1. What are the short- and long-term effects of drought on tropical forest biota and biogeochemical cycling?

Under Question 1, we continue to analyze and study the impacts of the 2015 drought as an analogue for the type of droughts we expect to become more frequent with time in the LEF. For each of our hypotheses we distinguished short- vs. long-term effects of drought; the recent drought allows us to address short-term effects and conduct modeling activities that will allow us to project these impacts into the future.

A. Describe and model the impacts of the 2015 drought on vegetation dynamics.

We continue to analyze the dynamics of flowering, seed rain, litterfall, seedling dynamics, and adult tree dynamics in response to the 2015 drought. We reported last year that the 2015 drought caused a spike in litterfall at the start of the drought in May and resulted in a 30% reduction in diameter increment of the largest trees in the Luquillo Forest Dynamics Plot (LFDP). During the past year, Uriarte and her students have used data from the LFDP and a series of plots of younger forest called the Chronosequence Project to elaborate our understanding of drought effects. Her student Naomi Schwartz showed that growth reduction in species was influenced by important functional traits linked to life history variation (Fig. 1).

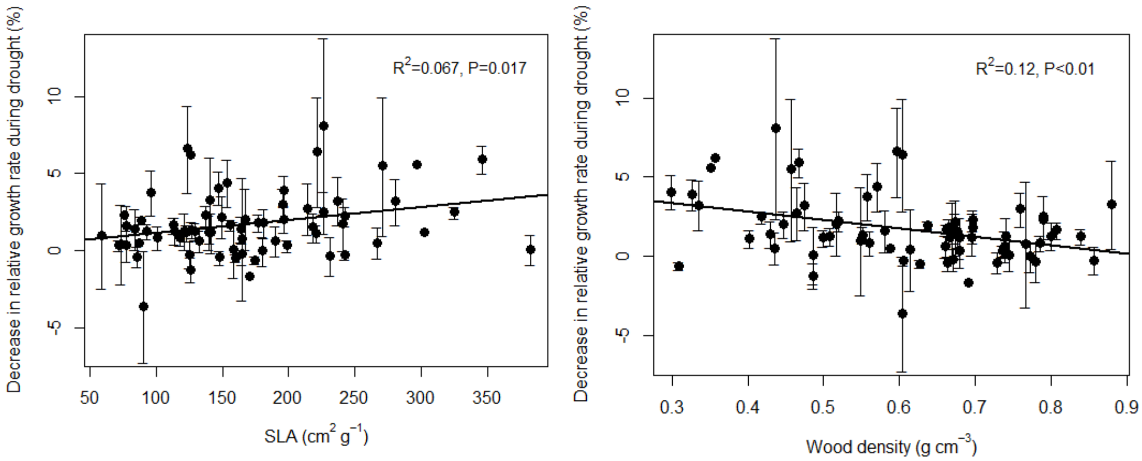

Fig. 1. Decrease in growth rate (diameter at breast height) in 2015 compared to previous years as a function of (left) specific leaf area (SLA or leaf thickness) and (right) wood density (WD). Fast-growing pioneer species have high SLA and low WD and are, therefore, more susceptible to drought than late successional species.

The relationships are, admittedly, weak. Naomi is attempting to refine this approach using a hierarchical Baeysian approach taking into account topographic variation within and among the sampled plots.

Sunny Feng, a post-doctoral associate working with Uriarte has incorporated data from the LFDP and the Chronosequence project into a version of the Ecosystem Demography model (ED2). ED2 aggregates species into three plant functional types (PFTs) based on whole leaf physiology but largely consonant with the life history variation demonstrated above. This effort was required a continuous 1-hr resolution record of climate record going back to 2002, utilizing LTER-collected data as well as data from USDA Forest Service, NOAA, and satellites (TRMM) to cross-check and fill gaps.

Net Ecosystem Productivity (NEP) in runs of the ED2 model incorporate the physiological responses of the PFTs to climate change scenarios. As an example of future climate change, they developed a projection of a gradual decline of precipitation to 50% present accompanied by 2 °C warming over time. The results showed that NEP (Fig. 2) would fall to 0 in the year 2036 when a drought of 30% was reached (along with a 1.2 °C increase in temperature). Beyond this time, one might speculate mortality among some species would occur, with a concomitant shift in species composition. Thus, they are beginning to define the impacts of increasing drought and when key points of rapid change might occur.

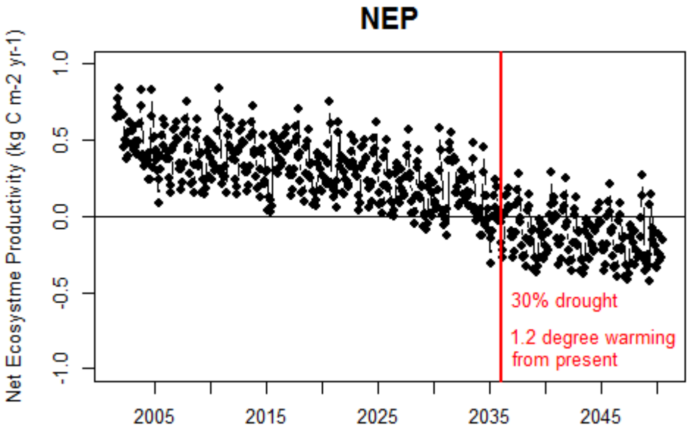

Fig. 2. Net ecosystem productivity (NEP) estimated from the ED2 model for tabonuco forest in Puerto Rico showing the impact of progressively increasing drought (to a 50% reduction in precipitation) and temperature (2 C) over time. Red line indicates where NEP falls to near 0, suggesting conditions under which tree mortality may become widespread, heralding a change in species composition.

B. Describe and model the impacts of the 2015 drought on soil biogeochemistry

Silver and laboratory personnel are monitoring an automated sensor array within a catena near El Verde Field Station (funded by the Department of Energy). This array records pseudo-continuous measurements of soil moisture, oxygen (O2) availability (as an indicator of redox) and greenhouse gas fluxes across a topographic gradient, with replicate transects running from ridge to valley. The 2015 drought effects on soil conditions continued into 2016 and resolved in winter 2016 (Fig. 3), indicating long lag times may result from extreme drought. They tracked the impact of that drought and its pattern of recovery on greenhouse gas emissions and key biogeochemical variables.

The 2015-6 drought led to rapid and dramatic declines in soil moisture and corresponding increases in soil aeration across topography. Soil carbon dioxide (CO_2) emissions increased by 60% on slopes and by 163% in valleys. Methane (CH_4) fluxes fell with drought in valleys, leading to a landscape-scale net consumption of 43 t CO_2 equivalents per ha over four months of drought. However, high post-drought CH_4 emissions offset 90% of this consumption over just 7 weeks. Drought and soil aeration led to significant declines in inorganic phosphorus (P) concentrations, an element commonly limiting to net primary productivity (NPP) in tropical forest ecosystems. This may explain, in part, the reduced growth of vegetation during the drought.

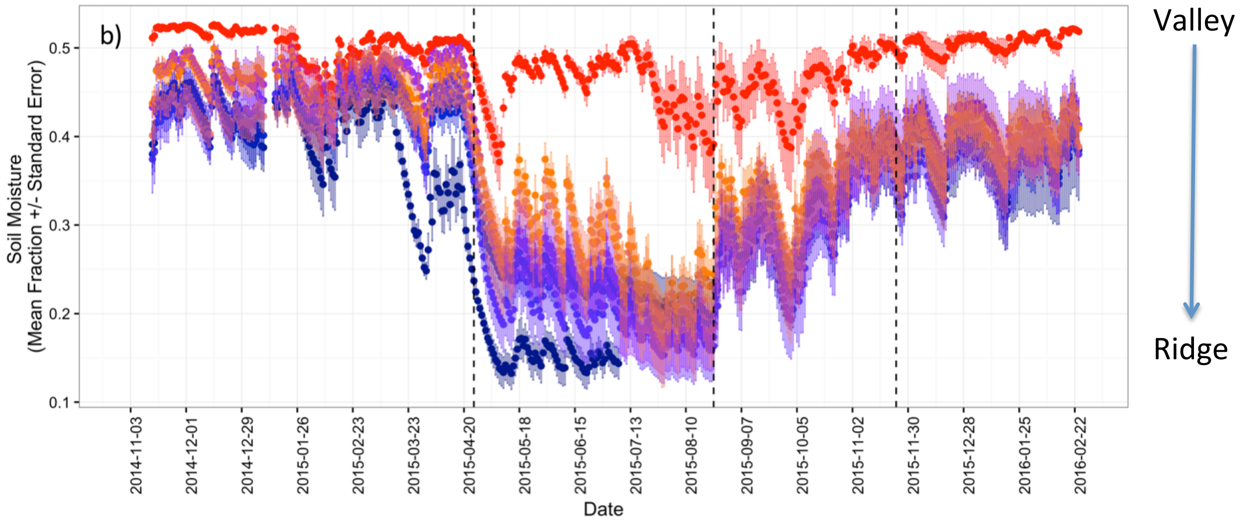

Fig. 3. Soil moisture levels measured in an automated sensor array along a catena in tabonuco *forest reveals the impact of the 2015 drought. Trend analysis divided the responses into four time periods, the latter two encompassing the long recovery period that carried into early 2016.*

They used controlled laboratory experiments (funded by LTER) on forest soils from different geomorphologies (slopes and valleys) to investigate the impacts of drought on phosphorus (P) and carbon (C) dynamics. The soils were amended with P and C and incubated under aerobic or anaerobic headspace. Results showed that the turnover of soil P fractions is governed by redox-induced Fe dynamics. More specifically, we found that oxidation events reduced the extractability of inorganic P, as oxidation of reduced Fe species likely enhanced P sorption/occlusion. On the other hand, reduction-induced release of P did occur but was much smaller in magnitude relative to the dissolution of Fe minerals. They also found that repeated redox oscillation gradually diminished the magnitude of soil Fe and P turnover.

Periodic anaerobic conditions had no effect of the P dynamics in valley soils but dramatically affect the P mobility in slope soils. The microbial biomass has the ability to immobilize soluble P but have no access to the less labile P fractions. Our laboratory incubation experiments also showed that iron oxidation contributed to soil C loss, explaining approximately 30% variability in soil CO_2 production.

Finally, Silver student Omar Gutiérrez de Arroyo designed, built, and established a throughfall exclusion experiment in Luquillo Experimental Forest. They began pre-treatment measurements, including soil moisture, temperature, and oxygen concentrations. The new exclosures are large enough to accommodate measurements of impacts on soil biogeochemistry as well as key organisms found in the exclosures such as microbes, litter arthropods, and gastropods.

Fig. 4. Photograph of throughfall exclusions being used to experimentally test the effect of drought on soil biogeochemistry and litter/soil organisms.

The results of the sensor array, laboratory incubations, and throughfall exclusion experiment will be incorporated into a modeling study using DAYCENT to be conducted by Gutiérrez as part of his dissertation and as described in our proposal. This will allow us to examine cumulative effects of more frequent droughts on soil biogeochemistry.

C. Describe the impact of the 2015 drought on stream and riparian habitats.

As we reported last year in detail, during the 2015 drought, streams draining the Luquillo Mountains almost dried up completely. This natural phenomenon provided a unique opportunity to study stream responses to flow reductions. We took advantage of ongoing long-term monitoring to understand how the 2015 drought impacted different components of stream ecosystems. LUQ streams are series of pools connected by riffles and small water drops. The drought eliminated all riffles leaving the streams as series of isolated pools. Water physico-chemistry was similar among pools at the onset of the drought and differed considerably during peak drought conditions. Inputs of leaf litter peaked during May 2015, both in terms of litter entering streams and in other locations of the forest.

Drought caused algal communities to decrease, possibly the result of an increase in consumer abundance. Benthic macroinvertebrates, in particular larval Chironomidae and Oligochaetes, increased in abundance during the middle part of the drought and collapsed towards the end. Decapod populations, which are highly mobile, did not respond to drought during the early part, but most pools lost their shrimp populations toward the middle and end of the drought. We are currently summarizing results to prepare a publication about the 2015 drought.

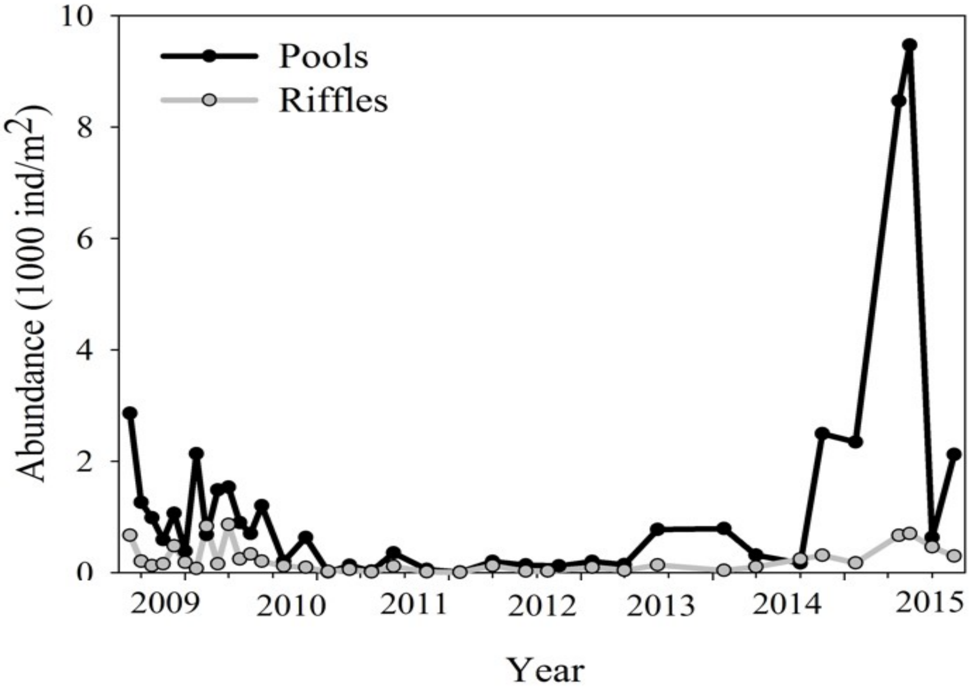

Fig. 5. Abundance of insects in a focal stream showing the increase in insects in stream pools during the 2015 drought.

D. Initiate a stream drought experimental array for long-term manipulation of stream flow and other drought related impacts to streams and riparian areas.

As described in the last proposal, we are starting a flow reduction experiment that will simulate the effects of drought on streams in the LUQ-LTER. The project is now called StreamFRE. Two tributaries of one of our focal streams were selected for the experiment; one will serve as a treatment stream and the other as a reference. Both streams will be sampled over time for one year before manipulations. The flow reduction will consist of a by-pass that will reduce base flow at the treatment stream for a few weeks during the early part of the year when precipitation is normally low and again during the mid-summer at the time when droughts are expected to become more frequent. The reference stream will remain un-manipulated to quantify natural variability in ecosystem processes. Progress to date: We started pre-manipulation sampling during 2016 and will have enough data to start manipulating flow during 2018. The following table shows the variables being monitored.

Table 1. List of physicochemical and biological variables currently measured in the Stream Flow Reduction Experiment.

Variables	Start date	Periodicity
Physicochemical		
Water temperature	2014	Hourly
Dissolved oxygen	Jun 2016	15 min
Water pH	Oct 2016	Weekly
Water conductivity	Oct 2016	Weekly

Water pressure (level)	2014	15 min
Discharge	2014	As needed
Water level (manual)	2014	As needed
Pool bathymetry	Oct 2016	As needed
Biological		
Macroinvertebrates	Oct 2016	Monthly
Algae	Oct 2016	Monthly
Chlorophyll	Oct 2016	Monthly
AFDM	Oct 2016	Monthly
Diversity	Oct 2016	Monthly
Shrimp	Oct 2016	Monthly
Riparian	Oct 2016	Monthly
Other		
Canopy cover	Jan 2017	Every 2 months
Benthic organic matter	Oct 2016	Monthly
Dissolved greenhouse gases	Oct 2016	Weekly
Nutrients	Oct 2016	Weekly
Seston	Oct 2016	Monthly
Litter fall	2009	Every 2 weeks
Leaf litter export	Dec 2016	Every 2 weeks
Leaf litter decomposition	January 2017	Annual

E. Complete planning of sampling of the Sonadora elevation gradient

The next major accomplishment for the LTER is to complete the once every six-year sampling of key organisms and abiotic variables along the elevation gradient represented by the Sonadora River. Our long-term goal is to track changes in the environment and biota along the gradient as climate changes. We have spent much of the past year organizing this effort and obtaining necessary permissions. Since the gradient study was established, the US Congress declared portions of the upper elevations of the LEF a Wilderness Area. For this it was necessary to design sampling methods that will maintain the untrammeled nature of the forest. We provide a diagrammatic representation (Fig. 6) of the sampling of upland forest (blue), palm-dominated riparian areas (for which we needed to reconfigure the shape of the 20x50 m plots to maximize riparian vegetation), and nearby stream reaches. We began sampling of the vegetation in the Fall 2016 and will continue with the sampling of all organisms and other variables through 2017.

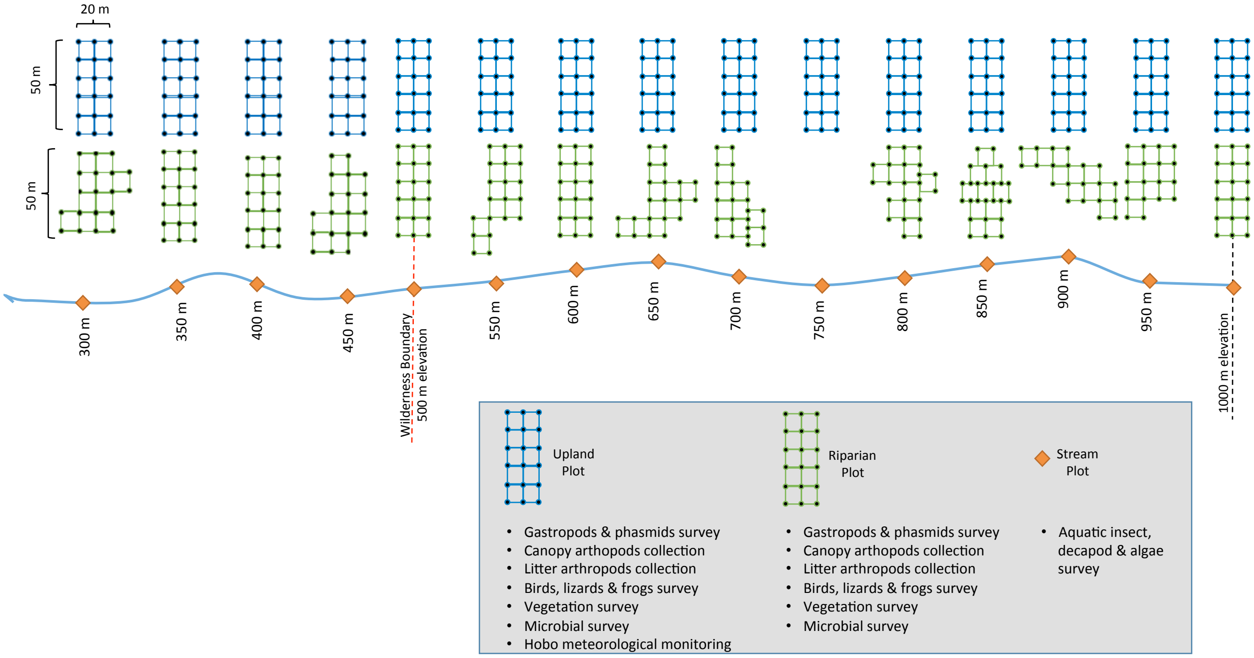

Fig. 6. Layout of sampling plots for the elevation gradient represented the Sonadora River. The gradient starts at 300 m elevation and extends to near the summit at 1000m. This diagram was developed for the USDA Forest Service to show the sampling to be done in the El Toro Wilderness Area, which starts at an elevation of 500 m

2. What are the effects of increased frequency of intense hurricanes on tropical forest biota and biogeochemical cycling?

A. Describe major results from a second trim manipulation in the Canopy Trimming Experiment (CTE).

As planned, we conducted a second set of manipulations in the CTE in Fall 2014, one decade after the initial treatments were established. We simplified the design by only conducting a hurricane-like treatment (trimming and debris deposition combined) abandoning the treatments of trimming only and debris deposition in untrimmed plots. This is aligned with our long-term goal of determining the impact of frequent intense hurricane disturbance on the species composition of the vegetation and key consumers as well as on long-term changes in soil organic matter and related impacts on soil nutrient availability. The simplified design assures we can logistically maintain the long-term measurements in the CTE. We continue the basic monitoring of key variables as outlined in our proposal.

For this report, we focus on research at the litter-soil interface conducted by Cantrell, Lodge, and González, as this was a key for understanding responses to the hurricane-like treatments. The group has completed two years of intensive sampling to monitor the impacts of the treatments (and the drought of 2015) on soil and litter microbial communities and nutrient limitation. Utilizing innovative Plant Root Simulator Probes developed by Western AG, they found significant increases in levels of many nutrients (total N, ammonium, [but not nitrate], P, S, K, Ca, and Mg in response to the trim treatments. There was also a flush of nutrients from litter at the end of the drought of

2015. Student Ivia Moreno conducted a litter decomposition experiment in the CTE. She decomposed a green leaf litter mixture of three species and, so far, has found no difference in decomposition rates between treatments. She did find an effect of litterbag mesh size on decomposition and nutrient mineralization, indicating that the increase abundance of arthropods allowed by the larger mesh size influenced decomposition and mineral release.

B. Describe the long-term dynamics of canopy arthropods in response to hurricanes and other disturbances

Schowalter, Willig, and Presley (*Environmental Entomology*, in press) quantified long-term successional trajectories of canopy arthropods on six tree species in LEF. The site experienced two intense hurricanes during the study period (Hugo in 1989 and Georges in 1998). Based on succession theory, we expected: (1) differential species performances to result in taxon- or guild-specific responses to disturbance, with complementarity among taxa or guilds that are adapted to different stages of succession; (2) differences in initial conditions at the time of each hurricane to result in distinct successional responses to each disturbance event; and (3) the legacy of hurricane-created gaps in the canopy to persist despite subsequent disturbances. At least one significant effect of gap, time after hurricane, or interaction of gap and time occurred for 53 of 116 analyses of taxon abundance, 31 of 84 analyses of guild abundance, and 21 of 60 analyses of taxonomic biodiversity (e.g., richness, evenness, dominance, diversity). Responses were ~60% more common for time after hurricane than for gap creation, indicating that temporal changes in habitat during recovery were of primary importance. Differential responses were pervasive, with both increases and decreases in abundance or biodiversity occurring in response to each factor. Guild-level responses were driven by changes in the abundance of resources on which they rely. For example, detritivores were more abundant soon after hurricanes due to increased litter fall, whereas sap-suckers were more abundant in gaps where new foliage growth was greatest. The legacy of canopy gaps created by Hurricane Hugo persisted for at least 19 years, despite droughts and other minor and major hurricanes that caused forest damage. This reinforces the need to consider historical legacies when seeking to understand responses to disturbance.

C. Describe the impact of hurricane-felled logs on soil development.

Jean Lodge and colleagues continue to describe the effects of decomposing logs from trees felled by both Hurricanes Hugo (1989) and Georges (1998) on soil formation (Fig. 7). The decomposing wood causes consistent increases in soil C but not other variables. Many of the responses are influenced by seasonal effects.

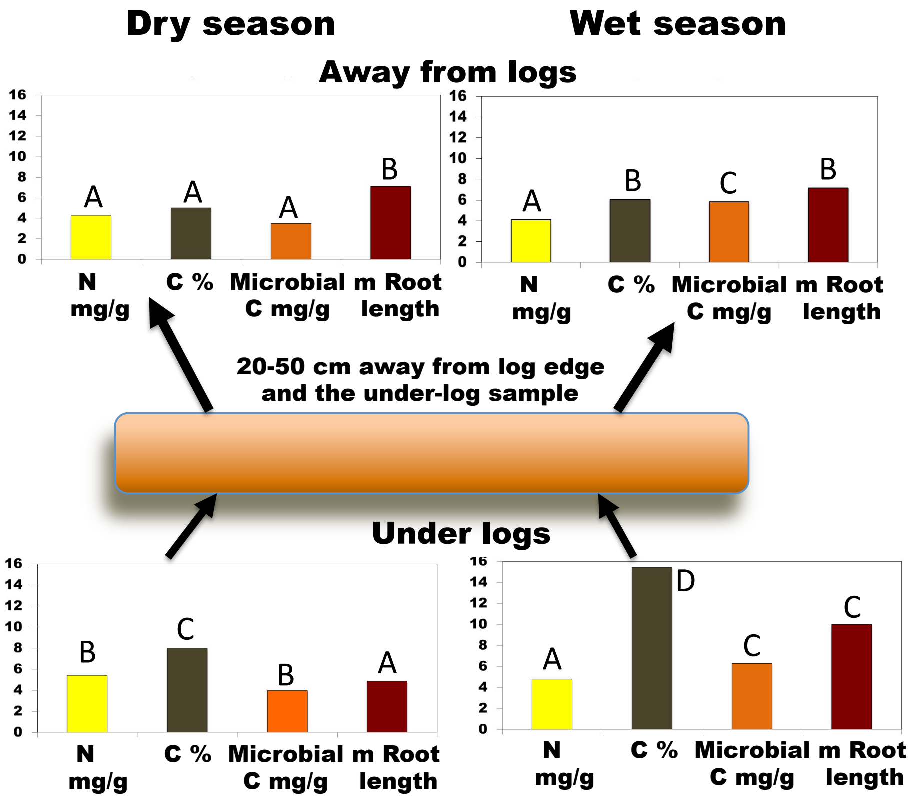

Fig. 7. The effects of decomposing logs on patterns of soil development. Logs were felled in Hurricanes Hugo (1989) and Georges (1998).

3. How do changes in climate interact with hurricane disturbance, land cover, and land use legacies to shape tropical forest ecosystems of the future?

Under question 3 we include two hypotheses. The first seeks to understand how the LEF landscape interacts with climate systems to produce precipitation variability and to then project future changes due to a changing climate. The second hypothesis reflects our interest in how land use history affects biotic communities and interacts with increased drought frequency and hurricane disturbance to cause ecosystem change. In 2016 we collaborated with the Luquillo Critical Zone Observatory to determine how variation in geological substrate and geomorphology influences vegetation structure.

A. Describe efforts to downscale and project precipitation variability throughout the LEF.

Mote and his students continue to study methods of downscaling precipitation variability in the LEF. They find that:

- Historic drought in Puerto Rico is associated with atmospheric regimes consisting of high wind shear and dry air in the low- to mid- troposphere across the eastern Caribbean.

- Future atmospheric regimes in Puerto Rico, as predicted by climate models, will introduce new atmospheric conditions which include drier air in the low- to mid-troposphere.
- The 2015 drought was driven by strong and frequent intrusions of hot, dry air in the low- to mid- troposphere. The Saharan Air Layer is largely responsible for this anomalously hot, dry air that produced very stable air and limited convective activity across multiple scales of motion. The 2015 drought was unlike previous droughts-of-record (e.g., 1994) in that it was most severe over the eastern portion of the island.
- Future projections of climate change in the CMIP5 model projections indicate that the 2015 drought may represent a precursor to future dry years, in terms of changes in seasonality and magnitude of rainfall departures.

B. Describe a remote sensing perspective of the impacts of the 2015 drought on the LEF

The effects of droughts on tropical forests are likely to depend on environmental heterogeneity. Uriate and her students examined the effect of drought on a Neotropical forest in eastern Puerto Rico using two vegetative indices derived from 30 m Landsat 7 ETM+, the Enhanced Vegetative Index and the Normalized Difference Water Index. We also considered some of the factors that may mediate the intensity of the response including forest age, elevation, slope and fragmentation (distance to edge). The effect of drought was clear in the remote sensing products with a significant decrease in EVI and NDWI from 2011 compared to 2015 across the landscape. However, there was differential response with respect to forest age, topography and environmental drivers. For both metrics, the effect of drought was stronger in old-growth forests, steep terrain, at higher elevations, and closest to fragment edges.

C. Assess the mechanisms underlying land use impacts on the composition and diversity of soil fungal communities in the Luquillo Forest Dynamics Plot.

Soil fungi are critical for forest function, playing an important role in carbon sequestration and in structuring tree communities. Over 70% of all remaining tropical forests are growing in former agricultural or logged areas. Yet our understanding of the long-lasting effects of human land use on soil fungal communities in tropical forests is limited. Uriarte and her student Bene Bachelot investigated the relationship among land use history, biotic and abiotic factors, and soil fungal community composition and diversity in a second-growth tropical forest in Puerto Rico. They coupled high-throughput DNA sequencing with tree community and abiotic environmental data to determine whether land use history had an effect on soil fungal community descriptors. They also investigated the biotic and abiotic factors that underlie such differences and asked whether the relative importance of biotic (tree diversity, basal tree area, and litterfall biomass) and abiotic (soil type, pH, iron, and total carbon, water flow, and canopy openness) factors in structuring soil fungal communities differed according to land use history.

They demonstrated long-lasting effects of land use history on soil fungal communities. At our research site, most of the explained variation in soil fungal composition (R^2 = 18.6%), richness (R^2 = 11.4%) and evenness (R^2 = 10%) was associated with edaphic factors. Areas previously subject to both logging and farming had a soil fungal community with lower beta diversity and greater evenness of fungal OTUs than areas subject to light logging. Yet, fungal richness was similar between the two areas of historical land use. Together, these results suggest that fungal communities in disturbed areas are more homogeneous and diverse than in areas subject to light logging. Edaphic factors were the most strongly correlated with soil fungal composition, especially in areas subject to light logging, where soils are more heterogenous. High functional tree diversity in areas subject to both logging and farming led to stronger correlations between biotic factors and fungal composition than in areas subject to light logging. In contrast fungal richness and evenness were more strongly correlated with biotic factors in areas of light logging, suggesting that these metrics might reflect long-term associations in old-growth forests.

D. Demonstrate the effects of an abrupt change in forest structure at geomorphological knickpoints in the LEF.

Most research on vegetation in mountain ranges focuses on elevation gradients as climate gradients, but elevation gradients are also the result of geological processes that build and deconstruct mountains. Recent findings from the Luquillo Mountains from the Luquillo CZO have raised questions about whether erosion rates that vary due to past tectonic events and are spatially patterned in relation to elevation may drive vegetation patterns along elevation gradients. Here theyuse airborne light detection and ranging (LiDAR) technology to observe forest height over the Luquillo Mountain Range. theyed show that models with different functional forms for the two prominent bedrock types best describe the forest height - elevation patterns. On one bedrock type there are abrupt decreases in forest height with elevation approximated by a sigmoidal function, with the inflection point near the elevation of where other studies have shown there to be a sharp change in erosion rates triggered by a tectonic uplift event that began approximately 4.2 My ago. The findings are consistent with broad geologically mediated vegetation patterns along the elevation gradient, consistent with a role for mountain building and deconstructing processes.