Significant Findings

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

A. Development of a definition for drought effects on wet tropical forest.

Droughts are poorly defined in space and time and, as a result, researchers have developed a plethora of indices to describe drought, including the Palmer Drought Index, Crop Moisture Index, Surface Water Supply Index, deciles, daily streamflow percentiles, and percent of normal precipitation (reviewed by Larsen 2000). A drought severity classification developed jointly by the National Oceanic and Atmospheric Administration Climate Prediction Center, U.S. Department of Agriculture, and the National Drought Mitigation Center (NOAA/USDA/NDMC) lists five levels of drought. The pattern of drought severity in 2015 showed that drought was widespread over eastern Puerto Rico (Fig. 1), including the LEF, beginning in April. Moderate drought persisted through the end of the year.

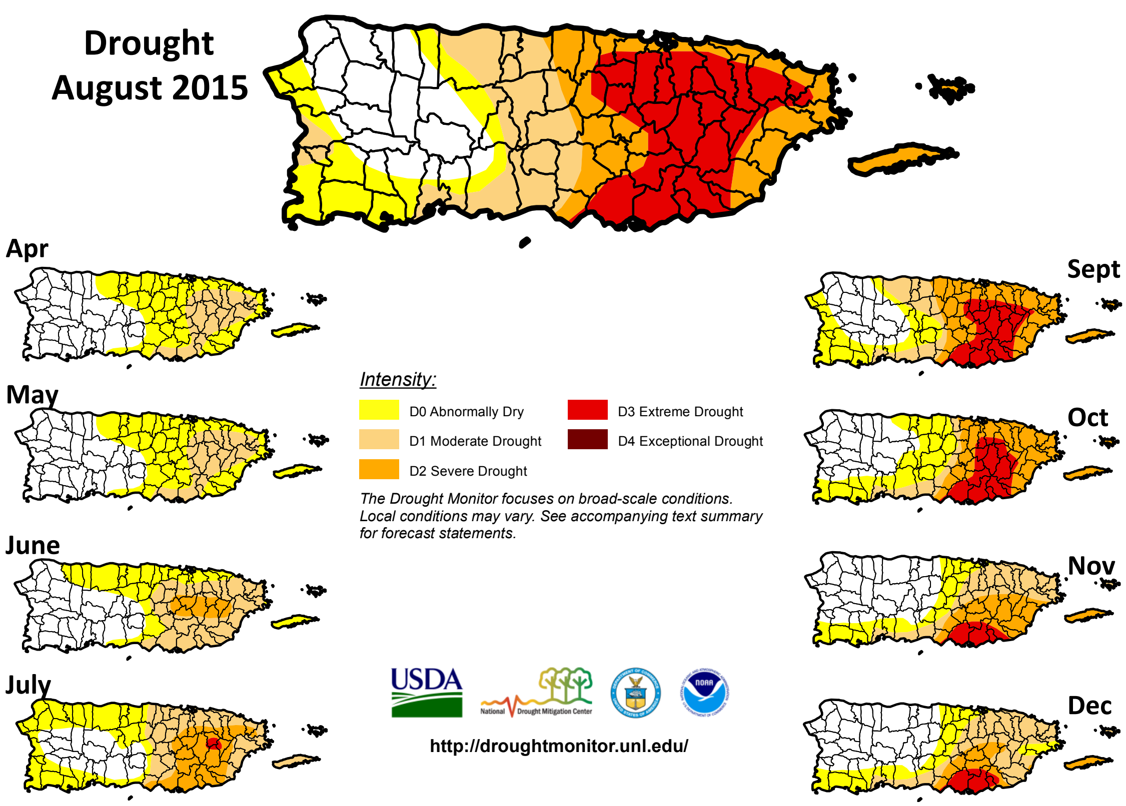

Fig. 1. Distribution of US Drought Monitor index in Puerto Rico 2015 starting in April when drought conditions first appeared.

Larsen (2000) suggested distinguishing meteorological, soil, and hydrological droughts, which the US Drought Monitor combines into single index. Meteorological droughts are periods of below-average precipitation. Soil droughts, also described as agricultural or vegetative droughts, follow meteorological droughts and affect natural flora and fauna and crops. A hydrological drought signifies reduced streamflow, reflecting lowered groundwater. The onset of the different droughts indicates increasing drought intensity as lowered precipitation must precede a decline in soil moisture, which, in turn, must precede a lowered water table. Thus, droughts typically begin in this sequence and recovery occurs in the reverse order, that is, by increased precipitation, which enhances soil moisture, which, in turn results in greater surface- and groundwater levels. As we continue to assess the impacts of the 2015 drought, we will determine how this scheme dovetails with our conceptual framework, which emphasizes the progressive impact of droughts on biogeochemistry and the biota and their interactions (Smith et al. 2009).

B. <u>Characterize the 2015 drought in the LEF by contrasting patterns of precipitation, soil moisture, and stream flow for the past year with long-term records.</u>

Meteorological drought began in Puerto Rico in April of 2015, marked by the departure of cumulative rainfall from the 40 year average (Fig. 2). By the end of 2015, a series of rainstorms (including TS Erika on August 28) had raised the rate of precipitation accumulation to near normal levels (but not totals). The severely dry summer experienced in 2015 mimics well (or is the result of) predicted changes in seasonality caused by global warming, that is, significant

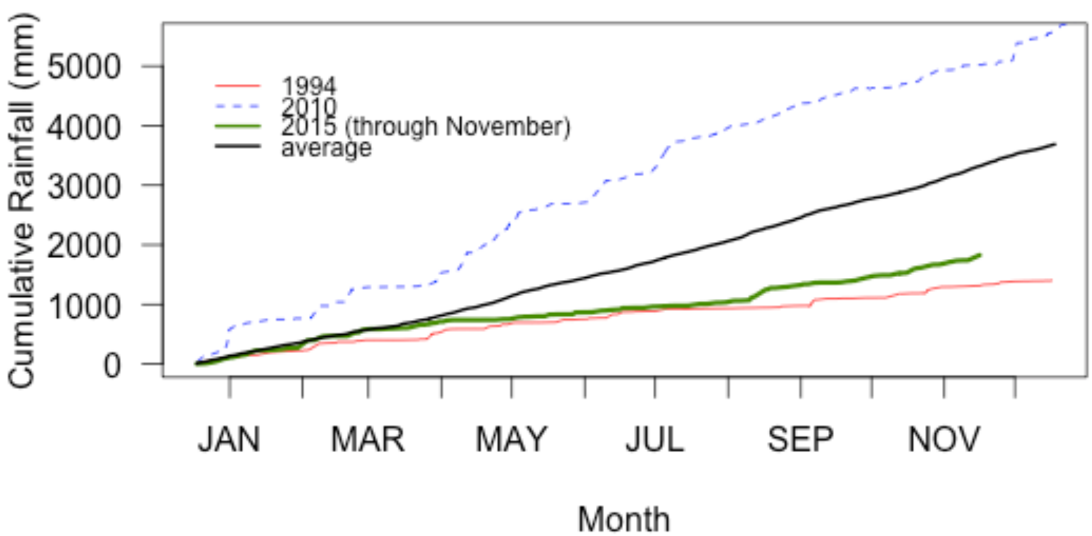

Fig. 2. Cumulative annual rainfall recorded at El Verde Field Station showing the average (1975-2015) contrasted with 2015 and two other individual years, a significantly dry one (1994) and extremely wet one (2010).

amplification of the bimodal seasonal pattern of rainfall manifested as a strong "veranillo" or summer dry period. Thus, 2015 might be considered a "dry run" for anticipated changes in seasonal rainfall in the future.

Impacts on soils were studied in an array placed (this work funded by a grant from DOE to LTER co-PI W. Silver) along a catena at El Verde. The study is designed to capture the biogeochemical response to extreme climate events, such as the drought that occurred in the forest in 2015. We are using automated soil O_2 sensing coupled with measurements of soil chemical and physical properties, climate, and greenhouse gas concentrations and fluxes. These results will be used to derive quantitative relationships linking climate and soil physical properties to redox sensitive biogeochemical processes in tropical forests (see publications by Hall, Silver and colleagues in Products). To better model C and nutrient cycling and greenhouse gas fluxes in Earth system models we need to develop a more mechanistic understanding of the spatial and temporal dynamics and drivers of soil O_2 availability in tropical forest soils. In the LTER, these results will inform plans to experimentally alter precipitation and determine the impacts on linked biogeochemical and biotic responses.

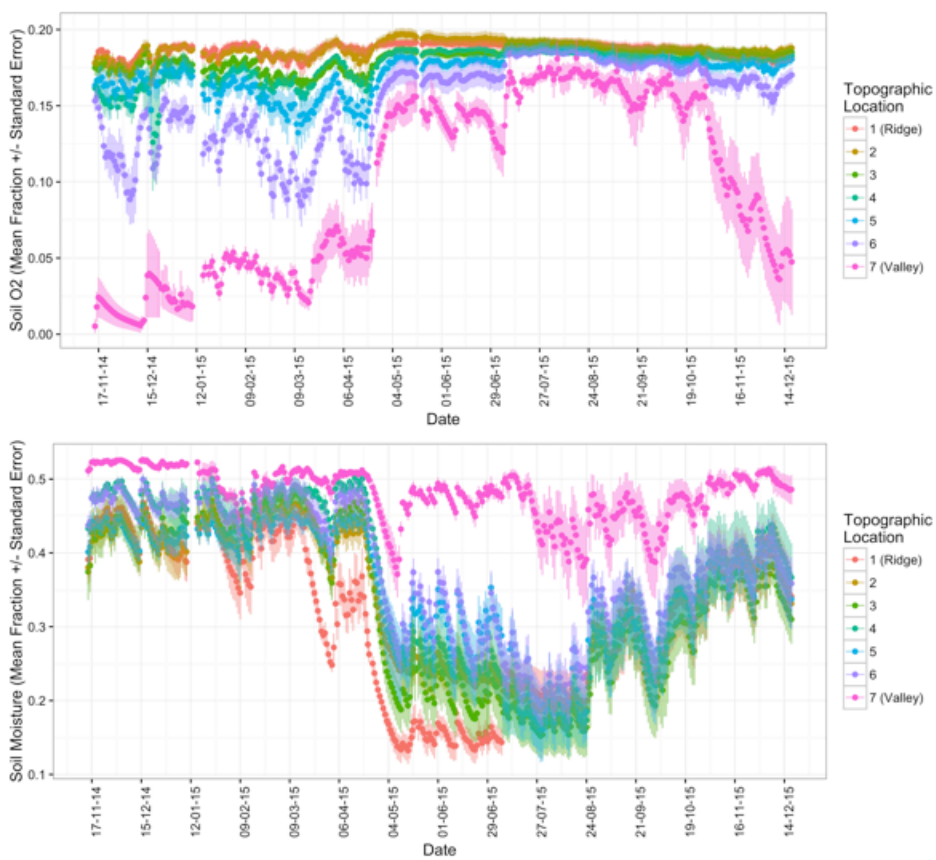

Fig. 3. Changes in (a) soil moisture and (b) soil O_2 in an array of sensors placed along a catena (valley to ridge geomorphological unit) in tabonuco forest near El Verde Field Station during 2015.

As an example of the 2015 drought on hydrology in the LEF, we contrast streamflow in the Mameyes River (one of three focal watersheds we have studied since the beginning of our LTER) with a 25-year average, as well as with patterns observed in1994 and 2010. Streamflow began to show a departure from the long-term average in May and remained quite low until late August. Despite the storms in August and September, the trend remained below the long-term average through late 2015.

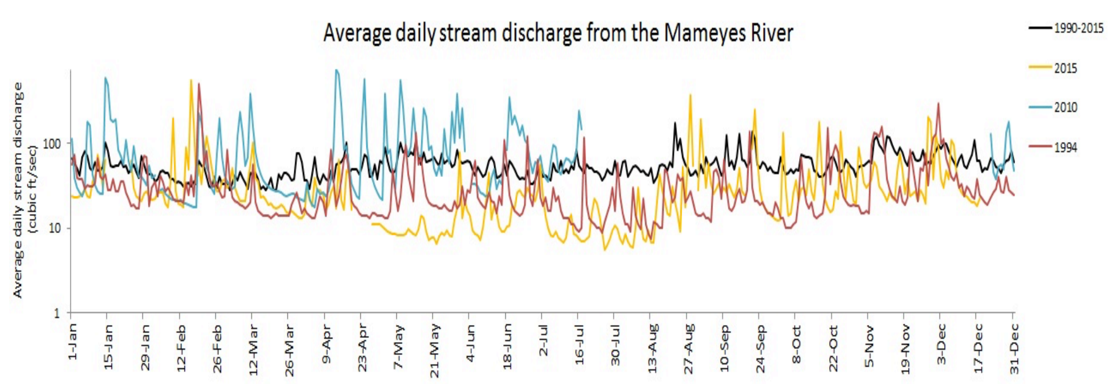

Fig 4. Streamflow in the Mayames River in the LEF. The 25 year average (1990-2015) is contrasted with the most recent year as well as one other extremely dry year (1994) and an unusually wet one (2010).

C. <u>Describe the impact of the drought on seasonal patterns of forest vegetation and terrestrial animals.</u>

One of the earliest responses to the 2015 drought that we noticed was the large input of litterfall from the canopy in May (Fig. 5) that required extra helpers to gather the material from collection baskets. Typically, there is a peak in litterfall at this time of year as a number of species normally turnover leaf mass (Zalamea and González (2008). The increased litterfall represented a wide range of species and was accompanied by many aborted fruits (J. Bithorn, pers. obs.), suggesting it was a stress response simultaneously experienced in much of the vegetation. This distinct pattern was not noticed in 1994, although increased litterfall is one aspect of drought in our wet forests (Beard et al. 2005). This result seems to challenge the notion of “progressivity” of drought effects in our forest. Understanding and experimentally measuring drought responses of the vegetation at relevant spatial scales is one of the challenges we will tackle during the next funding cycle.

A secondary peak in litterfall accompanied the passage of TS Erika on August 28. These events are not unusual at this time of year in our forests and help explain the secondary fall peak in litterfall shown in the averaged data.

We continue to assess the impacts of the 2015 drought on terrestrial and stream habitats with the goal of a major publication on the 2015 “dry run” for long-term climate change. For vegetation, we are especially interested in seedling

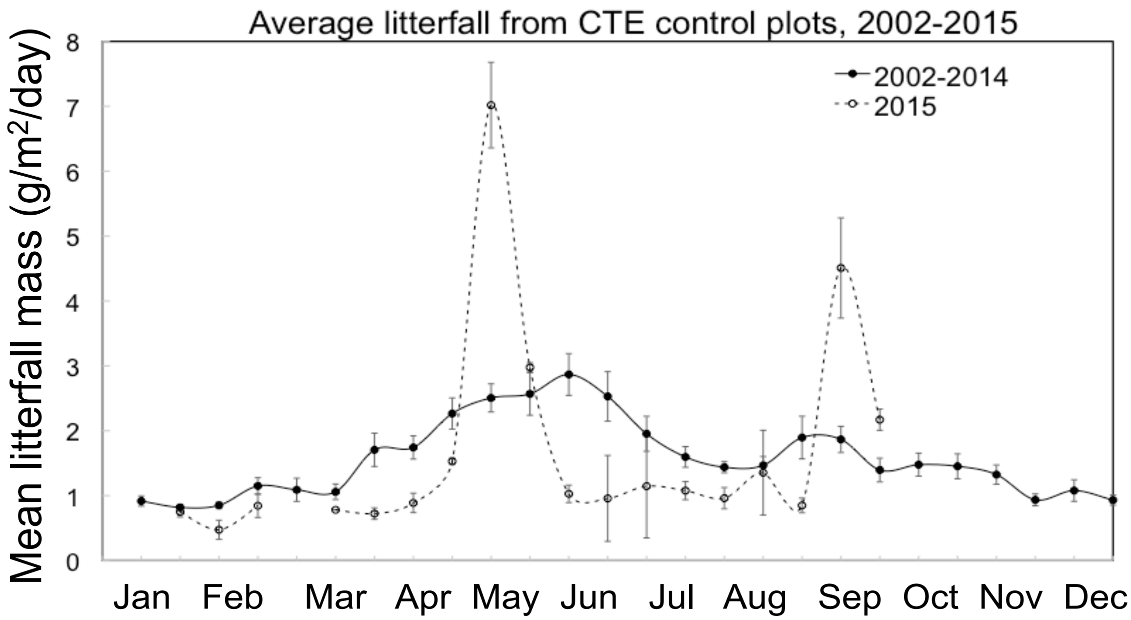

Fig. 5. Biweekly litterfall recorded in the unmanipulated control plots of the Canopy Trimming Experiment, contrasting patterns observed in 2015 with the previous 12 years.

censuses (funded in part by an LTREB grant to Zimmerman) that will provide an opportunity to parameterize models of species-specific seedling mortality to drought. This work will be conducted by Uriarte's group in collaboration with Zimmerman. They are also analyzing tree tree growth data from dendrometers, which showed a 30% reduction in overall growth of trees during the drought year.

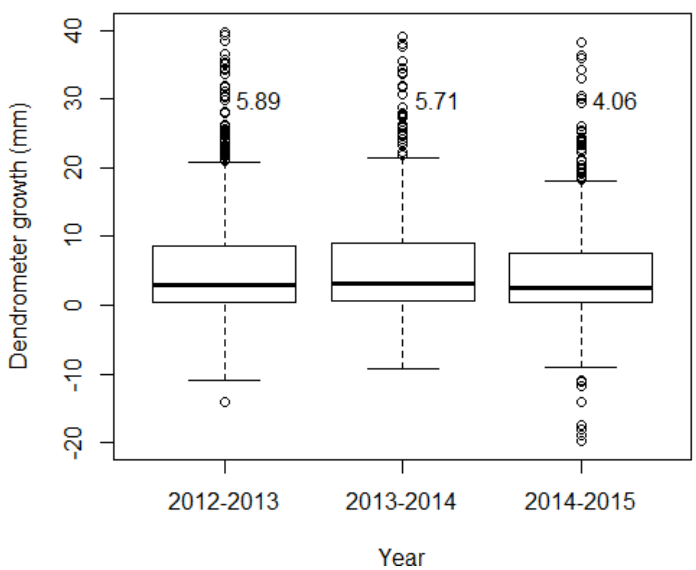

Fig. 6. Average growth (mm diameter) of the largest 1000 trees in the Luquillo Forest Dynamics Plot registered using dendrometer measurements taken each October. Values are averages.

We continue to analyze data on key terrestrial animal groups. Detailed information is available on the response of coquis, the iconic and abundant tree frog in our forests. Arboreal amphibians should be especially susceptible to an intense drought. Woolbright has found that adult frogs largely survived the 2015 drought, being found in aggregations near the ground in the wet valley bottoms. This drought avoidance behavior was accompanied by low calling rates and a lack of aggression among the normally territorial males. Females appeared to retain eggs until the rains resumed, resulting in a large number of small juveniles by November when rains returned. The drought was also accompanied by a reduction in the size of the smallest gravid females, a result that could not be explained by reduced growth rates. Such shifts in the smallest size class of gravid females have not been noted in previous droughts, such as 1994. Behavioral, physiological, and life history responses to drought will be our main focus as we investigate recorded impacts in other key fauna.

D. Describe the impact of the drought on stream habitats.

In response to the severe drought in 2015, Covich, Crowl, Pringle, and Ramirez intensified their sampling of shrimp, algae and other physico-chemical parameters, (from 2 - 5X per year) in the two LUQ LTER focal streams. They conducted integrated sampling of stream pools and riffles at the reach scale in both Bisley-3 and Prieta, with three sets of samples conducted during the drought. During the three drought sampling events, we also measured stream conductivity, NO_3, PO_4-P and TP in stream pools of both focal streams.

They expanded their sampling into Prieta-B, tributary of Prieta-A focal stream that is the “experimental” stream identified in our recent proposal as the site of a major stream-dewatering experiment. Toward this end, we identified and labeled seven stream pools as ‘refugia’ that had formed during the summer-fall drought. These refugia were sampled for shrimps, algal standing crop (chl. *a* and AFDM), stream solute chemistry, and conductivity. Sampling shrimp in very small pools required us to develop and test new, smaller traps for recording their population numbers.

Effects of low flows on decapod-dominated food webs during the drought (from April to September) were similar to those observed in 1994. However, the effects were more prolonged and the directional movement of large predatory species appears to have differed. As pools contracted in volume, the densities of most species increased. For the first time in the last 26 years of study, the pulse of leaf-litter input to the slow-flowing, shallow pools created an excessive amount of leaf litter that led to periods of deoxygenation. Movements of some larger predatory species are still being analyzed to determine if their upstream directional migrations was different from the pattern first observed in 1994. The movement to higher-elevation habitats was initially unexpected because small, shallow pools were thought more likely to be more at risk of deoxygenation than larger, deeper pool habitats at lower elevations.

The LUQ algal data set is unique because of its long-term nature and because it provides integrated quantitative measures of algal basal resources/standing crop (AFDM, chlorophyll *a)* at a relatively large scale (1 km stream reach). Since 2013 we have also analyzed the C;N:P of epilithon to assess potential temporal changes in the quality of algal food resources, thus improving the functionality of our dataset. They group has made good progress on the manuscript resulting from this data that will be submitted to the journal *Freshwater Biology*.

They found dramatically lower levels of algal standing crop during peak drought conditions in 2015 (July-August) in both focal streams: In Bisley-3, algal standing crop was 5-9 fold lower in pools and 2-6 fold lower in riffles compared to the long-term (2003-14) summer average. Inorganic sediments in pools were highly variable and ~2 fold greater in riffles compared to the long-term summer average. In Prieta, algal standing crop was 16-22 fold lower in pools and 11 -18 fold lower in riffles, compared to the long-term summer average (Fig. 7).

They also measured extremely high spatial variability in conductivity and solute chemistry between pools in Prieta and Bisley-3 in July- August 2015 due to the lack of flow in riffles connecting pools. Conductivity in both streams was 1.5 - 1.6 fold greater than mean conductivity over the last decade (2002-12).

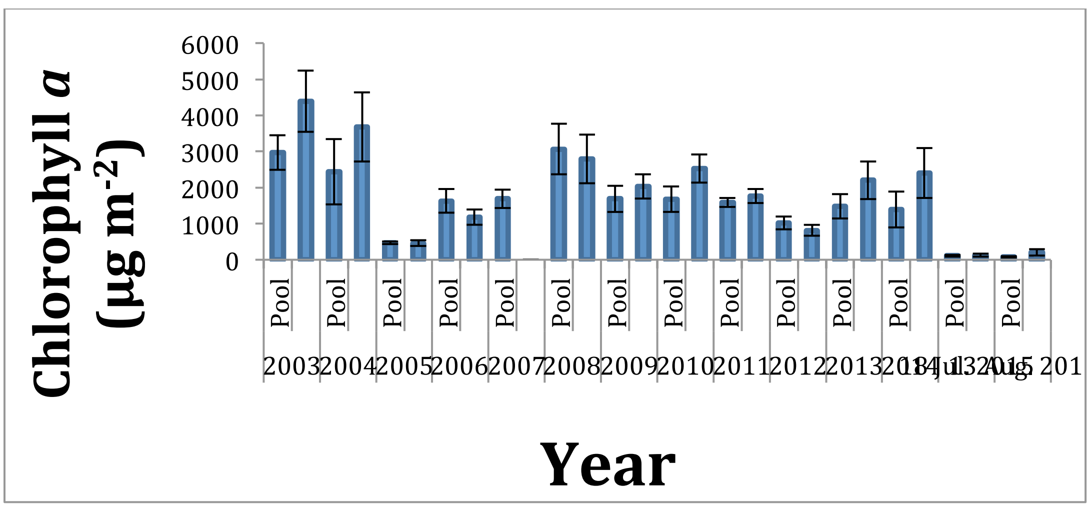

Fig. 7. Chlorophyll a *levels recorded in the Preita A stream from 2003 through the recent drought.*

E. <u>Describe patterns of diversity in gastropod communities along the elevation gradient in the LEF</u>

In our most recent proposal, we describe plans to continue long-term monitoring of elevational variation of key biogeochemistry and biota. We continue to analyze available data sets to establish baseline conditions for long-term climate change. Willig and his crew recently submitted a manuscript directed at understanding the spatial organization of gastropod communities in the LEF. Gastropods, like tree frogs, are likely to be strongly influenced by changes in precipitation. In this manuscript they argue that biodiversity at larger spatial scales (γ) can be driven by within-site components (α), with little variation in composition among locations, or can be driven by among-site components (β) that signal the importance of spatial heterogeneity at landscape or regional scales. For the elevational gradient, they determined (A) if variation in γ is primarily driven by variation in α or β components, (B) the form (e.g. linearly decreasing, mid-elevational peak) of the relationship of each component with elevation, and (C) if elevational gradients in α, β, and γ are molded primarily by changes in vegetation or by gradients in abiotic factors associated with productivity (e.g. temperature, insolation, precipitation). They sampled terrestrial gastropods along two parallel transects in the Luquillo Mountains of Puerto Rico. One transect passed through multiple vegetation types, and one passed through only palm forest. They quantified variation in multiple metrics of taxonomic biodiversity (i.e. species richness, evenness, diversity, and dominance) and decomposed each metric into hierarchical spatial components (α, β, and γ). The contributions of α and β to γ were evaluated via simulation analyses whereas elevational relationships were evaluated via orthogonal polynomial regression.

The relative contributions of α and β to γ were similar for mixed forest and palm forest transects. After accounting for variation in abundance, variation in hierarchical components was associated with elevation in a consistent manner along both transects. Moreover, abundance-based metrics of biodiversity evinced mid-elevational peaks, whereas species richness declined monotonically with increasing elevation. The spatial organization of gastropod biodiversity was not affected by elevational zonation of vegetation (elevational patterns were similar along both mixed forest and palm forest transects). Rather, it was molded by: (1) elevational variation in productivity, (2) the spatial configuration of palm forest, and (3) the cloud condensation point acting as a transition between low and high elevation faunas. Gradual variation in productivity and its correlates played a dominant role in molding elevational gradients in multiple aspects of taxonomic biodiversity as well as in accounting for differences between gradients along mixed forest and palm forest transects.

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

A. Describe the major impacts of canopy trimming in tabonuco forest.

Shiels, González, Lodge, Willig, and Zimmerman recently published a summary of hurricane simulations conducted in the Canopy Trimming Experiment (CTE). This follows the publication of an Special Issue describing the near decade long results from the CTE. This most recent article was part of Special Feature in BioScience on large-scale experiments edited by Shiels and González. In the CTE we used a replicated factorial experiment to determine the mechanisms of forest change associated with canopy openness and organic matter (debris) addition. Cascading effects from canopy openness accounted for most of the shifts in the forest biota and biotic processes (Fig. 8), which included increased plant recruitment and richness, as well as the decreased abundance and diversity of several animal groups. Canopy opening decreased litterfall and litter moisture, thereby inhibiting lignin-degrading fungi, which slowed decomposition. Debris addition temporarily increased tree basal area. Elevated soil solution nitrate was a dominant response after past hurricanes; this effect only occurred in our experiment with simultaneous canopy-opening and debris treatments. Although debris is an important carbon and nutrient source, short-term responses to cyclonic storms appear to be largely driven by canopy opening.

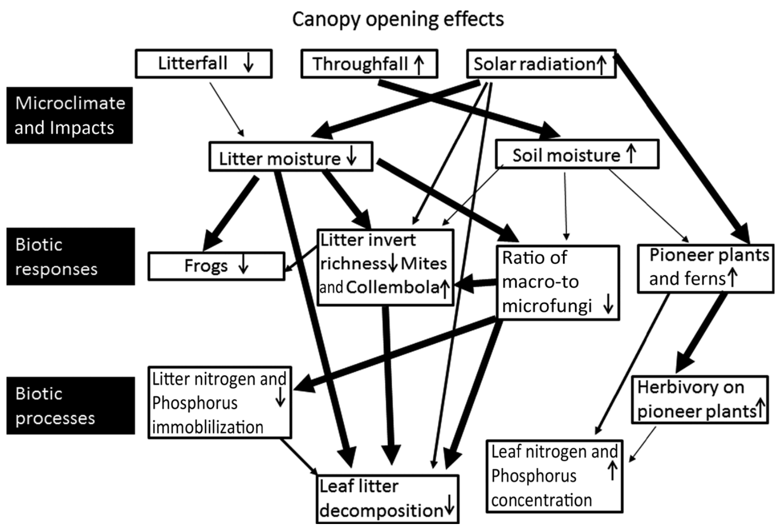

Fig. 8. The effects of canopy opening (trim + no debris) during the first 1–7 years postmanipulation relative to unmanipulated reference plots (no trim + no debris) in tropical wet forest in the Luquillo Mountains of Puerto Rico. The changes in microclimate (first 1 year) and litterfall inputs (first 2.5 years), and responses in the biota and biotic processes are shown, including the effects that cascaded through the food web. In the boxes, the arrows depict increases (the upward arrow) or decreases (the downward arrow); the arrows connecting the boxes represent the influential flows of three levels of strength: strong (the thickest arrows), medium (the medium arrows), and small (the thinnest arrows).

Silver and her lab recently sampled and analyzed soils samples from the CTE To determine the long term impacts of canopy trimming and debris deposition on soil carbon and nutrients, and identify the depth to which these disturbance impacts can be detected. They found a strong depth dependence of soil moisture and pH, with higher water content and acidity in the top soil (> 40 cm), where biological activity is concentrated. After a decade of recovery, we measured significantly higher soil carbon and nitrogen content within the top 20 cm. Soil phosphorus—mainly bicarbonate-extractable organic phosphorus— also responded positively to debris deposition, with significantly higher values in the top 30 cm. Concentrations of reactive iron (Fe) species, including citrateascorbate and HCl extractable Fe, showed marked decreases with depth, and no apparent treatment effects. Finally, preliminary results from soil carbon fractionation suggest that debris deposition increased the free light fraction in the top 10 cm over 10 years.

Considering all four treatments, debris deposition without canopy trimming caused the largest changes in soil carbon and nutrients over the 10 y period, with disturbance impacts being detectable down to ~30 cm depth (for soil organic phosphorus). Interestingly, the effects of debris deposition combined with canopy trimming (i.e., hurricane simulation), did not lead to large changes in soil carbon and nutrients, highlighting the longer-term resistance and resilience of soil biogeochemistry to hurricane-associated disturbances in this wet tropical forest. Large pulses of organic matter deposited during hurricanes appear to subsidize the forest floor but are coupled with rapid and efficient decomposition leading to no detectable changes in C and P stocks over time.

B. Describe major results from a second trim manipulation.

As planned, we conducted a second set of manipulations in the CTE in Fall 2014, one decade after the initial treatments. We simplified the design by only conducting a hurricane-like treatment (trimming and debris deposition combined) abandoning the main effect 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. For this report, we focus on research at the litter-soil interface conducted by Cantrell, Lodge, and González. Their research considered a) the spatial distribution of microbial communities and b) arthropod diversity and nutrient mineralization in green litter decomposition

a) Spatial distribution of soil and leaf litter microbial communities in a simulated hurricane experiment. Microbial communities play important roles in litter decomposition and nutrient cycling. The Canopy Trimming Experiment, started in 2003 at the Luquillo Experimental Forest in Puerto Rico, focused on the immediate effects of hurricanes on forest floor processes and recovery in a tropical wet forest ecosystem. Changes in microbial community structure in the forest soil and litter layer may influence ecosystem recovery. Canopy trimming was applied again in October-November 2014 with the purpose of understanding long-term effects of increased hurricane frequency on forest productivity and carbon sequestration. We used the treatment to study unresolved short-term effects of canopy opening and debris deposition on litter and soil processes. Nutrient leaching and mineralization from green leaves was determined using WesternAg Plant Root Simulator (PRS) Probes placed in the leaf litter fermentation layer (above the mineral soil) one week prior trimming (T0), and one (T1), two (T2), three (T3), five (T4), and 12 (T5) weeks post trimming. Differences between treatments and among times were analyzed using a linear model ANOVA in MiniTab. Soil and leaf litter were collected at T0, T1, T2, T3 T4 and T5. DNA was extracted using MoBio Power Soil DNA Isolation kit. The TRFLP technique was used to obtain profiles of the fungal communities in each sample using the fungal ITS region and the 16S for the bacterial communities. Changes in microbial community structure between samples were analyzed using NMDS and UPGMA. TRFLPs relative abundance data was analyzed using Two-Way PERMANOVA and Bray-Curtis Similarity Index. Significant differences in nutrient concentrations between unmanipulated control and -trimmed plots were observed for total N, NH_4, Ca, K, P, S and Mg in leachates. Leachate nutrients were higher in the trimmed plots. Total leachate N, NH_4, P and S also changed significantly with time, and there was a significant treatment by time interaction for N, NH_4 and P. Leaching of P, K, S and Mg began immediately in trimmed plots. All nutrients showed a peak at T4 (5 weeks). Significant differences are observed for both soil bacterial and fungal communities through time. On the other hand, significant differences between treatments and through time is observed for both bacterial and fungal communities of leaf litter (Fig. 1). These results show that leaf litter microbial communities are sensitive to environmental changes caused by canopy opening and debris addition.

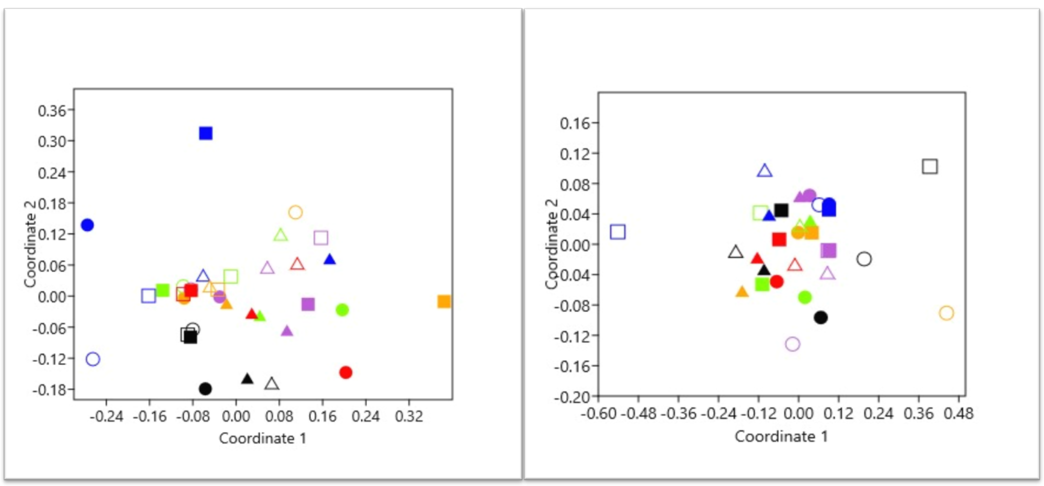

Fig. 9. NMDS of leaf litter fungal (top) and bacterial (bottom) communities. Blocks: A (Circle), B (square), C (triangles); Time (DAYS): T0, T1 (7), T2 (14), T3 (21), T4 (35), T5 (84); Treatment: Control (solid), T+D (open)

b) Arthropod diversity and nutrient mineralization in green litter decomposition in a simulated hurricane experiment

Hurricanes generate disturbances in forests such as canopy opening, fallen trees and leaves which in turn alter physicochemical characteristics of the habitat, as well as, decomposer activity and nutrient fluxes. Litter decomposition depends primarily on the interaction among climate, litter quality and biota, as a consequence any change in habitats will result in changes in these factors. Our objective is to evaluate the effects of hurricane driven changes to forests on decomposition, decomposer communities and nutrient mineralization. Specifically, we will study the effect of a hurricane in green litter decomposition, decomposer fauna and nutrient mineralization. This study is part of the Canopy Trimming Experiment 2 performed by the Luquillo LTER at El Verde Field Station. For this, three blocks (A, B and C) were selected; each with two plots of 20m x 20m, one plot was used for control and the other Canopy opening (Trim). Each plot was subdivided into 16 sub-plots, from which three sub-plots (5m x 5m) were randomly selected. In each subplot, litterbags with different mesh sizes were placed. This experimental design represents 3 blocks x 2 plots/block (1 trim/ 1 control) x 3 subplots x 3 litterbag mesh sizes x 4 collecting times, for a total of 216 litterbags. Each of these litterbags were used as the sampling unit. In each one, decomposer fauna and nutrients were measured. Decomposer fauna were retrieved using Berlese Funnels and mineralized nutrients were quantified using WesternAg PRS probes. Preliminary results suggest significant differences in abundance of decomposer fauna and in available nutrient concentration between trim and control plots, and among litterbags. For example nitrogen and phosphorous were significantly higher in trim plots and in large mesh litterbags. Also, decomposer arthropod abundance was higher in large mesh litterbags. These results suggest that when all decomposer arthropods are present, available nutrients are higher. These results will be further analyzed, and interpreted in the context of food web dynamics.

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

A. <u>Describe efforts to model and predict precipitation variability in the LEF</u>

To investigate how changes in climate influence the LEF, Mote and his student Craig Ramseyer are working to a) determine the climate forcing mechanisms (moisture, wind, pressure patterns) that in conjunction with a dynamic landscape control precipitation in and around LUQ LTER; b) to identify leading modes of variability in atmospheric circulation in the Eastern Caribbean and "downscale" to reconstruct precipitation in LUQ LTER, and c) to understand how changing regional circulation leads to projected changes in drought and precipitation under various future climate change scenarios through the use of an empirical-dynamical downscaling framework. This last goal was incorporated into plans for the next funding cycle.

To date, they have focused on this first objective, finding moisture anomalies and the wind profile in the lower troposphere are the significant controls on precipitation variability. Low precipitation and dry days in the LEF are linked to high wind shear regimes over the eastern Caribbean in the lower 3km of the atmosphere. If moisture is high in this layer, precipitation may still be limited if wind shear is high and/or winds shift to a more southeasterly flow. During certain circulation patterns leading to dry conditions in the LEF, near-surface winds and moisture may be near climate norms but 3 km moisture and winds may be anomalous. During the onset of the 2015 drought, the winds at 3 km in May deviated 20 – 50° from May climate norms across the eastern Caribbean, resulting in predominantly southeastern winds. Additionally, there was a 20 –

40% reduction in moisture at 3 km. These atmospheric conditions contributed to only 84 mm of rainfall falling at El Verde Field Station, approximately a 70% reduction compared to the May average monthly rainfall at El Verde. A manuscript titled, "Atmospheric Controls on Puerto Rico precipitation using Artificial Neural Networks", is in review with *Climate Dynamics*. A manuscript is in preparation regarding the downscaling results.

Meanwhile, González and colleagues have studied micro-climatic trends trends along the elevation gradient in northeastern Puerto Rico. Study results showed that differing patterns of precipitation and temperature change through time across seasons and with elevational position. They examined precipitation and temperature records collected over twelve years at twenty sites, ranging from sea level in the coastal zone of the San Juan Metropolitan area up to 1000 m at the top of the Luquillo Experimental Forest. An analysis of the driest and wettest months of the rainfall seasons revealed that the driest months are getting slightly wetter over time, while no trend was perceived for the wettest months. Precipitation also appears to increase faster at higher elevations. As for temperature, the daily minimum was observed to increase slightly, and the daily maximum decreased, suggesting that the range of temperatures along the elevation gradient is narrowing. Unlike with precipitation, the pace of temperature change did not vary with elevation position. These results emphasize that differing patterns of climate change across tropical elevation gradients should be explored in order to understand the effects of future climate scenarios on biological life and the ecosystem services they provide to human communities.

B. Characterize the impacts of loss of connectivity streams draining the LEF and update the water budget for the LEF

In addition to a changing precipitation regime, the structure and function of streams draining the LEF are strongly influenced by the presence of dams that divert water for human uses. Pringle and her student Pedro Torres are completing two manuscripts on this topic. The first paper presents data from *in situ* macroconsumer exclusion experiments, that were designed to experimentally isolate effects of native biota on rates of leaf decomposition in two study streams (one above a large dam and one without a dam). To assess if observed differences in leaf decomposition rates persisted at a landscape-scale across the island, we analyzed data on *in situ* leaf decomposition rates in 14 different streams (seven above large dams and seven with no dam). The second paper focuses on how nutrient uptake and respiration differ between streams with and without native biota (i.e. undammed and dammed streams, respectively). They found a surprising absence of functional redundancy in streams of Puerto Rico where shrimp have been extirpated (i.e. above dams): no other organisms (e.g., insect shredders) replaced the functional role of extirpated shrimp in driving the process of leaf decomposition – despite the absence of shrimp consumers over decadal time scales.

Completing a major goal of the current funding cycle, Pringle and colleagues developed a new water budget for the EYNF that updates and expands past water budgets (Naumann 1994, Crook et al. 2004) to provide a 20 year record of change. The budget was completed through collaboration with Jason Christian (UGA Engineering), Kyle McKay (US Army Corps of Engineers and UGA Forest Resources) and two UGA graduate students. Completion of this budget is very timely given the severe drought in Puerto Rico during 2015 and can be used to help manage the hydrologic resources within the forest boundaries.

They also developed an advanced hydrological analysis of water resources from the EYNF to the ocean using physics-based models. As the USDA Forest Service implements its “all lands” approach to quantifying contributions of the national forests to surrounding areas, this model will provide approximations of the hydrologic resources in areas outside the forest boundaries. Unlike the mass balance hydrologic approach used previously (Naumann 1994, Crook et al. 2004), they used coupled physical models that partition water between appropriate compartments using a dynamic and physics-based approach. This model system uses time-series precipitation data to calculate a time-series water partition between surface water and soil moisture.

C. Describe the effects of land use on tropical forest succession.

Much of our work on succession is conducted in the Luquillo Forest Dynamics Plot (LFDP) where we have studied the mechanisms influencing species diversity for 25 years. The plot has land use history dating to the early part of the 20^{th} Century such that functions as a laboratory for studying and modeling how a tropical forest with a history of land use will respond to a changing climate. During the coming year we will be using our data from the LFDP to determine how the forest dynamics were influenced by the 2015 drought. Meanwhile, we report a recent study on the increase in lianas in the LFDP. From our recently published studies from the LFDP and Puerto Rico, some of which was conducted with a large number of collaborators around the world, we show how functional traits influence such things as competition, patterns of succession, and how species influence soil resources. We also study interactions with microbes and how they influence tree species diversity in the context of climate change. This work involves collaborations between Uriarte, Brokaw, Zimmerman, Thompson and their students and other colleagues.

In 2015 we counted, identified, and determined canopy coverage of lianas (woody vines) in twenty 20 x 20 m plots in the LFDP. Lianas are studied because their number and biomass are expected to increase disproportionately with CO_2 fertilization. The plots were divided evenly in the two land use area of the plot. We had previously censused lianas in the same plots in 2001. Since 2001, liana stem density increased in the less mature forest that had been subjected to various land uses in the 1930s. Liana stem density did not increase in the pre-hurricane, more mature forest. In the 2001 census, three years after Hurricane Georges, liana density had been lower in the less mature forest than in the more mature forest. The increase during the study period more or less equalized densities between less and more mature forest plots. Percent canopy coverage of lianas increased over all plots. Species richness of lianas over all plots increased by seven species. This REU project will be submitted for publication in the coming year.

The role of tree species variation in growth and survival rates across ontogeny is a potentially important mechanism for promoting forest diversity, particular in high-diversity systems such as tropical forests (Lasky et al 2015). In the LFDP, traits were more strongly associated with average growth and survival than with neighborhood interactions, and were highly consistent across ontogeny for most traits. The associations between trait values and tree responses to crowding by neighbors showed significant shifts as trees grew. Large trees exhibited greater growth as the difference in species trait values among neighbors increased, suggesting trait associated niche partitioning was important for the largest size class. Our results identify potential axes of niche partitioning and performance-equalizing functional trade-offs across ontogeny, promoting species coexistence in this diverse forest community.

Leaf litter inputs have an important role in mediating heterogeneity in soil nutrient content in a successional forest (Uriarte et al 2015). The models developed captured the effects of tree size and location on spatial variation in leaf litterfall (R2 ¼ 0.31–0.79). For all 12 focal species, most of the leaf litter fell less than 5 m away from the source trees, generating finescale spatial heterogeneity in leaf litter inputs. Secondary forest species, which dominate areas in earlier successional stages, had lower leaf litter C:N ratios and produced less litter biomass than old-growth specialists. In contrast, P content and N:P ratios did not vary consistently among successional groups. Interspecific variation in leaf litter quality translated into differences in the quantity and quality (C:N) of total leaf litter biomass inputs and among areas with different land use histories. Spatial variation in leaf litter C:N inputs was the major factor associated with heterogeneity in soil C:N ratios relative to soil physical characteristics. In contrast, spatial variation soil N:P was more strongly associated with spatial variation in topography than heterogeneity in leaf litter inputs. The modeling approach presented here can be used to generate prediction surfaces for leaf litter deposition and quality onto the forest floor, a useful tool for understanding soil–vegetation feedbacks. A better understanding of the role of leaf litter inputs from secondary vegetation in restoring soil nutrient stocks will also assist in climate change on secondary forests in tropical regions (Uriarte et al 2015, Ecol Applications).

We also studied the effects of diversity and host specificity of natural enemies in maintaining tropical tree diversity (Bachelot et al 2015). We found that the relationships between local and (conspecific seedling density) and community scale (conspecific basal area of adult trees) abundance and both richness of above-ground enemies and foliar damage were hump-shaped. Seedlings of tree species existing at intermediate levels of abundance, at both local and community scales, suffered more damage and experienced pressure from a greater diversity of enemies than those existing at high or low densities. We hypothesized that greater damage at intermediate abundance level could arise from a rich mixture of generalist and specialist enemies targeting seedlings of intermediate abundance tree species. Consistent with this hypothesis, we found that generalist enemies were more diverse on species at rare or intermediate abundance relative to common tree species. However, specialist enemies showed no significant trend across tree species abundance at either the local or community scales.

Revisiting data collected on forest age, structure, and composition in plots found throughout Puerto Rico, we studied the role of functional and phylogenetic diversity of tree in mediating successional shifts in of post-agricultural tropical forests and used these data to investigate niche partitioning or competitive dominance hierarchies as drivers of successional change (Muscarella et al 2015). We found increases of community-weighted mean leaf mass area and max height and seed mass with forest age reflected a shift in dominance of species with acquisitive resource-use strategies and small seeds towards species with more conservative resource use and larger seeds. A negative relationship between forest age and local diversity of max height and seed mass suggested increased importance of competitive hierarchies for light capture and shade-tolerant regeneration in older forests. In contrast, the colonization of palms in older forest plots led to a positive relationship between forest age and local phylogenetic diversity, suggesting functional convergence of distantly related lineages on traits that confer competitive dominance.

Data collected in the LFDP contributed to two publications in highly influential journals on tropical forests, diversity, and ecosystem function. The first by Kunstler et al. forthcoming in Nature, found that phenotypic traits and their associated trade-offs have been shown to have globally consistent effects on individual plant physiological functions, but it has remained unclear how these effects scale up to influence competition – a key driver of community assembly in terrestrial vegetation. The paper used growth data from the LFDP and other plots, totaling more than 3 million trees in plots around world to show how three key functional traits – wood density, specific leaf area and maximum height – consistently influence competitive interactions. The trait-based approach to modelling competition developed in the article makes generalization possible across the forest ecosystems of the globe and their highly diverse species composition.

The second article, by Poorter et al. (2015), studied the relationship of aboveground biomass (AGB) to forest attributes (diversity and structure) and environmental drivers (annual rainfall and soil fertility) using data from 144,000 trees, 2050 forest plots and 59 forest sites including the LFDP. Biodiversity was found to have an independent, positive effect on AGB and ecosystem functioning, not only in relatively simple temperate systems but also in structurally complex hyperdiverse tropical forests.

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