Brokaw et al. 2012a, proofs at: http://luq.lternet.edu/sites/default/files/2012LUQLTERbook.pdf). Harris et al. (2012) also summarize LUQ research. Other synthetic books and papers largely from LUQ cover tropical elevation gradients (González et al. 2012), post-agricultural succession (Myster 2008), hurricanes (Lugo 2008), and landslides (Restrepo et al. 2009). Synthetic works inspired by LUQ c ecological theory (Scheiner & Willig 2011), forest dynamics (Zimmerman et al. 2008, Uriarte et al. 2009, 2012), carbon-nutrient-climate relationships (Cleveland et al. 2011), redox drivers of biogeochemical cycling (Burgin et al. 2011), island ecology (Walker & Bellingham 2011), cloud forests (Bruijnzeel et al. 2010), ferns (Mehltreter et al. 2010), tropical stream ecology (Heartsill-Scalley et al. 2001, Boulton et al. 2010), earthworm ecology (Sastre-De Jesús & González 2006), insect ecology (Schowalter 2006), restoration (Walker et al. 2007), and environmental disasters (del Moral & Walker 2007, Lundquist et al. 2011). LUQ also contributed to syntheses of LTER Network contributions (Crowl et al. 2008, Hopkinson et al. 2008, Jones et al. 2012, Robertson et al. 2012) and of long-term trends (Peters et al. 2012). Among the 269 peer-reviewed and 65 other LUQ publications appearing in the last six yr, the 10 most important (underlined in text) are those that report important results and guide future research.

1.5 BROADER IMPACTS

In the last six yr 58 graduate and 88 undergraduate students have been involved in LUQ. During LUQ 4 we leveraged $19,327,345 (grant totals) for 31 research and education projects related to LUQ, including a recent NSF Macrosystem Biology project on warming and biodiversity (J. Brown, R. Waide). Our Schoolyard LTER program reached 1050 students in Puerto Rican high schools and 954 teachers and 1662 students via our interactive teaching website *Journey to El Yunque* (http://elyunque.net/journey.html). The leveraged funds included a $1,100,000 grant from the US Dept. of Education for an ongoing evaluation of how *Journey to El Yunque* affects motivation and learning. Since 2006 a site REU program based at El Verde Field Station, and strongly connected to LUQ, has involved 56 students, 55% of whom represent minorities, and produced 12 publications, eight with the student as first author. The Luquillo Forest Dynamics Plot, the CTE, and other LUQ field projects have been supported by volunteer internships for recently graduated students seeking experience in tropical research. Sixty students participated during LUQ 4 (more than half women and 35% minorities), and many have gone on to pursue academic studies. Our outstanding broader impact is that, in just the past six yr, LUQ scientists have led the establishment of NEON/STREON (Lugo, McDowell), ULTRA-Ex (Lugo), IGERT (Brokaw), and CZO (Scatena) sites (full names Sect. 2.3.4) in Puerto Rico. These programs strongly complement LUQ research and create a unique, broad, and strong synergy for ecological science in the tropics.

Section 2 Proposed Research

2.1 INTRODUCTION

The Luquillo Long Term Ecological Research Program addresses changing ecosystems and services in the tropics by developing ecological understanding and management recommendations that are based on long-term observations, experiments, and synthesis (March et al. 2003, Walker et al. 2007, Shiels et al. 2010, Brokaw et al. 2012a, Lugo et al. 2012a, b, Willig et al. 2012a). Results from LUQ have improved our fundamental understanding of tropical ecosystems and disturbance dynamics and provided an important foundation to anticipate the long-term effects of change associated with natural events and anthropogenic activities. Tropical ecosystems are characterized by high diversity, large plant and soil carbon pools, and the highest rates globally of net primary productivity (Sitch et al. 2003) and respiration (Raich & Schlesinger 1992), and they are key sources and sinks of greenhouse gases (Matson & Vitousek 1990, Bousquet et al. 2011). Land use, urbanization, and climate change are transforming the tropical forest biome and have the potential to significantly decrease biodiversity, lower ecosystem carbon storage, and alter biogeochemical cycling (Grau et al. 2003, Aide & Grau 2004, Lugo & Helmer 2004, Laurance & Peres 2006, Terborgh 2007, Asner et al. 2009). The interacting, long-term impacts of human-mediated disturbances are producing ecosystems with no previous analog and are threatening key ecosystem services such as potable water (MES 2005). A fundamental task for ecologists is to better predict the impacts of local, regional, and global perturbations on biodiversity and biogeochemistry in tropical forests (Clark et al. 2001, Smith 2011). Therefore, in LUQ 5 we will build on our research history to ask:

> *How do long-term changes in climate and land use interact with other disturbances to affect biodiversity, biogeochemistry, and their interactions to determine ecosystem services in northeast Puerto Rico?*

The Luquillo LTER program began in 1988 with a focus on the effects of natural disturbances on the population, community, and ecosystem ecology of mid-elevation forests and streams in the Luquillo Mountains (LM) of northeastern Puerto Rico. During successive research phases, LUQ expanded its studies to include higher and lower elevations in the LM and extended beyond the forest boundaries into the suburbs and city of San Juan, a metropolitan area of 1,300,000 inhabitants located within 25 km of the LM. The early phases of research revealed how forests and streams of the LM respond with remarkable resilience (return to pre-disturbance conditions) to natural, pulse disturbances (Sect. 2.2) such as hurricanes, landslides, and floods (Walker et al. 1991, 1996, Zimmerman et al. 1996, Schaefer et al. 2000, Beard et al. 2005, Brokaw et al. 2012a). These pulse disturbances alter ecosystem structure and function, but the return to pre-disturbance conditions is typically rapid (Zimmerman et al. 1996, Brokaw et al. 2012b). By contrast, more recent work suggests that press disturbances, such as climate and land use change, may cause enduring changes in ecosystems and their services, with potential negative effects on societal wellbeing (Lugo & Helmer 2004, Peters et al. 2007, Marin-Spiotta et al. 2007, Ramírez et al. 2009, Murphy et al. 2010, Potter et al. 2010). Results of LUQ research that have contributed significantly to understanding of environmental change are:

- The frequency of drought and inter-annual variation in rainfall are increasing in the Caribbean (Comarazamy & González 2011). Drought is likely to decrease soil respiration and phosphorus (P) availability in tropical forests (Wood & Silver 2012).
- Nitrogen availability and greenhouse gas emissions are affected by DRNA and Feammox, which are novel nitrogen cycling pathways in terrestrial ecosystems (Silver et al. 2001, Pett-Ridge et al. 2006, Templer et al. 2008).
- Changing rainfall and rates of N deposition affect the way N is cycled and feeds back to soil nutrient availability, greenhouse gas fluxes, and water quality (Ortiz-Zayas et al. 2005, Cusack et al. 2010, McDowell et al. 2012).
- <u>Carbon cycling in LM forests is highly sensitive to climate. Small increases in temperature can decrease the ability of tropical forests to store carbon</u> (Silver et al. in prep.).

- Leaf litter decomposition in the LM is among the fastest observed globally in both forests and streams (González & Seastedt 2001, Crowl et al. 2006, Parton et al. 2007, Cusack et al. 2009). Detritus is a main energy source for higher trophic levels (Lodge 1996, McDowell et al. 2012).
- Although hurricane-produced debris is substantial, decomposition, nutrient export, and trace gas emissions after hurricanes change only briefly (Silver et al. in prep), as rapid regrowth reasserts control over most ecosystem processes within 1-2 yr (Scatena et al. 1996).
- Patterns in biodiversity affect responses to disturbance and ecosystem processes by minimizing physical impacts, providing residual species pools, and enhancing nutrient and biomass turnover (Silver et al. 1996, Crowl et al. 2012).
- Organisms of the LM are more resilient after natural than human disturbances (Brokaw et al. 2012b).

Puerto Rico's natural disturbance regime (Scatena et al. 2012), socio-economic situation (Grau et al. 2003), land use dynamics, and land use and elevation gradients (Fig. 5) make the

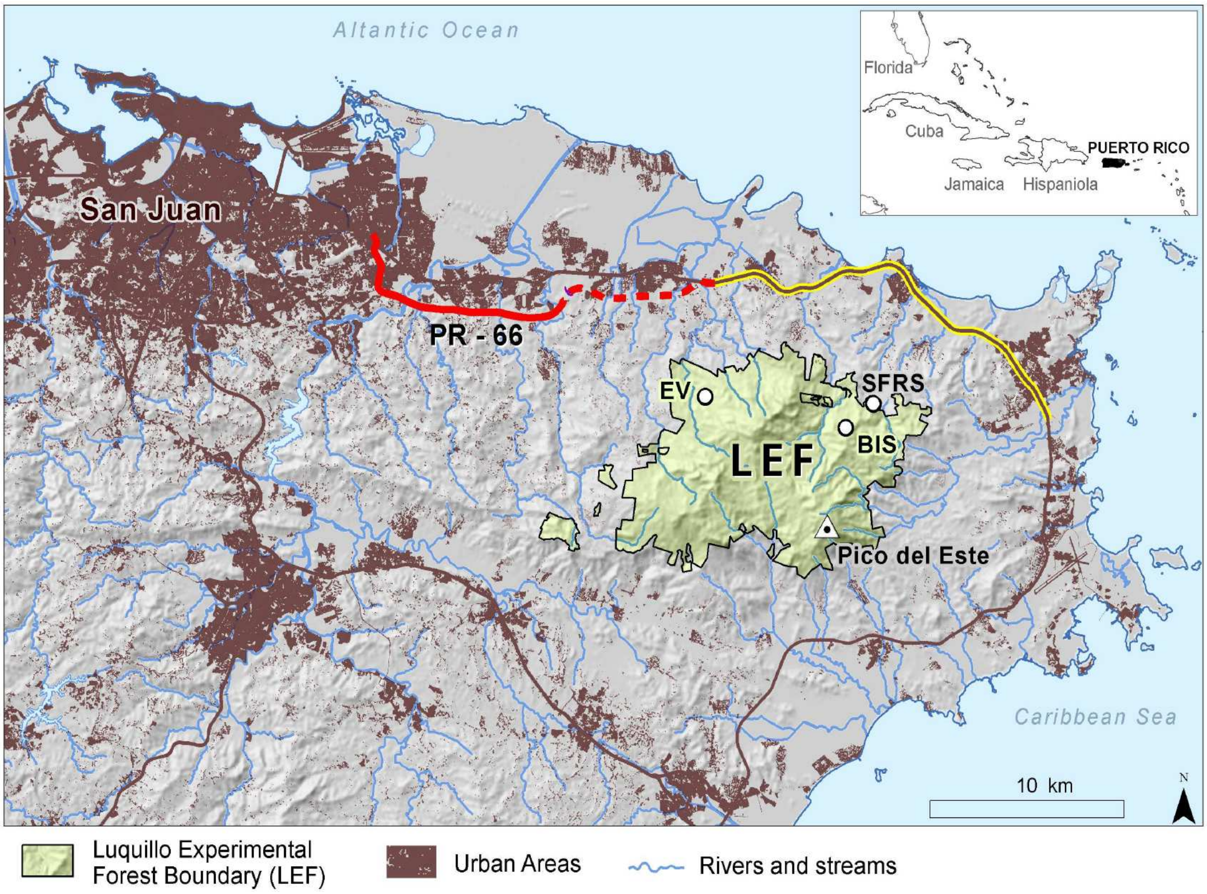

Figure 5 – Northeastern Puerto Rico, with main LUQ study sites highlighted. LEF = Luquillo Experimental Forest in the Luquillo Mountains. The LEF is coterminous with El Yunque National Forest, a unit in the U.S. National Forest System. EV = El Verde Field Station; SFRS = Sabana Field Research Station; BIS = Bisley Experimental Watersheds; PR-66 is Puerto Rico Route 66, showing road segments that are existing (filled red), under construction (dashed red), and planned (yellow). Pico del Este is 1051 m asl. (Map by Olga Ramos)

island an excellent laboratory for study of the interactions between natural, pulse disturbances and long-term, typically human-caused, press disturbances and climate change. The Caribbean and large areas of the tropics are undergoing similar social, economic, and ecosystem changes (Asner et al. 2009). Thus LUQ research addresses local, regional, and global environmental issues. To carry this research forward LUQ 5 builds on the many long-term data sets that have been synthesized in LUQ 4 (Table 1, Sect. 1.4); it enters a synergy among LUQ and programs in Puerto Rico representing four other research networks (Sect. 2.3.4); and it will continue one long-term, large-scale field experiment, launch two new field experiments, and begin a long-term, landscape project. Each of these projects is designed to reveal the mechanisms and consequences of key, long-term drivers of change in the tropics: 1) increased hurricane frequency or intensity, 2) greater variability of rainfall, and 3) accelerating land use change. Four of the six main projects in LUQ 5 focus on water, as a key ecosystem component and important ecosystem product.

2.2 CONCEPTUAL FRAMEWORK

Our conceptual framework, developed over 24 yr of LUQ and founded on decades of previous work (Odum & Pigeon 1970, Reagan & Waide 1996, Lugo et al. 2012b), integrates scales of natural and anthropogenic disturbance and response. In the LM, short-term ecosystem changes are typically caused by episodic, natural disturbances such as hurricanes, droughts or landslides (Zimmerman et al. 1996), corresponding to *pulse disturbances* (Ives & Carpenter 2007, Collins et al. 2012, Waide & Willig 2012). Long-term changes are typically caused by anthropogenic drivers associated with climate, land use, or water use (Pringle 2000, Murphy et al. 2010, van der Molen et al. 2010). These long-term drivers correspond to *press disturbances*. We define a pulse disturbance as a discrete event in time that is of relatively short duration. In contrast, a press disturbance is an event of longer duration that is directional and continuous in nature. Some disturbances have both direct and indirect manifestations that may be pulses or presses. For example, a direct manifestation of increased CO_2 emissions is a gradual increase in atmospheric temperature (press disturbance) but an indirect manifestation is an increase in the frequency of intense hurricanes (pulse disturbances) arising from increased temperature interacting with oceanic and atmospheric circulation patterns (Knutson et al. 2010). The responses of ecosystems to disturbance can be described by *resistance* – the extent to which system attributes are unaffected by the disturbance; *resilience* – the rapidity with which a system returns to pre-disturbance conditions; and *vulnerability* – the likelihood that the system will not return to pre-disturbance conditions (Carpenter et al. 2001, Waide & Willig 2012).

The LUQ conceptual framework has evolved from an initial emphasis on pulse-driven patch dynamics (Levin & Paine 1974, Waide & Lugo 1992, Lugo & Waide 1993, Lodge et al. 1994) to a broader model incorporating both pulse- and press-driven dynamics (Peters et al. 2011, Waide & Willig 2012), with a long-term focus on the vulnerability of ecosystems and their services. The concepts that frame research in LUQ 5 (Fig. 1) are expressed in three, sequenced points:

1. Pulse disturbances drive short-term changes, characterized by high ecosystem resilience with respect to aspects of biodiversity and biogeochemistry.
2. Press disturbances interact with pulse disturbances to drive long-term changes, characterized by low ecosystem resilience and possible vulnerability of biodiversity, biogeochemistry, and ecosystem services.
3. To foresee change and vulnerability of ecosystems and their services, we must understand how press and pulse disturbances interact and affect the responses of biodiversity and

biogeochemistry (including their interactions) at short- and long-term temporal scales and at multiple spatial scales.

The first of these points, regarding short-term change in response to natural, pulse disturbance, is clearly illustrated with LUQ results at the level of populations, communities, and biogeochemical processes (Brokaw et al. 2012b). These results include the degree of resilience of forest tree species composition, terrestrial invertebrate populations, litterfall, and stream chemistry after hurricanes (Zimmerman et al. 1994, 2010, Schaefer et al. 2000, Bloch & Willig 2007, Willig et al. 2007, 2011a); of freshwater shrimp populations after floods and droughts (Covich & Crowl 2002, Covich et al. 2006); and of forest succession after landslides (Zarin & Johnson 1995).

Long-term observations supply examples of the second point: interactions between pulse and press. The pioneer tree *Cecropia schreberiana* showed high resilience by recruiting abundantly in response to canopy opening (pulse) by a hurricane in 1989 (Zimmerman et al. 1994, Brokaw 1998), suggesting that it would be more common with more hurricanes (O'Brien et al. 1992). But after a second strong hurricane 9 yr later, *Cecropia* recruitment was low, likely due to a dense understory that developed after the first storm and inhibited establishment. More frequent hurricanes (interacting pulse and press) might produce low, dense vegetation with few storm-created gaps and few *Cecropia*, because its resilience mechanism, gap colonization, is thwarted. In streams, a consequence of more frequent and longer droughts (interacting pulse and press) is greater water extraction (press) for potable water supplies, which kills migratory shrimps and fishes (Crook et al. 2009) and reduces water quality and genetic resources.

The third point, that long-term observations and experiments are needed to document continuing, interacting pulse and press disturbances and their long-term, cumulative impacts is supported by the above examples and many other results (Willig & Walker 1999, Brokaw et al. 2012b). Thus LUQ 5 will continue documenting these interactions, while carrying out experiments to elucidate mechanisms.

2.3 RESEARCH APPROACHES

LUQ 5 research will take place in the LM and adjacent areas of northeast Puerto Rico (Fig. 5, Harris et al. 2012, McDowell et al. 2012). Work in the LM focuses on mid-elevation sites at El Verde Research Area and Bisley Experimental Watersheds and along elevation transects from sea level to LM peaks (Fig. 5). Our studies also extend along the present and projected route of a four-lane highway that cuts across the base of the mountains, and from old growth forest into the metropolitan area of San Juan. LUQ 5 research on long-term environmental change includes four integrated approaches: 1) long-term observations of change in time, 2) gradient studies of change in space, 3) experiments to understand mechanisms of change, and 4) synthesis and modeling to generalize and extend results. The main features of major established studies are given below; new projects are described in more detail in Section 2.4 (with more detail at: http://luq.lternet.edu/research/projects). LUQ research is conducted by 29 Senior Personnel (http://luq.lternet.edu/people/luq5researchers). Project teams are listed in parentheses, leader named first, after each hypothesis in Section 2.4.

2.3.1 Long-term measurements – The core research of LUQ includes long-term measurements of abiotic and biotic characteristics designed to reveal dynamics in space and time (Table 1). Many long-term measurements are from forest plots and stream reaches at El Verde or Bisley and along the elevation gradient in the LM (Covich et al. 2009, Heartsill-Scalley et al. 2010, Willig et al. 2011b). The Luquillo Forest Dynamics Plot (LFDP) covers 16 ha of mid-elevation forest, in which c. 150,000 individual trees and shrubs ≥ 1.0 cm dbh of 140 species (accumulated totals of tree and species) and several animal groups (e.g., gastropods, birds) have been censused for up to 22 yr (Willig et al. 2007, Zimmerman et al. 2008, 2010, Uriarte et al. 2010b). The LFDP is part of the Center for Tropical Forest Science (CTFS) global network of 42 large, long-term forest plots, the source of many syntheses describing global patterns in tropical forests (e.g., Losos & Leigh 2004, Wills et al. 2006).

Table 1 – Long-term monitoring in LUQ. B = Bisley, E = El Verde, L = landslides, LM = other site in the Luquillo Mountains, P = Pico del Este. Complete list at: http://luq.lternet.edu/data

MEASURE	INITIATION	SITE	FREQUENCY
Meteorology			
Rainfall	1975, 1988, 1993, 2002	E, B, P, LM	hourly, daily
Temperature (air and soil)	1975, 1988, 1993, 1997, 2002	E, B, P, LM	hourly, daily
Humidity, wind speed and direction	1995, 1993, 2002	B, E, P, LM	hourly, daily
Light (PAR, total radiation, albedo)	1995 1993	E, B, P, LM	hourly, daily
Hydrology			
Stream discharge	1983, 1987	B, LM	daily
Throughfall	1988	B, LM	daily, weekly
Chemistry			
Rain	1983, 1988, 2010	E, B, P	weekly, bulk and wet only
Throughfall	1988	B	weekly
Streamwater	1983, 1988	B, E, LM	weekly at 9 sites
Groundwater	1988	B, LM	weekly to periodic
Soil (O_2, trace gas flux, solution)	2003	E	monthly
Microbes			
Fungal mats	1983	B, E, LM	periodic
Fatty Acids (EL-FAME)	2002-2006	E	every 4 months
Plants			
Algae (stream) standing crop	2002	E, B	twice yearly
Forest structure, biomass, composition	1988, 1993	B, E, LM	1-5 yr intervals
Biomass	2006	E	yearly
Tree species composition	2003	E	yearly
Canopy structure	1989	E, B, EP	every 3 yr
Leaf area index	1989	E, B	every 3 yr
Coarse wood distribution	2002	B	every 3 yr
Seedling dynamics	1992, 2003	B, E	monthly, every 3 yr
Flowering phenology	1992	B, E	weekly to monthly
Herbivory	2002	E	yearly
Litterfall, litter decomposition	1987, 1990, 1994, 1996, 2005	B, E, L, P, LM	weekly, yearly, every 3 yr
Landslide revegetation	1988	LM	yearly
Abandoned pasture revegetation	1998	LM	yearly
Understory structure & composition	1988, 1991, 1993, 2003	E, P	yearly
Animals			
Invertebrates (several)	1991, 2002	E, P, LM	yearly
Arthropods (scorpions, shrimps, spiders, walking sticks)	1988, 1991	E	yearly
Gastropods (snails)	1991	E	yearly
Birds	1989	E	yearly
Frogs	1987		yearly
Disturbance			
Treefall gaps, landslides, stream channel change	1988	B, E, LM	yearly to periodic

2.3.2 Gradient studies – LUQ conducts studies along both elevation (a qualified proxy for climatic variation) and land use gradients (Fig. 5, Table 1). The LM present a gradient of climate and vegetation change that extends through four ecological life zones and forest types. These forest types include *tabonuco* forest (up to 600 m asl), *colorado* forest (600-900 m), *elfin* forest (900-1074 m), and *palm* forest at all higher elevations. Rainfall rises from 2450 mm yr^{-1} at lower elevations to 5000 mm yr^{-1} at higher elevations (Brown et al. 1983, McDowell et al. 2012). Mean annual temperature is about 5 ˚C warmer in the lowlands than on the peaks (McDowell et al. 2012). During LUQ 3, we established the Long-Term Elevation Plots, a series of study plots at intervals of 50 m elevation in two watersheds within the LM and an extended set of plots from sea level to mountain peaks (Gould et al. 2006, Barone et al. 2008, González et al. 2012). We also study the strong land use gradient along the 23 km from the fully protected, 11,000-ha El Yunque National Forest (in the LM) into San Juan (Fig. 5). At the urban end of the gradient, our work is complemented by research of San Juan ULTRA-Ex (Urban Long-Term Ecological Research Areas) and the University of Puerto Rico's IGERT (Integrative Graduate Education and Research Traineeship) Program, the latter supporting students working on "Natural-Human Systems in the Urbanizing Tropics". LUQ has a strong leadership role in these programs.

2.3.3 Experiments and landscape project – LUQ 5 includes one ongoing and two new field experiments, as well as a new landscape study. These projects are designed to reveal and quantify the mechanisms and consequences of the key drivers of long-term change in Puerto Rico: hurricane regime, variability of precipitation, and land use.

<u>Change in hurricane regime</u> – *The Canopy Trimming Experiment* (CTE) is a continuing, long-term field experiment that evaluates the effects of a change in hurricane regime on tabonuco forest biodiversity and biogeochemistry (Richardson et al. 2010, Shiels et al. 2010). The experiment began in 2004 and will extend at least 20 yr. The experiment simulates the two main direct effects of a hurricane: the removal of forest canopy (change in microclimate) and the consequent deposition of detritus on the forest floor (change in nutrient dynamics). The first set of treatments was designed to distinguish these effects from each other, using a 2 x 2 factorial design-with four treatments, each covering a 30 x 30 m area, in each of three blocks. The treatments were (Fig. 6): A) canopy not trimmed and no canopy biomass added to forest floor, as a reference, B) canopy not trimmed, but canopy biomass from a trimmed plot distributed on the forest floor, to simulate the changes in redistribution of biomass created by the hurricane but without the associated change in microclimate, C) canopy

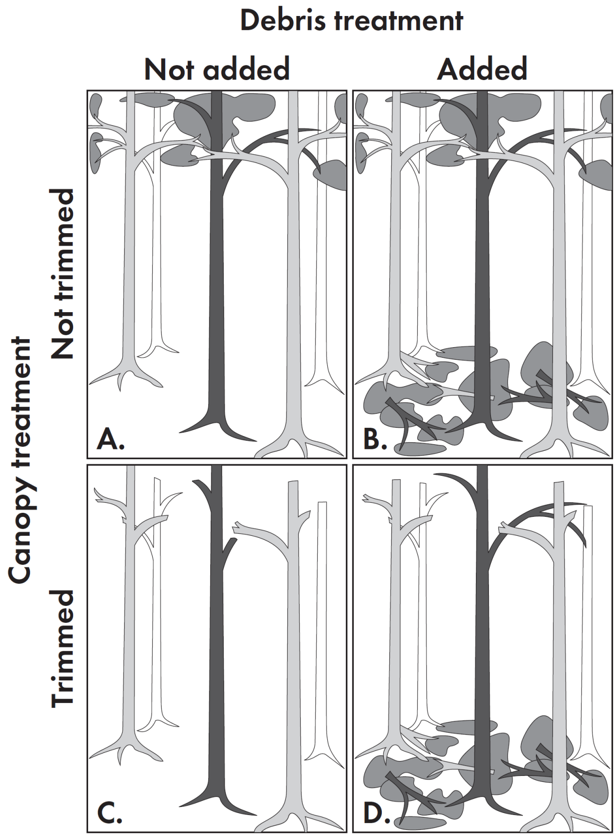

Figure 6 – Experimental manipulations in the CTE, which simulates hurricane impacts on tropical forest structure and function (see text). (Willig et al. 2012b)

trimmed, with trimmed detritus removed from the plot, to simulate changes in microclimate created by the hurricane but without the associated redistribution of biomass, and D) canopy trimmed, with trimmed detritus distributed on the forest floor, to change both microclimate and distribution of biomass. Measurements in the CTE began one yr before treatments were applied and have continued at variable intervals, depending on the identity of monitored characteristics. Measurements include microclimate, soil and soil solution nutrients, trace gas fluxes, litter inputs and decomposition, and dynamics of microbial, plant, and animal communities. Because we will repeat treatment D and measurements in the control (treatment A) during LUQ 5 and again in later years, the CTE will also assess the effects of an increase in hurricane frequency (Royer et al. 1998) and will test long-term predictions of the CENTURY model for soil organic matter accumulation and nutrient dynamics in tabonuco forest (Sanford et al. 1991, Zimmerman et al. 1995, Johnson et al. 2011).

Change in variability of precipitation and reduced detrital inputs to streams – *The Litter Exclusion Stream Experiment* is a new field experiment that will explore the effects of reduced terrestrial detrital inputs to streams. Litter inputs are expected to change due to a predicted increased variation in precipitation and are expected to affect trophic dynamics and water quality (Sect. 1.1.2). Fundamentally, the experiment tests the idea that trophic relations in headwater streams are driven by energy from detrital inputs rather than by algal primary production (details in Sect. 2.4.1, Hypothesis 1.4). This experiment will extend at least 10 yr.

Change in variability of precipitation (drying) – *The Throughfall Manipulation Experiment* is a new field experiment that tests the effects of predicted more variable rainfall and climatic drying on biogeochemical fluxes (details in Sect. 2.4.2, Hypothesis 2.2). This experiment is will extend 6 to 10 yr.

Change in land use – *The Landscape Project* is a new, long-term (~20 yr) field project that quantifies the effects of urbanization (highway construction and subsequent development) on terrestrial and aquatic biodiversity, biogeochemistry, and ecosystem services (details in Sect. 2.4.3, Hypothesis 3.2). This project integrates, and tests predictions based on LUQ research and will be a basis for long-term study of land use effects over the next LUQ research cycles.

2.3.4 Cross-site and cross-network research – Important efforts by LUQ are cross-site and cross-network research. LUQ contributes to cross-site, Network-level databases on climate and hydrology (ClimDB, HydroDB, StreamchemDB). Cross-site studies have included participation in LIDET (Long-term Intersite Decomposition Experiment Team), LINX (Lotic Intersite Nitrogen eXperiment), and CTFS (Sect. 2.3.1). Cross-network collaborations are conducted with NEON (National Ecological Observatory Network), STREON (Stream Experimental and Observatory Network), LCZO (Luquillo Critical Zone Observatory), IGERT, and San Juan ULTRA-Ex. These programs are discussed where relevant in the research plans (Sect. 2.4). LUQ is a member of NeoSelvas and Cloud Forest Research Coordination Networks (RCN).

2.3.5 Models – LUQ uses conceptual, system, statistical, and process/mechanism models to guide and extend our research. Much of LUQ 5 is based on the conceptual models we have developed since LUQ 1 and described in our synthesis book and elsewhere (Willig & Walker 1999, Willig et al. 2007, Crowl et al. 2012, Waide & Willig 2012). These models focus on the interactions of disturbance, biodiversity, biogeochemistry, and ecosystem services (Fig. 1). We also use process ecosystem models to test hypotheses and extend observations, for example, the CENTURY model to understand the watershed-scale distribution of soil carbon (Johnson et al. 2011) and effects of hurricane-generated coarse woody debris on nutrient cycling (Zimmerman et al. 1995). Topoclim (http://www.esf.edu/luq/climate/) is our spatially-explicit model of climate in the LM, and is the basis for process models of soil carbon (Wang et al. 2002a, b) and the distribution of evapotranspiration (Wu et al. 2006). These climate models are also used by LCZO to understand the influence of climate on soil development, and will be used in LUQ 5 to understand environmental drivers along the LM climate gradient. Ongoing modeling efforts in LUQ 5 include a landscape model of water provisioning (Uriarte et al. 2011), and statistical models to evaluate the influence of natural and anthropogenic drivers on forest dynamics (SORTIE-PR, Uriarte et al. 2004, 2009) and on biodiversity, populations, and communities of aquatic and terrestrial organisms (Willig et al. 2007, Hein et al. 2010, Prates et al. 2010).

2.4 RESEARCH PLAN

We apply the approaches above to answer our overarching question: *How do long-term changes in climate and land use interact with other disturbances to affect biodiversity, biogeochemistry, and their interactions to determine ecosystem services in northeast Puerto*

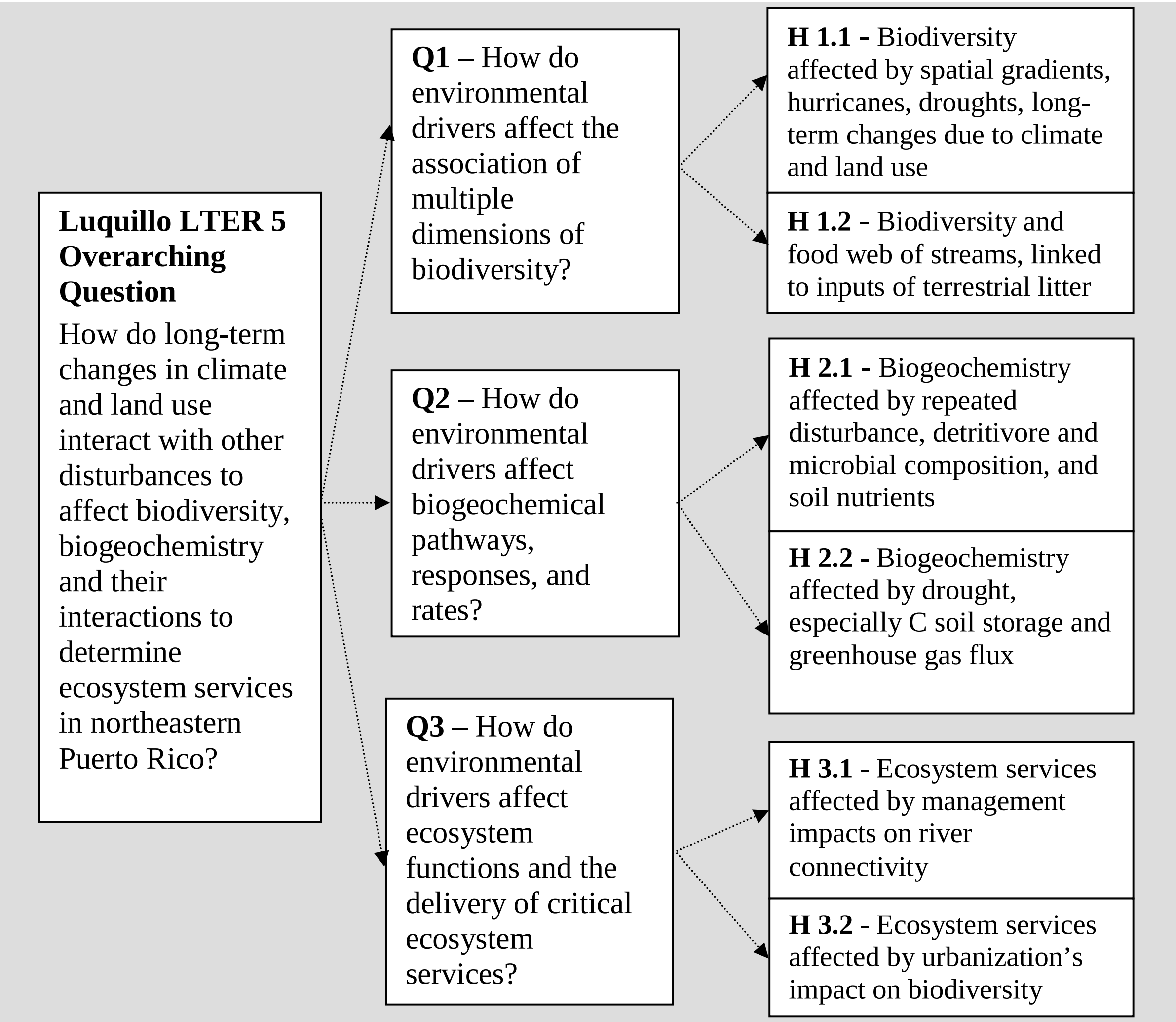

Figure 7 – LUQ 5 Program Framework, showing the logical progression from overarching question to focal questions (Q) to hypotheses (H) and projects.

Rico? LUQ 5 embodies a coherent progression from this question to three focal research questions and six hypotheses and associated projects (Fig. 7) that address long-term changes in biodiversity (Sect. 2.4.1) and biogeochemistry (Sect. 2.4.2) and how changes in the two interact with each other and affect ecosystem services (Sect. 2.4.3). Water is an integrating theme in LUQ 5 (Fig. 8). It is a driver, in the form of predicted changing rainfall and as a manipulated variable in five of our six hypotheses and associated questions, and it is a response variable, important in ecosystem function and as an ecosystem product, in four hypotheses.

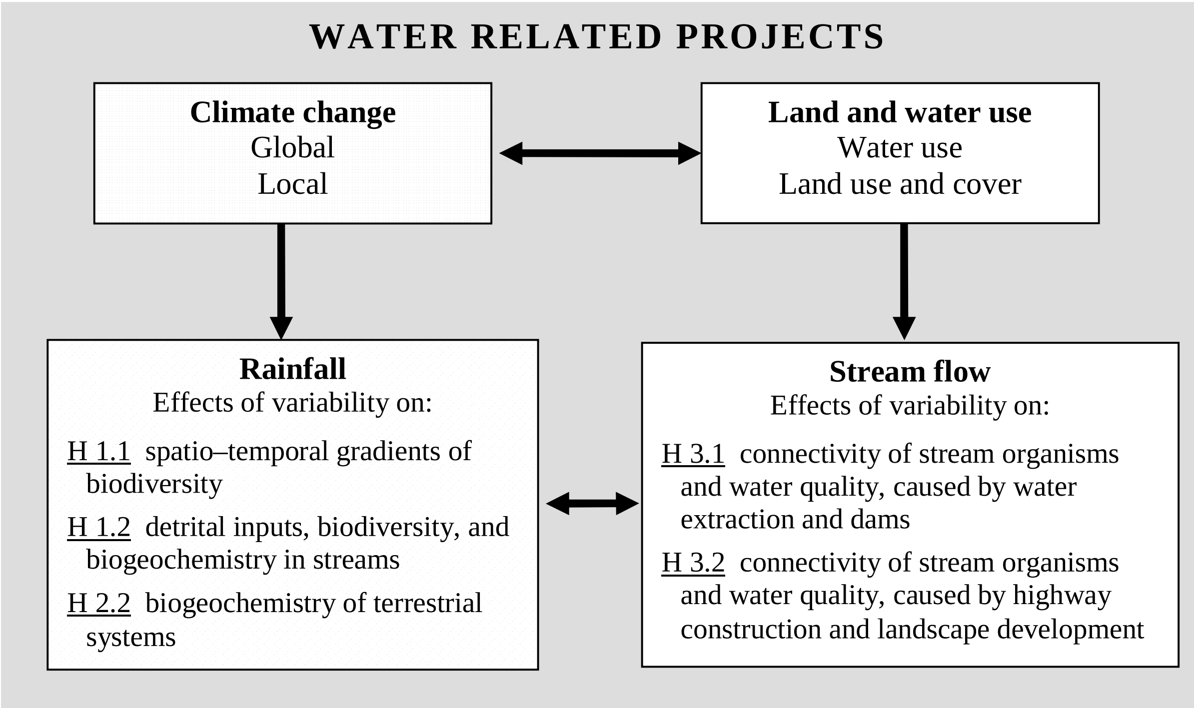

Figure 8 – Water is a unifying topic in LUQ 5. In the LM, two main drivers change water quantity, variability, and quality. **Climate change**, both global and local, affects the quantity and variability of **rainfall**, which, in turn, affects biodiversity, biogeochemistry, and their interactions (Fig. 1) in linked aquatic and terrestrial systems. These processes are addressed in Hypotheses (H) 1.1, 1.2, and 2.2 and associated projects (Sect. 2.4). **Land and water use** by humans affects **stream flow**, which, in turn, affects connectivity (see text) of stream organisms and water quality. These processes are addressed in Hypotheses 3.1 and 3.2 and associated projects (Sect. 2.4). The direct effects of climate change on rainfall, and of land and water use on stream flow, have indirect effects on biodiversity, biogeochemistry, their interactions and ecosystem products. Other indirect effects and interactions are implicit in the diagram. Hurricanes have pulse effects on rainfall and stream flow, which we detect in long-term observations (Table 1), while we study hurricane terrestrial effects in Hypothesis 2.1.

2.4.1 Question 1 – *How do episodic disturbance events and long-term climate and land use change affect multiple dimensions of biodiversity and related ecosystem functions?*

Understanding the spatio-temporal variation in biodiversity and its connection to ecosystem function is one of the Grand Challenges in Environmental Science (NRC 2001) and an essential task of long-term research in LUQ 5. We propose hypotheses concerning the effects of press and pulse disturbances on: 1) spatio-temporal variation in the multiple dimensions of biodiversity and

2) the importance of terrestrial inputs to stream biodiversity and water quality. In addressing this question, we will leverage our spatially explicit long-term data on a number of key taxa in the LM with the collection of new data based on observational and manipulative experiments designed to explore resistance, resilience, and vulnerability to interacting disturbances. Theories concerning the inter-relationships among taxonomic, functional, and phylogenetic biodiversity, and their integrated responses to environmental variation and disturbance, are at an early stage of maturation. Consequently, we expect that our empirical findings will catalyze the development of theory regarding multiple dimensions of biodiversity.

Hypothesis 1.1: Biodiversity in multiple dimensions over multiple scales – *Each of the multiple dimensions of biodiversity (taxonomic, functional, and phylogenetic) in terrestrial and aquatic systems responds differently to*: *1) spatial gradients in environmental characteristics, 2) hurricane-mediated disturbance and drought, and 3) long-term change associated with climate and land use, and these responses are taxon-specific*. *Functional biodiversity is more tightly linked to environmental characteristics and responds more strongly to both press and pulse disturbances than do taxonomic and phylogenetic biodiversity*. (Willig, Bloch, Brokaw, Cantrell, Crowl, González, Lodge, Presley, Pringle, Ramírez, Richardson, Thompson, Uriarte, Waide, Woolbright, Zimmerman)

Most biodiversity research focuses on the taxonomic dimension, as expressed by species richness, diversity, or evenness (Loreau 2000, Mittelbach et al. 2001). Less studied are the functional, phylogenetic, and genetic dimensions of biodiversity and how they vary with each other in space or time (Reiss et al. 2009, Meynard et al. 2011). Functional biodiversity refers to the diversity of organismal strategies for resource acquisition and stress tolerance, and studying it is essential for understanding the connection between ecosystem structure and function. Phylogenetic biodiversity considers the phylogenetic relationships among taxa in a community, and studying it is essential for understanding how evolution shapes community composition. We have long studied the dynamics of taxonomic biodiversity in the LM (e.g., Lodge & Cantrell 1995, Willig et al. 1998, 2007). In LUQ 5 we will expand these studies and explore the resistance, resilience, and vulnerability of the taxonomic, functional, and phylogenetic dimensions of biodiversity, using existing data from LUQ 1-4 and projects in LUQ 5. LUQ 5 will provide the foundation for future research on genetic biodiversity.

Changes in any aspect of biodiversity arise as a consequence of turnover in species with respect to space or time (Figs. 2, 9). Taxonomic turnover generally increases with productivity and declines with disturbance, and several hypotheses may account for these patterns, including variation in stochastic processes or changes in habitat heterogeneity (Chase & Leibold 2002, Chalcraft et al. 2004, Scheiner & Willig 2005, Fox et al. 2011). Functional biodiversity arises through evolutionary trade-offs associated with heterogeneous environments (Roff 1992), as exemplified by turnover in functional traits along environmental gradients (Willig et al. 1996, Díaz & Cabido 2001, McGill et al. 2006, Cantrell et al. 2012). Understanding how taxonomic, functional, and phylogenetic biodiversity change together along environmental gradients would allow us to differentiate among hypotheses regarding turnover along gradients. The joint study of taxonomic, functional, and phylogenetic dimensions will also provide insights into how biophysical factors, including long-term climate and land use change, alter biodiversity and thus affect ecosystem function and services.

A multi-scale approach is needed to understand the spatio-temporal dynamics of biodiversity because species distributions may shift due to global change (Pimm 2009, Laurance et al. 2011), affecting alpha, beta, and gamma components of each dimension of biodiversity. In the LM, we have assessed changes in taxonomic biodiversity along environmental gradients (Willig et al. 2012b, Richardson & Richardson 2012) and in response to disturbance (Willig et al. 1998, Willig et al. 2007), but we do not understand how the other dimensions of biodiversity respond to these drivers. We will address this hypothesis with interrelated projects that focus on 1) spatial gradients in environmental characteristics, 2) effects of episodic disturbances such as hurricane and drought, and 3) effects of press disturbances associated with climate and land use.

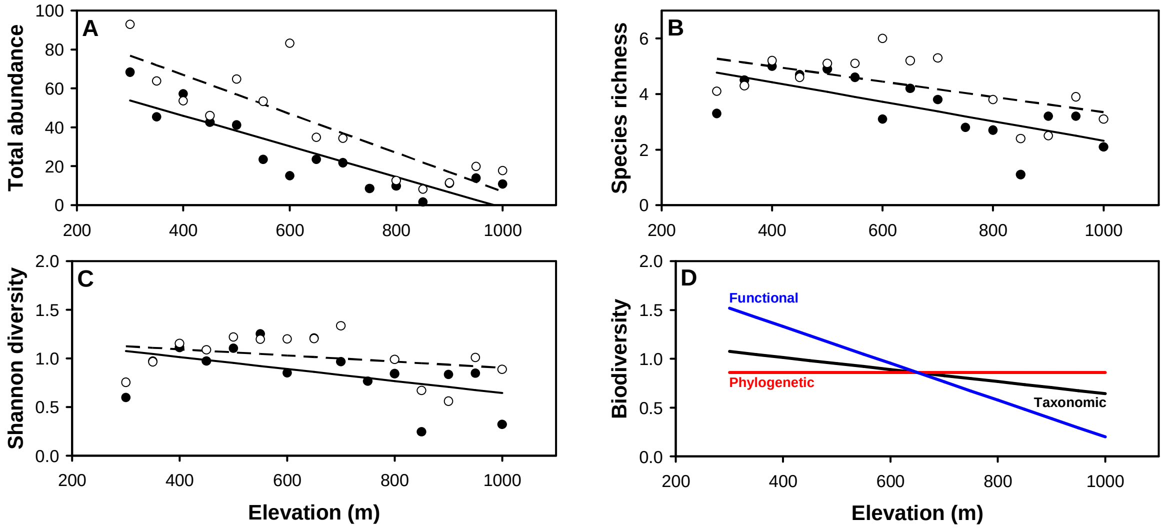

Figure 9 – Empirical relationships (A-C) between elevation and three aspects of mean taxonomic biodiversity of gastropods along two transects (mixed forest and palm forest) in the Luquillo Mountains, as well as hypothesized elevation relationships (D) of taxonomic (black line), functional (blue line), and phylogenetic (red line) biodiversity. Mixed forest transects (solid symbols) and palm forest (open symbols) shown with best fit linear fits.

Hypothesis 1.1 workplan

<u>Biodiversity and spatial gradients</u> **–** To test this hypothesis, we continue spatially-explicit monitoring of various terrestrial and aquatic taxa in the Luquillo Forest Dynamics Plot (LFDP, Sect. 2.3.1), the Long-Term Elevation Plots (LTEP, Sect. 2.3.2), and the Canopy Trimming Experiment (CTE, Sect. 2.3.3), and we begin monitoring in our new field experiments (Sect. 2.3.3). The LFDP provides spatially explicit data beginning in 1990, and the LTEP provides data at multiple spatial scales (plots, elevation strata, watersheds), beginning in 2003. The field experiments quantify the strength of abiotic drivers associated with gradients in the LM. The treatment plots in the CTE (Sect. 2.3.3), the Litter Exclusion Stream Experiment (Hypothesis 1.2, below) and the Throughfall Manipulation Experiment (Sect. 2.4.1, Hypothesis 2.2, below) create contrasting environmental conditions for testing the mechanisms that mold patterns in multiple dimensions of biodiversity. In the CTE, we monitored treatment effects on taxonomic diversity but did not assess effects on other dimensions (except some aspects of microbial functional diversity). We expect trimming to affect functional diversity more than phylogenetic or taxonomic biodiversity because of the close linkage between functional traits, niche characteristics, and the observed environmental distribution of species. The Litter Exclusion Stream Experiment manipulates the link between terrestrial and aquatic ecosystems. By severing this link, theory predicts negative cascading effects on the biodiversity of all trophic levels in food webs (Dodds & Whiles 2010), with larger effects on functional diversity than on other

dimensions. The Throughfall Manipulation Experiment will provide treatments with contrasting soil moisture, helping us to understand how heterogeneity in water availability affects microbial biodiversity. The Landscape Project (Sect. 2.4.3, Hypothesis 3.2) will provide an ideal landscape gradient on which to evaluate how multiple dimensions of biodiversity vary in response to local conditions within the context of the composition and configuration of a changing landscape (Peters et al. 2007, Willig et al. 2007).

For each study a number of taxa (trees, microbes, gastropods, litter invertebrates, reptiles, amphibians, and birds) will be evaluated for functional characteristics and phylogenetic relationships of constituent species (Villeger et al. 2008, Pavoine et al. 2011) to estimate the multiple aspects of each dimension of biodiversity at different sites (e.g., 40 sampling points in the LFDP, 10 plots in each elevation stratum in the LTEP). Functional classifications can be based on guild membership (Blaum et al. 2011, Cardoso et al. 2011) or functional traits (Mason et al. 2005, Ricotta 2005). Metrics of functional and phylogenetic biodiversity (e.g., Rao's Quadratic Entropy [Q], Vellend et al. 2011, Weiher 2011) will be weighted by the relative abundances or biomasses of species and compared to results based on incidence alone (i.e., presence and absence). Long-term data from the LFDP and LTEP, collected during LUQ 1-4 and continuing through LUQ 5, will be used to quantify spatio-temporal associations among different dimensions of biodiversity, or among aspects within dimensions (e.g., richness and evenness for taxonomic biodiversity), by means of univariate and multivariate correlations, including path analysis. Gradients in functional or phylogenetic biodiversity can arise due to differences in species richness; sites with more individuals or species will more likely contain more functional groups or more distantly-related taxa, due to chance alone. Thus we will conduct simulation analyses to evaluate whether gradients in functional or phylogenetic biodiversity simply reflect gradients in species richness or, instead, represent unique phenomena requiring additional mechanistic explanation.

<u>Biodiversity and pulse disturbance workplan</u> **–** Spatially explicit long-term monitoring of selected taxa on the LFDP occurs regularly, as part of our core monitoring of population and community dynamics, whereas such monitoring on the LTEP will be scheduled over longer intervals (2-5 yr, depending on taxon). These long-term data will provide the temporal component needed to assess resistance, resilience and vulnerability (Waide & Willig 2012) of multiple dimensions of biodiversity to pulse disturbance events such as hurricanes and droughts. As we have done previously for the taxonomic dimension, we propose to model temporal variation in multiple aspects of the other dimensions of biodiversity (see above) in response to such disturbance events using statistical models, including time series analysis, intervention analysis (Prates et al. 2010), multivariate repeated analyses of variance (Willig et al. 2011a), Gaussian or Markov random field approaches (Prates et al. 2010), and hierarchical Bayesian approaches (Uriarte et al. 2012). Responses of multiple dimensions of biodiversity to hurricane disturbance and climate change will also be evaluated in the CTE (Sect. 2.3.3), the Litter Exclusion Stream (Hypothesis 1.2, below) and Throughfall Manipulation Experiments (Hypothesis 2.2, below), and the Landscape Project (Hypothesis 3.2, below). These long-term experiments simulate changing pulse and press environmental drivers in the LM (Scatena et al. 2012, Willig et al. 2012a).

<u>Biodiversity and interacting pulse and press disturbance workplan</u> **–** The long-term biotic data that we continue to gather on the LFDP and LTEP, and new data in the Landscape Project and in dammed rivers (Sect. 2.4.3, Hypothesis 3), will enable us to quantify how presses, or temporal changes in climate or land use, interact with pulses, or episodic disturbances, to affect the

resistance, resilience, and vulnerability of multiple aspects of biodiversity as well as their spatial associations. To maximize our ability to relate biodiversity patterns to microclimatic characteristics across experiments and study areas, we will create synoptic networks of sensors using LTER standard monitoring protocols. As already established in the Canopy Trimming Experiment, and partially in the LTEP, networks will monitor abiotic and climatic variables (e.g., air, soil, and stream temperature; soil moisture, solar radiation) on all experiments and projects. Such monitoring will enable us to compare changes along the elevation gradient over time and associate them with observed changes in multiple aspects of biodiversity.

We have already quantified elevation gradients in taxonomic components of biodiversity in the LM (González et al. 2012) as well as the current meta-community structure of trees, gastropods, and other biota (Barone et al. 2008, Willig et al. 2011a, 2012b, Presley et al. 2012). As in other tropical mountains, the cloud condensation point appears to be rising in response to climate change (Lawton et al. 2001), and plant, animal and microbial species will shift elevation distributions in response (Pimm 2009, Lodge et al. 2008, Forero-Medina et al. 2011), altering gradients in biodiversity and community structure. We will capture these changes with further analyses of meta-community structure (coherence, turnover, boundary clumping) and hierarchical components of biodiversity (alpha, beta, and gamma) over time (Leibold & Mikkelson 2002, Willig et al. 2007, Presley et al. 2010).

Hypothesis 1.2: Biodiversity of streams, productivity, detrital inputs, and climate change – *Tropical stream food webs are regulated by inputs of terrestrial detritus. Therefore, reduction of litter inputs from forests to streams will strongly affect freshwater biodiversity, food web structure, secondary production, and water quality.* (Ramírez, Covich, Crowl, McDowell, Ortiz, Pringle, Scatena)

Understanding trophic controls on stream ecosystems is critical for understanding how stream biodiversity, biogeochemistry, and water quality respond to long-term environmental change. Current theory in stream ecology, based on research in temperate regions (Wallace et al. 1997, Nakano et al. 1999), states that small, canopy-covered, headwater streams are heterotrophic systems that rely on inputs of detritus from adjacent terrestrial areas (Thorp et al. 2008, Dodds & Whiles 2010). Tropical headwater streams are expected to follow this pattern, but recent studies challenge the importance of detritus as a major energy resource for tropical stream food webs and suggest, instead, the importance of primary production by algae (March & Pringle 2003, Douglas et al. 2005, Dudgeon et al. 2010). Our long-term studies in the LM have shown that litterfall creates a strong connection between terrestrial and stream ecosystems (Covich et al. 1991, Zimmerman & Covich 2003, 2007, Cross et al. 2008a). However, the quantity and quality of detrital inputs to streams are greatly influenced by hurricanes, droughts, and climate variability (Sect. 1.1.2, Fig. 10). For example, leaf-litter delivery is mediated by mat-forming, forest fungi that trap and release litter slowly and improve its nutritional quality for stream organisms (Lodge et al. 2008). But droughts kill the fungal mats, so that subsequent floods deliver detritus of inferior quality in large pulses to headwater systems. Thus, if headwater streams truly rely on detritus as the main energy source, they are vulnerable to changes in drought, flood, and hurricane regimes that affect the adjacent terrestrial ecosystems. In addition, the loss of riparian-stream connectivity is commonly observed after watershed urbanization and other land use changes (Paul & Meyer 2001, Allan 2005). But if streams rely more on primary production, they should be more resistant to changes in the surrounding forest.

We propose the Litter Exclusion Stream Experiment, a “whole-stream exclusion” (complete exclusion on a stream reach) of leaf litter, that will allow us to quantify the degree of connectivity between stream and terrestrial ecosystems. We will also quantify the resistance of stream ecosystems to reductions in allochthonous inputs from riparian vegetation, which may occur with increasing variability of drought and flood. Moreover, by manipulating leaf detritus under persistent canopy cover, we will be able to assess the importance of terrestrial detritus to aquatic biodiversity and food webs in isolation from other confounding factors (e.g., changes in total rainfall, inputs of contaminants).

In the proposed experiment we will assess changes in the energy source of stream ecosystems that could lead to changes in ecosystem services. For example, nitrogen removal is a major ecosystem service provided by headwater streams (Meyer & Wallace 2001). The ability of streams to remove nitrogen is strongly influenced by factors controlling microbial communities, such as energy sources and food web interactions (Findlay 2010). Studies at Hubbard Brook showed that after major disturbances forest ecosystems tend to lose nitrogen while streams tend to retain it (Bernhardt et al. 2003). For tropical streams, we lack information on how such ecosystem services might be affected by changes in energy to the stream.

Hypothesis 1.2 workplan – In the Litter Exclusion Stream Experiment we will entirely exclude terrestrial detritus, mostly leaf litter, from entering a reach of headwater stream in the LM for at least 10 yr, to assess responses of multiple dimensions of biodiversity (Hypothesis 1.1), algal and macro-invertebrate biomass, and primary and secondary productivity of the stream. We will also monitor changes in water quality in response to litter exclusion. The experiment will parallel successful designs used in the USA (Coweeta LTER, Wallace et al. 1997) and Japan (Nakano et al. 1999). We will select two perennial headwater streams (c. 1 m channel width) close to each other in the LM. One stream will be manipulated (litter excluded) and the other will serve as a reference.

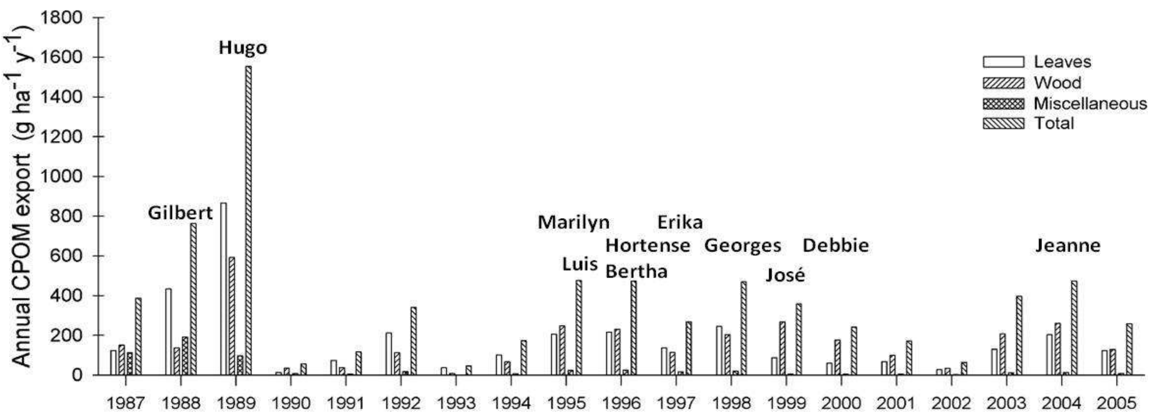

Figure 10 – Long-term annual exports of coarse particulate organic matter (CPOM) from the Bisley Experimental Watersheds. The names over the bars refer to tropical storms or hurricanes that affected the area. Peak CPOM exports correspond to major hurricanes (e.g., Hurricane Hugo in 1989), but periods of frequent storm activity (e.g., 1995-2000) can result in low but continuous exports. (Re-drawn from Heartsill-Scalley et al. 2012)

Along the entire length (150 m) of the experimental stream, a tent-like screen with roof and side walls will prevent vertical and lateral inputs of litter from entering the channel. Nets placed across the permanent channel will block input of litter from surface flow during episodic storms. A similar reach will be selected and marked in the reference stream, but no screen or walls will be constructed around it. Because no two streams are exactly the same, this experiment cannot be truly replicated. Instead, we will design the experiment to use Randomized Intervention Analysis (RIA, Carpenter et al. 1989), a design well-suited to the analysis of un-replicated whole-ecosystem manipulations. RIA requires a manipulated system and an undisturbed reference system. As required for RIA, all measurements will be conducted concurrently in both streams to create a time-series for each characteristic. Similar to other whole-stream manipulations using RIA (Wallace et al. 1997), we will gather 3 yr of monthly pre-manipulation data and 3 yr of post-treatment data. Most variables will be measured monthly, thus increasing the power of our analysis. We will measure the effects of litter exclusion on multiple dimensions of biodiversity, biomass, and monthly productivity of all major food web components in the streams. Algal biomass will be monitored monthly by sampling benthic biofilms on rocks using a modified Loeb sampler. Primary production will also be measured on rocks in situ, using chambers. Aquatic insect composition and biomass will be measured monthly by sampling riffles and pools. Insect secondary production will be estimated monthly using the instantaneous growth method (Benke 1984), with growth rates for major taxa determined in situ in growth chambers. Shrimp and crab populations will be sampled in pools using minnow traps, following standard protocols (Zimmerman & Covich. 2003, Covich et al. 2006). Shrimp secondary production will be measured following methods similar to those described for insects (Cross et al. 2008a). We will also monitor standing crops of detritus in the stream bed and changes in stream dissolved organic matter and nutrients monthly. We will closely compare our results with those from the Coweeta LTER.

2.4.2 Question 2 – *How do episodic disturbance events and long-term climate change affect biogeochemical pathways, responses, and rates?*

Understanding the response of biogeochemistry at local, regional, and global scales to episodic disturbance events (pulses) and press disturbances such as climate change is a fundamental issue in ecosystem ecology. Past work in the LM shows that many biogeochemical processes have been resistant to, or resilient after, significant hurricane disturbances. Stream and groundwater chemistry (McDowell et al. 1996, Schaefer et al. 2000, Shanley et al. 2011, McDowell et al. 2012), elemental fluxes in stream water (Schaefer et al. 2000), soil carbon and nutrient pools (Silver et al. 1996, Teh et al. 2009), rates of litter decomposition (Sullivan et al. 1999) and trace gas fluxes (Erickson & Ayala 2004) are either resistant to hurricane disturbance (e.g., Si and Ca in streams), or return to pre-hurricane levels within a year or two (e.g., N_2O flux from soils). The resilience of these biogeochemical processes in the face of increased hurricane frequency is unknown, however.

Despite the apparent resilience of the forested landscape to hurricane disturbance, it appears that the biogeochemistry of this tropical landscape may be relatively sensitive to episodic wetting and drying events. Alternating wet and dry periods likely result in flushes of microbial activity that release nutrients and organic matter (Lodge et al. 1994), and may shift conditions past biogeochemical thresholds that result in a change in redox status. In upland soils, we have documented shifts from oxic to anoxic conditions in response to increased soil moisture, and changes in the frequency and magnitude of redox fluctuations (Silver et al. 1999, 2012, Liptzin et al. 2011). These responses result in corresponding changes in redox-sensitive processes in upland soils such as greenhouse gas production and consumption (Silver et al. 1999, 2012, Teh et al. 2008, Liptzin et al. 2011), nitrogen cycling (Silver et al. 2001, 2005, 2011, Templer et al. 2008), and soil iron and phosphorus dynamics (Chacon et al. 2006, Liptzin & Silver 2010). It can also lead to large differences in the N chemistry of soil solution collected from wetter and drier environments (McDowell 1998). In the riparian zone, we have shown that the forms of N in groundwater differ dramatically with redox status (McDowell et al. 1992, 1996) and that topographic transitions, where these redox changes occur, are hot spots for N_2O emissions from surface soils (McSwiney et al. 2001).

LUQ takes three approaches to understanding the long-term drivers of biogeochemistry in this landscape. First, we are documenting long-term patterns in fundamental biogeochemical parameters such as litterfall mass and nutrients (Scatena et al. 1996, Zalamea & González 2008, Heartsill-Scalley et al. 2011), stream nutrient chemistry and export (e.g., Schaefer et al. 2000, Shanley et al. 2011, McDowell et al. 2012), and trace gas flux (Table 1, Silver et al. 2012 and in prep.). These baseline measurements help determine how biogeochemical processes respond to both long-term drivers (press) and episodic (pulse) disturbances. Second, we will continue the CTE, which simulates effects of hurricanes on a set of biogeochemical parameters over the long term. Third, we will begin the Throughfall Manipulation Experiment that will alter the delivery of water to forest plots to help us understand the long-term effects of more extreme wetting and drying events on forest biogeochemistry.

Hypothesis 2.1: Biogeochemistry, system productivity, and hurricanes – *Repeated pulse disturbances associated with hurricanes lead to repeated pulses of nitrogen loss in soil solution, repeated decoupling of soil CO_2 flux from litter inputs, long-term changes in soil decomposer communities, and decreased net primary productivity. Soil C storage, which reflects the balance between carbon inputs and carbon mineralization, will decrease with repeated disturbance.* (González, Cantrell, Lodge, McDowell, Richardson, Silver, Willig, Zimmerman)

The responses of biogeochemical cycling to episodic pulse disturbances and climate change are closely linked to changes in community composition, primary production, and nutrient availability. During the first phase of the Canopy Trimming Experiment (CTE, Sect. 2.3.3, Fig. 6) we showed that the simulated hurricane treatment altered the ratio of fungi to bacteria, fungal connectivity, and diversity of microarthropod functional groups, as well as rates of mass loss of litter and nutrient translocation, thus clearly linking changes in biodiversity to changes in ecosystem function (Sect. 1.1.1, Richardson et al. 2010). We expect that repeated application of the trim-and-deposit-debris treatment of the CTE (treatment D, Fig. 6) will result in long-term alteration of the composition of the decomposer community, soil nutrient dynamics, and carbon mineralization and storage.

Past work in the LM shows that soil C balance can be altered by changes in biogeochemical inputs. Experimental N fertilization resulted in an increase in heavy fraction soil C (Cusack et al. 2010), a change in microbial community structure (Lodge et al. 2008, Cusack et al. 2011), and an increase in storage of C in mineral soil. However, one of the striking biogeochemical results from the long-term data in the CTE is the decoupling of litter inputs and soil CO_2 efflux following disturbance (Fig. 3). Prior to manipulation, litter inputs and CO_2 fluxes were tightly coupled in all plots, with both tracking changes in temperature and light availability. Following canopy trimming, soil respiration in treated plots diverged from controls for only 1.5 yr, even though litterfall remained lower in the trimmed plots 6 yr after the original manipulation. Leaf area index, soil nitrate levels, and microarthropods responsible for litter decomposition responded to canopy opening and debris addition on the same time frame as did soil CO_2 efflux, with a return to pre-treatment levels in 1.5 yr. The prolonged reduction of litter inputs to the forest floor, when combined with the return of CO_2 efflux to pre-treatment levels, suggests that repeated hurricane disturbance will reduce standing stocks of soil C, alter the quality of soil C, and change the composition of the soil litter decomposer community. Although we have seen that microbial communities in forest soils of the LM are affected by disturbance (Lodge et al. 2008), we know little about the identity of particular microbial species or fungal functional groups that may have been affected by the original canopy trimming manipulations. We will focus additional attention on the responses of soil organic matter and soil decomposer communities (taxonomic, functional and phylogenetic biodiversity) to hurricane simulation in LUQ 5. By repeating the trim-and-deposit-debris treatment in the CTE, during LUQ 5 we will build the long-term record needed to understand the linkages among C fluxes and the composition and activity of decomposers.

Hypothesis 2.1 workplan – As mentioned, we will repeat the trim-and-deposit-debris treatment of the CTE (treatment D, Sect. 2.3.3, Fig. 6) in 2013, measuring CO_2 flux, soil solution nutrients, litterfall, tree growth, litter decomposition, composition of litter decomposer communities, and the amounts and forms of soil C in response to the manipulation. In addition we will continue to measure abiotic characteristics (air and soil temperature, light, soil moisture) continuously in each of the control and treatment plots. Litterfall will be collected every two weeks. Greenhouse gas flux (CO_2, CH_4, and N_2O) and nutrients in soil solution (NH_4^+, NO_3^-, PO_4^{3-}, DOC, and DON) will be measured monthly. Changes in litter microarthropods, including taxonomic, functional, and phylogenetic biodiversity, and microbial functional group diversity (through Terminal Restriction Fragment Length Polymorphism [TRFLP], clone libraries, and fungal:bacterial ratio) will be measured quarterly. Rates of litter decay, stem growth, and seedling recruitment will be measured annually. Soil C fractions will be measured at the beginning and end of the study (methods in Cusack et al. 2010).

Hypothesis 2.2: Biogeochemistry, soil C, and climate drying – *Soil C storage and loss are tightly coupled with the magnitude of precipitation on long temporal scales (months to years), whereas greenhouse gas fluxes respond to the timing of rainfall events on shorter temporal scales (days to weeks). These differences in response times derive from the relative sensitivity of nutrient availability and microbial communities to changes in redox*. (Silver, Cantrell, González, Lodge, Mayol, McDowell)

In the Caribbean, climate change will likely lead to lower and more seasonal rainfall (Angeles et al. 2010, Comarazamy & González 2011). Past research in the LM showed that tropical forest biota and biogeochemistry are sensitive to drought (Sect. 1.1.2). A predicted

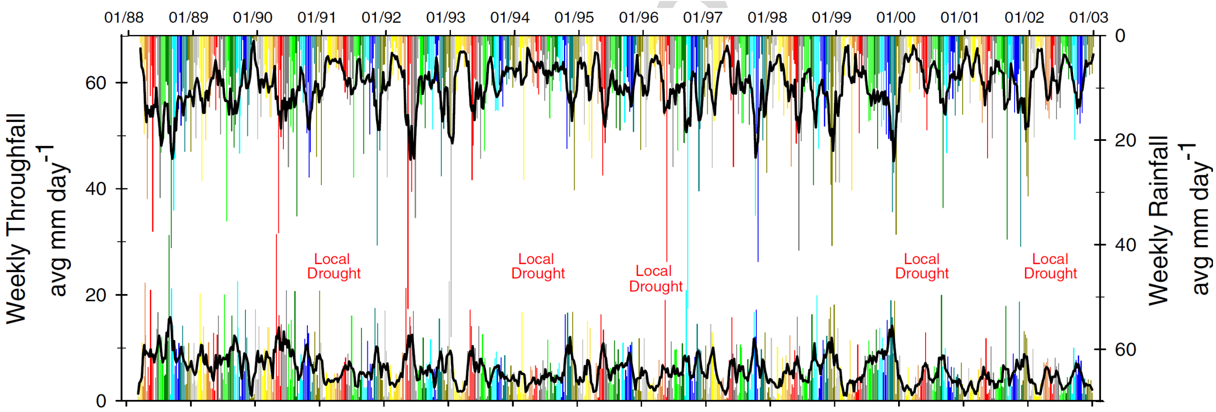

Figure 11 – Throughfall (bottom) and rainfall (top) with periods of local drought indicated (lowest 5% mm d^{-1}). Individual colored bars are weekly values coded by month (red is May). Thick black line is running average. (Heartsill-Scalley et al. 2007)

increase in the magnitude or intensity of particular rainfall events (Knutson et al. 2010) can also affect ecosystem processes (Fig. 11). This is particularly true of redox-sensitive biogeochemistry including the production and consumption of greenhouse gases (Sect. 1.1.2, Liptzin et al. 2010, Burgin et al. 2011). Understanding the resilience of tropical forests to fluctuations in precipitation will help us to predict the vulnerability of ecosystems to climate change. Therefore, we propose to manipulate throughfall over the long term to examine the effects of changes in soil moisture on biogeochemical pools and fluxes, and on patterns in microbial community composition and multiple dimensions of biodiversity, on which these biogeochemical processes depend. Previous throughfall manipulation studies in tropical forests produced conflicting results with regard to C and N cycling (Davidson et al. 2008, Cleveland et al. 2010, Wieder et al. 2011, Wood & Silver 2012) and generally explored only one level of throughfall change. We propose to determine the effects of multiple levels of throughfall change to help us identify the mechanisms that link biogeochemical fluxes to microbial community composition and multiple dimensions of biodiversity. LUQ has the world's longest continuous record of throughfall measurements (Heartsill-Scalley et al. 2007), an informative context for this experiment.

Hypothesis 2.2 workplan – To determine the effects of changes in soil moisture on soil microbes and biogeochemistry, we will establish the Throughfall Manipulation Experiment in tabonuco forest. We will add or exclude throughfall for 6 to 10 yr to explore the effects of changes in soil moisture on root biomass, soil microbial diversity, soil C and nutrient storage and loss, and greenhouse gas dynamics. To manipulate throughfall we will use clear, corrugated plastic roofs (four 1.1 x 1.1 m sheets) placed on a PVC frame, about 1.5 m above the soil surface (Wood & Silver 2012). These clear shelters facilitate replication, have minimal effects on microclimate apart from water diversion, and are considered the best approach for exploring mechanisms driving patterns in biogeochemistry and microbial composition (Fay et al. 2000, Cleveland et al. 2010, Wood & Silver 2012). We will establish five replicate 2 x 2 m plots of each of the following four treatments: 100% throughfall removal, 50% throughfall removal, throughfall doubling, and un-manipulated control (20 plots total). In a pilot study we used a similar design to reduce throughfall at this site, and found a 16-36% decrease in soil moisture over three months in the 0-10 cm depth (Wood & Silver 2012). The roofs on all plots will be set at an angle to capture all runoff in a trough. Water captured from the 100% throughfall removal will be applied to the throughfall doubling plot via a passive rainfall simulation system (Rubol et al. submitted). Half of the captured water will be distributed on the 50% throughfall removal plots, and all captured water will be placed back on the control plots, using a passive, automatic watering system. Litter falling onto the shelters will be distributed weekly onto the plots. We want to alter but not completely exclude soil moisture; therefore we will not trench around the plots, which has the unwanted side effect of a prolonged change in root biomass and soil hydrologic dynamics (Silver & Vogt 1993, Silver et al. 2005). Tensiometers in each plot will document the effectiveness of our throughfall manipulations in altering soil moisture content.

Soils will be sampled for microbial communities at the beginning of the experiment and quarterly thereafter. Soil cores will be sampled for fine root biomass at the beginning of the experiment (n = 3 per plot) and yearly thereafter (Silver & Vogt 1993). Soil moisture, temperature, and O_2 concentrations will be monitored hourly using automated sensors at 10 cm depth. Trace gas fluxes (CO_2, N_2O, CH_4) will be measured every two weeks for the first year using two surface flux chambers per plot, after which fluxes will be monitored monthly. Porous cup tension lysimeters will be used to measure dissolved nutrients and organic matter in soil solution at the same frequency as trace gases. Concentrations of reduced Mn and Fe will be measured in lysimeter samples and soil extracts to provide an index of Mn and Fe reduction, which are dominant anaerobic biogeochemical processes in this system. Soils will be sampled quarterly for pH, Fe and Mn reduction potential, potential net N mineralization, and soil P concentrations. Shifts in microbial functional biodiversity will be determined through TRFLP, clone libraries, and fungal:bacterial ratios.

2.4.3 Question 3 – *How do changes in land and water use affect biodiversity and biogeochemical dynamics, which, in turn, affect ecosystem functions and the delivery of critical ecosystem services?*

Questions 1 and 2 address the impacts of climatic pulses and presses on ecosystems. The experiments we use to answer those questions – the CTE, Litter Exclusion Stream Experiment, and Throughfall Manipulation Experiment – will provide mechanistic understanding of how changing climatic drivers affect biodiversity and biogeochemistry. In Question 3 we use those experimental results, our long-term observations, and additional field work and modeling to ask how the climate drivers, the direct effects of human water and land use, and interactions between climate and human activity are affecting ecosystem services in the landscape in and around the LM (Figs. 1, 5).

The LM provides water, biodiversity, recreation, and other ecosystem services and products (González-Cabán & Loomis 1997, Scatena et al. 2002, Kartchner 2003, Santiago & Loomis 2009, López-Marrero & Hermansen-Báez 2011). These products and services are affected by land use in the lowlands surrounding the LM (Lugo 1994, Lugo & Helmer 2004, van der Molen et al. 2010) and by changes in the hydrologic connectivity between the lowlands and the LM (Pringle 1997, Greathouse et al. 2006a, Crook et al. 2009, Hein et al. 2010). Hydrologic connectivity refers to the water-mediated transfer of matter, energy, and organisms within or between elements of the hydrologic cycle (sensu Pringle 2001). Longitudinal riverine connectivity, between upstream and downstream reaches (in both directions), plays a key role in structuring streams draining the LM (Kikkert et al. 2009). Reduced stream flows, due to water withdrawals associated with urbanization (press disturbance), are exacerbated by more frequent and longer droughts (interacting pulse and press). This can result in the total cessation of flow and reduced connectivity in streams for up to several months each year, interfering with both the upstream and downstream migration of native fish and shrimps (Holmquist et al. 1998). The decrease in numbers of migratory aquatic organisms that feed on algae and decomposing leaves (March et al. 2003, Blanco & Scatena 2005, Greathouse et al. 2006a, Hein et al. 2010) potentially reduces water quality (Santos-Román et al. 2003) and recreation potential. On land, lowland deforestation fragments forests and can reduce rainfall in the LM (van der Molen et al. 2010) with effects such as reduced gene flow among frog populations (Barker et al. 2011).

How these long-term changes in connectivity and land cover affect the resilience and vulnerability of ecosystem processes and services is the focus of hypotheses and projects of Question 3. This question is also a focal point for integrating activities within our site and with other research programs, including NEON, STREON, LCZO, ULTRA-Ex, and IGERT in Puerto Rico. The projects for Question 3 span spatial scales that range from plots and stream reaches (Hypotheses 3.1) to regional scale studies of the urbanizing coastal plain that surrounds the LM (Hypothesis 3.2). By extending our long-term environmental sampling network and conducting shorter synoptic studies we will evaluate how changes in aquatic biogeochemistry and riparian soils influence local and regional biodiversity and the delivery of ecosystem services. Accordingly, Hypothesis 3.1 addresses how longitudinal riverine connectivity (between the LM and coast) has changed over the last 30 yrs, and how different levels of connectivity affect ecosystem function and services. This hypothesis complements mechanistic studies in the Litter Exclusion Stream Experiment (Sect. 2.4.1). Hypothesis 3.2 addresses how past and present construction of a four-lane highway adjacent to the LM influences the functioning and services of aquatic and terrestrial ecosystems. Hypothesis 3.2 provides a platform for future long-term studies of the changing landscape.

Hypothesis 3.1: Ecosystem processes, services, and riverine connectivity – *Longitudinal riverine connectivity between the LM and the coast decreased dramatically between 1994 and 2004. We predict that connectivity has increased since 2004, due to the implementation of water withdrawal infrastructure designed to increase the survival of migratory aquatic organisms. While streams draining the LM are vulnerable to increasing water withdrawals, the ecosystem processes of nutrient retention, respiration, primary production, and decomposition will be highly resilient as long as some stream flow is retained. In contrast, we predict that when a state of 'zero' connectivity exists (above large dams with no spillway flow) these ecosystem processes and associated ecosystem services will be significantly reduced due to the potential extirpation of many native organisms.* (Pringle, Scatena, Crowl, Covich, McDowell, Ortiz, Ramírez, Santiago)

LUQ research on the hydrologic budgets and water use of the LM has documented a dramatic increase in water extraction (mainly for potable water) and a corresponding decrease in the longitudinal connectivity of LM streams for migratory biota (Fig. 12; Nauman 1994, Crook et al. 2007, Crook et al. 2009). In 1994 only 50% of the water in streams draining the LM reached the coast on an average day, and by 2004 only 30% of the water reached the coast on average (Crook et al. 2007). In response to concerns about the impacts of water withdrawals on riverine connectivity, water managers adopted an ecologically-based hyporheic stream water extraction system suggested by LUQ (Benstead et al. 1999, Scatena & Johnson 2001, March et al. 2003). Two off-stream storage reservoirs designed to provide passage for aquatic organisms were also built on two large streams that drain the LM. By combining our existing long-term data with focused mechanistic studies, we now have the unique opportunity to ascertain if these management changes have increased riverine connectivity and/or altered biogeochemical processes and associated ecosystem services over the last 10 yr.

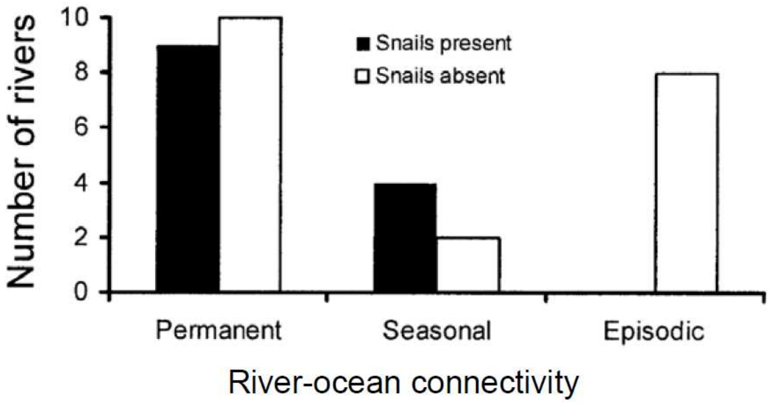

Figure 12 – Presence of populations of the snail *Neritina virginea* in 32 rivers of Puerto Rico with varying connectivity to the ocean. River connectivity is characterized as permanent, seasonal, or episodic. (Blanco & Scatena 2006)

Hypothesis 3.1 workplan – This hypothesis will be addressed by: 1) updating the hydrologic and water use budgets of the LM to determine how much water has been extracted in the past 10 yr, 2) assessing changes (between 1994, 2004, and 2014) in the relative vulnerability of native stream organisms to water withdrawals using a LUQ-derived *Index of bi-directional riverine connectivity* (Crook et al. 2009), 3) directly examining biological and geomorphic effects of the two new off-site reservoirs to test the impact of these new management strategies on biodiversity, and 4) comparing ecosystem processes (nutrient retention, respiration, and decomposition) and associated services in three types of streams: a) relatively free-flowing (flow to coast >80% yr), b) streams experiencing significant levels of water withdrawal (no flow to coast 50-80% per yr), and c) stream reaches above dams that have completely lost their connectivity with the coast. Coordinated sampling and studies in non-free-flowing stream reaches above large dams and other barriers will provide the opportunity to quantify how "zero" connectivity (accompanied by the complete loss of native macroconsumers) affects biogeochemistry, ecosystem processes and associated ecosystem services. By studying reaches that span a range of connectivity (free flowing to completely disconnected) we will be able to estimate the thresholds at which changes in connectivity influence biodiversity, ecosystem function, and services. Data from previous LUQ synoptic sampling of aquatic biota (Benstead et al. 1999, Blanco & Scatena 2005, 2006, Crook et al. 2009) will be combined with new sampling above and below different types of extraction sites to assess if the changes in biodiversity and connectivity that were predicted during LUQ 3 and 4 have occurred. In stream reaches that will be selected in coordination with studies proposed in Hypothesis 3.2 (and including both control and reference stream reaches in the Litter Exclusion Stream Experiment, Sect. 2.4.1), we will quantify and compare reach-scale geomorphic and hydraulic characteristics (Pike et al. 2010), biodiversity, nutrient demand (Tank et al. 2007), respiration (Ortiz-Zayas et al. 2005), and decomposition (March et al. 2003). In addition to whole-reach measurements, we will also use small-scale electric exclosures (modified from Pringle & Blake 1994) nested within stream reaches to experimentally examine how decomposition, respiration, and primary production are affected by macroconsumer exclusion caused by reductions in connectivity. By using standardized design elements from STREON (electric exclosures [Pringle & Blake 1994], sediment baskets, etc.) this project will promote cross-site analysis and inform the analytical framework of STREON. Finally the results of these studies on the influence of connectivity on stream ecosystem processes and services will be included in the landscape water model described in Hypothesis 3.2.

Hypothesis 3.2: Ecosystem processes, services, and landscape change – *Road building and urbanization at the base of the LM will reduce ecosystem services by simplifying the structure and biodiversity of aquatic ecosystems and reducing water quality. In addition, land use changes will fragment adjacent terrestrial plant communities, reducing biophysical connectivity and biodiversity. Consequently, we predict the development of "urban syndromes" in linked aquatic and terrestrial ecosystems along the flanks of the LM and a reduction in critical ecosystem services.* (Zimmerman, Uriarte, Brokaw, Crowl, Covich, McDowell, McGinley, Ortiz, Pringle, Ramírez, Santiago, Scatena, Willig, Yu)

Puerto Rico Route 66 is a four-lane highway under construction (Fig. 5) that exemplifies trade-offs between development and ecosystem services. The highway is being built at the base of the LM and provides a unique opportunity to evaluate and predict the long-term environmental changes resulting from highways, urbanization, and the interaction of pulse and press disturbances on tropical ecosystems (Laurance et al. 2009, DTPW 2011). A 13-km section of Route 66 has operated since 2006. A second section is under construction and will be operational during LUQ 5, and a third section near the LM will be developed after 2018. By 2030 the road will be part of a highway system that encircles the island and the northern semicircle of the LM (DTPW 2011). This combination of finished, under-construction, and planned sections of the road near the LM provides an "experiment" to track the development of urban stream and terrestrial syndromes (simplified or fragmented ecosystems with low biodiversity). During LUQ 5 we will develop a long-term platform to monitor and model ecological and human effects on these ecosystems such that their services can be predicted as highway construction and development proceeds. Although beyond the scope of LUQ, we will seek additional funding to develop scenario analysis based on this platform, as suggested in the Mid-Term Review (Section 4).

Hypothesis 3.2 workplan – Specific projects under Hypothesis 3.2 include: 1) studies of the region's land use history, 2) analysis of the effects of this history and recent highway construction on stream and floodplain geomorphology, and the biogeochemistry and biodiversity of aquatic and adjacent terrestrial communities, and 3) further development of a landscape-level model that links changes in water quality and quantity to physical, biological and socioeconomic drivers (Uriarte et al. 2011).

<u>Land use history</u> – Land use records, aerial photography, and remote sensing data will be compiled and analyzed to construct a historical record of how landscape pattern and structure changed in the study area before and after the construction of Route 66. This will extend our previous research on long-term environmental change and effects on biodiversity in northeastern Puerto Rico (Thomlinson et al. 1996, Thompson et al. 2002, Willig et al. 2004) to the coastal floodplain and provide a platform for future studies in the area.

<u>Impacts on aquatic and terrestrial ecosystems</u> – During LUQ 5 we will establish a network of sites for synoptic sampling of stream and floodplain geomorphology, water chemistry and quality, and the biogeochemistry and multiple dimensions of biodiversity of aquatic and adjacent terrestrial communities. At the start of LUQ 5 permanent stream-riparian plots will be established within representative 100-yr flooding zones along a gradient of urbanization to evaluate how land use change affects hydrographs and other elements of these aquatic/terrestrial ecosystems. The establishment and analysis of these permanent plots will be a central component of a PhD dissertation. The plots will be sampled every 2 yr as a training project for REU students and students working in the LCZO.

<u>Landscape-level model of water quality and quantity</u> – Recent LUQ research has begun to identify drivers of land cover change and their impacts on water provisioning (Uriarte et al. 2011). This component of the project will develop those techniques at a finer spatial resolution for the area surrounding the LM and affected by the highway. It will focus on: a) quantifying the impacts of spatial heterogeneity in land cover changes on several water quality indicators (Santos-Román et al. 2003), and b) determining the spatial scale at which this heterogeneity influences water quality. The result will be a statistically-based model that links physical, biological, and socioeconomic drivers to water quality and quantity (Uriarte et al. 2011). In LUQ 5 we will conduct sensitivity analyses of projected urbanization due to the expansion of Route 66, varying the amount and dispersion of urbanizations as key components of land use change and studying changes in landscape fragmentation and water quality. These results will provide the basis to seek additional funding to incorporate social components of land use change (land use planning and social perceptions that drive land use change) and scenario analysis.

2.5 SYNTHESIS AND PRODUCTS

LUQ 5 will represent a new peak of achievement for Luquillo LTER, catalyzed by recent syntheses of our work and by expanding connections to other research networks, and manifested by expansion in research approaches and products. There is an expansion in scale: to our studies on episodic natural disturbance and response we add more focus on long-term environmental change and more landscape-level work, to gain the understanding we need to foresee future states of ecosystem services. There is also an expansion in approach: the observations over 24 yr and the syntheses of LUQ 4 were prerequisites for the new field experiments and landscape-level studies on long-term environmental change proposed for LUQ 5. The broad relevance of the studies in LUQ 5 connects LUQ to other programs. Results from long-term observations in the LFDP are used in CTFS syntheses; the CTE links with hurricane research at the Harvard Forest LTER; the Litter Exclusion Stream Experiment connects with litter exclusion at the Coweeta LTER and will complement studies of riparian effects on streams in San Juan ULTRA-Ex; the Throughfall Manipulation Experiment complements Luquillo CZO studies of soil moisture and weathering; and the Landscape Project and the landscape water modeling will synergize with Puerto Rico NEON, STREON, and IGERT.

Major products of LUQ 5 will be definitive syntheses of results from tests of our hypotheses. About one yr after we begin LUQ 5, we will convene a workshop on "concepts and approaches for quantifying multiple dimensions of biodiversity as mechanisms for understanding succession and long-term change." Toward the end of the LUQ 5 cycle we will hold a workshop to synthesize our understanding of the resistance, resilience, and vulnerability of aquatic and terrestrial tropical ecosystems to interacting pulse (largely natural) and press (largely human) disturbances. Another workshop will synthesize our results on water in ecosystems and as an ecosystem product (Fig. 8). In a tropical world of changing hurricane regime, warming and drying, increasing variability of rainfall, and rapid urbanization, our syntheses will address the consequences for biodiversity, biogeochemistry, and ecosystem services. LUQ 5 research and education help fulfill the *Decadal Plan for LTER* (LTER 2007, Collins et al. 2011); it is an integrated program of long-term and experimental research, linked to education, and designed to help sustain ecosystem services in tropical environments.

Section 3 Education and Outreach

LUQ education and outreach programs 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 in Puerto Rico), Jess Zimmerman, Jorge Ortiz-Zayas, Eda Meléndez (LUQ Information Manager), and Ariel Lugo.

3. 1 SCHOOLYARD LTER

For nearly 20 yr, 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. Self-motivated teachers from each of these schools, with the assistance of their students, have established long-term plots on public and private lands near their schools to study forest structure and dynamics. In some schools, these investigations have had outstanding results, with teachers publishing in a peer-reviewed journal (*Acta Científica*, Vol. 13, 1999) and attending national conferences. During LUQ 4 we institutionalized Schoolyard LTER by hiring an Educational Coordinator for the project. This has strengthened our relationship with these four high schools, and helped guide teachers and students as they monitor their long-term plots and record biological and environmental data.

During LUQ 5, we will continue to improve the learning cycle for the participating schools. We will begin with a weekend internship at El Verde Field Station, where the teachers and students train in data collection protocols and management techniques under the guidance of UPR researchers and graduate students. This training prepares them to conduct similar investigations at their school sites throughout the academic year. Twenty students participate (five from each school), ranging in grade from sophomores to seniors. These students are selected by their teachers based on their leadership within the program, and returning students serve as mentors to their peers. During the school year, Schoolyard Educational Coordinator Noelia Báez visits each of the schools on a monthly basis, serving as a liaison between Schoolyard staff and the classroom and providing support in the implementation of the research. We recently added a data analysis and management workshop during the spring, held with the teachers from each institution and led by Ms. Báez, UPR researchers and the LUQ IM. The annual cycle culminates with a research symposium held at UPR, at which students from each of the four schools present the results of their research.

3. 2 *JOURNEY TO EL YUNQUE*

During LUQ 3 and 4, LUQ researchers supported the development of a four-week bilingual middle school curriculum unit called *Journey to El Yunque* (http://elyunque.net/journey.html). Students use LUQ data to investigate the effects of Hurricane Hugo and Hurricane Georges on the LM and consider the long-term implications of increased hurricane activity. Steven McGee and Jess Zimmerman have leveraged LUQ NSF funding for a 4-yr grant of over $1,100,000 from the U.S. Department of Education to conduct basic research, in collaboration with an educational psychologist, on how the program affects motivation and learning. The project will lead to a significant revision of the web site materials.

3. 3 REU, OTHER UNDERGRADUATE PROGRAMS

The University of Puerto Rico has led an REU site program in tropical ecology and evolution at El Verde Field Station since 2002; funding for the program was renewed in 2011. This program has involved 92 students, 55% of which came from under-represented minorities, and produced 23 publications, 12 with the student as first author, since 2002. REU funding for two students from LUQ will allow us to expand this program to ten students per year, as in past years with supplemental funds.

In addition to REU, research on the LFDP, LTEP, and CTE has been supported by volunteer internships filled by undergraduates or recently graduated students seeking experience in tropical research. About two hundred students, mostly women and over 35% underrepresented minorities, have participated in these programs, and many have gone on to pursue academic studies. In these internships, usually of three months, students receive per diem, travel, and lodging. Training in identification, field methods and data management, and seminars by researchers, enrich the field experience. Beginning in LUQ 5 we will establish the Alejo Estrado Fellowship Program by supporting two Fellows throughout the year to participate in the CTE, the Litter Exclusion Stream Experiment, and the Throughfall Manipulation Experiment. Of longer duration (as much as six months to one yr), these fellowships will target minority students seeking field experience as a step toward an academic career.

3. 4 UNDERGRADUATE AND GRADUATE PROGRAMS AT UPR

The creation of a Department of Environmental Science (ES) at UPR, formed from an existing ES program and the Institute for Tropical Ecosystem Studies (where LUQ is based), will increase the influence of LUQ research on the development of the undergraduate and graduate programs at the university. The funding of an IGERT Program in Human-Natural Systems in the Urbanizing Tropics at UPR during LUQ 4 was led by LUQ researchers in collaboration with the existing faculty in the ES Program. Receipt of IGERT funds provided the administrative imperative for the university and state agencies to complete approval of the ES Graduate

Program, now in its third year of operation. Classes in the undergraduate program in ES at UPR have frequently been taught by LUQ researchers; creation of the new department will ensure continued input of LUQ concepts and findings into the undergraduate curriculum.

LUQ has a strong program in graduate student training; 58 graduate students have been part of LUQ 4. Many are supported, at least in part, directly by the grant, at UPR or via subawards to collaborating institutions. Cohesion among students from the different institutions represented in LUQ is fostered by a Graduate Student Organization and by an elected Graduate Student Representative, who represents LUQ among students at the LTER Network level. We have a dedicated e-mail list for students (luq-students@lternet.edu) and activities devoted to graduate students at our annual and other meetings. Mr. Omar Pérez, current Graduate Student Representative, has developed an excellent education and outreach website about research on Puerto Rican rivers (https://sites.google.com/a/ites.upr.edu/luquillo-lter/home).

Section 4 Addressing the 2009 Mid-Term Review

The 2009 mid-term review of LUQ included four main recommendations for research, which we present here, with explanations of how we address them.

"**The PIs might consider a manipulative experiment that directly tests hypotheses about linkages between terrestrial and aquatic ecosystems**" We have amply documented the linkage of forest and stream ecosystems along riparian zones in the LM, in terms of leaf-litter inputs to detrital-based food webs in headwater streams (Covich et al. 1991, 1996, Wright & Covich 2005a, 2005b, Cross et al. 2008a, Crowl et al. 2000, 2006). To elucidate the linkage directly we propose the Litter Exclusion Stream Experiment in LUQ 5, in which we exclude terrestrial litter from headwater streams (Sect. 2.4.1).

"**The committee did not hear any characterization of secondary production**" Since the 2006 review we have described the secondary production of shrimps that consume detritus in streams (Cross et al. 2008a, b). We will also measure secondary production in the Litter Exclusion Stream Experiment (Sect. 2.4.1), and we recently began long-term sampling of benthic invertebrates in forested and urban sites to assess productivity. LUQ research is the first study of secondary production in a tropical urban river.

"**A scenario planning approach could be considered to address potential directions of monitoring and experiments to examine potentially important issues**" Our proposed work on spatial and temporal variation in biodiversity (Sect. 2.4.1) and, especially, our Landscape Project (Sect. 2.4.3) lend themselves to scenario planning. True scenario planning, however, involves intensive work with stakeholders and managers (Biggs et al. 2010), and at present we do not have the resources for the outreach and surveys needed. During LUQ 5 we will explore ways to begin scenario planning, building on our landscape work on ecosystems and services (Sect. 2.4.3)

"**research would benefit from digital access to comprehensive …GIS layers**…**How scaling is … handled is critical**" Spatial analyses are woven into several components of LUQ 5, including modeling, gradient analyses, and land use change studies. Long-term LUQ measurements inform spatial modeling of ecosystem structure and function and are used for modeling geospatial projections of future landscapes. LUQ legacy studies are being geo-referenced with appropriate metadata. LUQ 5 has the support of state-of-the art geospatial tools, expertise, and analysis from Dr. Mei Yu (Senior Personnel) at UPR-RP and the US Forest Service International Institute of Tropical Forestry GIS Remote Sensing Laboratory.

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