Understanding Tropical Forest Abiotic Response to Hurricanes using Experimental Manipulations, Field Observations, and Satellite Data

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Abstract. With projected increasing intensity of hurricanes and large uncertainty in the path of forest recovery from hurricanes, studies are needed to understand the fundamental response of forests to canopy opening and debris deposition: the response of the abiotic factors underneath the canopy. Through two manipulative experiments and instrumenting prior to hurricane María (2017) in the Luquillo Experimental Forest (LEF) of Puerto Rico, this study found a long recovery time of primary abiotic factors (light, throughfall, and temperature) influenced by the disturbance of canopy opening, and complex responses by the secondary abiotic factors (relative humidity, soil moisture, and leaf saturation) influenced by the disturbance of the primary factors. Recovery took 9 years for beneath canopy light, while throughfall recovery took 6 years and neither had recovered when hurricane María passed 3 years after the second experiment. Air and soil temperature seemingly recovered fairly quickly from each disturbance (<2.5 years in two experiments for ~ +1 °C of change); however, temperature was the most important modulator of secondary factors, which followed the long-term patterns of the throughfall. While the soil remained wetter and relative humidity in the air stayed lower until recovery, leaves in the litter and canopy were wetter and drier, with evidence that leaves dry out faster in low rainfall and saturate faster in high rainfall after disturbance. Comparison of satellite and field data before and after the 2017 hurricane showed the utility of satellites in expanding the data coverage, but the muted response of the satellite data suggest they measure dense forest as well as thin forest that is not as disturbed by hurricanes. Thus, quick recovery times recorded by satellites should not be assumed representative of all of the forest. Data records spanning the multiple manipulative experiments followed by hurricane María in the LEF provide evidence that intermediate hurricane frequency has the most extreme abiotic response (with evidence on almost all abiotic factors tested) versus infrequent or frequent hurricanes.

1 Introduction

Hurricanes are expected to increase in intensity with climate change (Emanuel, 1987; Knutson et al., 2010; Yoshida et al., 2017), thus understanding how tropical forests respond to hurricanes is critical to understanding future forest regimes. Tropical forests are in a cycle of non-equilibrium, a cycle driven by the response to the large step-changes of hurricanes (Burslem et al., 2000). Recently, new tools for understanding the nature and duration of the forest-hurricane response have become available for use; satellite data can provide landscape-wide qualities of the historical response (Schwartz et al., 2017) and earth systems models can provide long-term forest response given the projections of increased frequency of hurricanes (Lee et al., 2018). While these tools can provide a large amount of spatially-complete, cost-effective, and consistently-recorded data, the data needs to be placed in context of what is actually happening at the ecosystem level. There is a need for connection between disturbance and recovery at the critical forest scale: for the manner in which landscape-scale data downscales to the more critical forest landscapes, and for the measured response of the forest with repeated hurricanes that should be put into a long-term model (Bustamante et al., 2016; Holm et al., 2014). These connections can only be accomplished with the analysis of fine-scale field observational data. More than understanding when vegetation has recovered, it is important to understand how the abiotic environment affected by the vegetation changes recovers from the disturbance as cascading effects due to canopy openness can account for most of the shifts in the forest biota and biotic processes (Shiels et al., 2015). To this end, a manipulative experiment on hurricane disturbance effects was implemented in the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico. This is a wet tropical forest extending from sea level to 1 km peaks with high rainfall, very high productivity, and frequent hurricane disturbance (González et al., 2013; Scatena and Lugo, 1995; Wang et al., 2003).

The Canopy Trimming Experiment (CTE) was designed to study the key mechanisms behind such a forest's response after a major hurricane, and guide how repeated hurricanes might be expected to alter such ecosystems using these key mechanisms (Richardson et al., 2010; Shiels et al., 2015; Shiels and González, 2014). Multiple control and treated plots were created in the forest. In the treated plots, the forest canopy was trimmed and the canopy debris was littered to the forest floor to simulate the canopy changes from a category 3 hurricane (on the Saffir Simpson scale). On September 20, 2017, category 4 hurricane María made a direct hit on the CTE site, and the experimental sensors captured the acute changes as well as the forest recovery. A relatively small amount of disturbance was attributed to the offshore passing of hurricane Irma 2 weeks earlier; the CTE site was on the lee of hurricane Irma. After the hurricane, comparisons could be drawn between the experiment and the actual hurricane response, as well as an analysis of which aspects of the response were captured by satellite data, MODIS and AMSR2. It is important to note that hurricane María provided a much larger hurricane trimming effect than the CTEs were designed to simulate.

A simplified way of thinking about response to canopy opening and debris deposition is to consider three levels of response. Primary factors are only affected by the initial disturbance: more light and throughfall reach the forest floor and temperatures under the canopy increase. Secondary factors are affected by the primary inputs: relative humidity (in the air), soil moisture, and leaf saturation (wetness of canopy and litter leaves) levels change under the canopy. Tertiary factors are biotic, which are affected by primary and secondary factors, the abiotic factors. Research on biotic effects of hurricane disturbance are numerous (for synthesis efforts see: Mitchell, 2013; Shiels et al., 2015) but less researched is how the abiotic factors have changed to alter the biotic environment. This study attempts to quantify abiotic response as acute changes from a hurricane disturbance (experimental or otherwise) and recovery from the changes, for primary and secondary factors. Quantifying the responses makes it possible to assess if the experimental trimming data and satellite data are reasonable sources for studying the effect of hurricane disturbance and appear to be measuring the same abiotic system, as well as appreciate if different events cause substantially different responses. This study does not attempt to determine what amount of recovery is considered 'normal' conditions to biotic life, or in other words what would affect tertiary factors, but instead quantifies changes in the abiotic factors that can be used to frame the changes found in biotic factors post-hurricane in many previous studies including those of biotic abundance (Shiels et al., 2015), soil biochemistry (Arroyo and Silver, 2018), litter decomposition (González et al., 2014; Lodge et al., 2014), and plant reproduction (Zimmerman et al., 2018).

2 Methods

2.1 Homogenizing Time Series Data Types

In spring of 2005 (CTE1) and December of 2014 (CTE2), in 0.09 ha square plots near the El Verde Field Station (419 m; 18°20' N, 65°49' W), the forest canopy was trimmed, and the canopy debris was littered to the forest floor. The plot size and trim amounts were based on the patch disturbance after the two most recent hurricanes before 2017, both category 3 hurricanes at the location of El Verde: Hugo in September 1989, and Georges in September 1998 (Zimmerman et al., 2014). Details of the trimming and littering treatment, as well as the biotic response to the 2005 experiment have been extensively documented (Richardson et al., 2010; Shiels et al., 2014, 2015; Shiels and González, 2014). The data were collected in the inner 0.04 ha quadrants of the 0.09 ha trimmed plots to minimize edge effects. There were 3 control plots and 3 treated plots. The field data after 2015 were collected sub-hourly by automated sensors and averaged into daily values. The field data before 2015 were collected by different sensors or more intermittent methods (soil and litter gravimetric water contents (GWCs) and canopy photos), so the data had to be converted and calibrated from this first period to the post-2015 period in order to make one time series. Satellite data also had to be converted and calibrated to the post-2015 data type. Throughfall data were collected the entire time period with the same method of bi-weekly recordings of rain funnels. To account for spatial heterogeneity under the canopy, multiple sensors in each plot were used and the results were averaged in all control and treated plots (with quality control).

Many of the data types required calculation of a smoothed data pattern in order to convert and calibrate. In all cases, the smoothing was done using Local Estimated Scatterplot Smoothing (LOESS), which fits least squares polynomials locally to the points. The LOESS degree of smoothing is contingent on the size of the local neighborhood, which here was always chosen to be one year of data around each point. The yearly smoothing was done to extract the larger signal from the data and to homogenize the different collection intervals of the data. The automated sensor field data captured larger amounts of background noise than the temporally smoothed rain funnel data and the geographically smoothed satellite data; and to a lesser extent, the geographically smoothed soil and litter GWCs and canopy photo data. The one-year smoothing neighborhood was chosen to be longer than the longest length of time between repeat measurements across all data types and methods.

Calculations for abiotic responses were made on the resulting time series with the one-year smoothing. Recovery after a CTE experiment was defined as the point in time that the treated data time series crosses the time series of the control data, afterwards which the difference between the treated and control data stays within a 15% buffer of the control data for a year, or until the next event. This could be a conservative measure for biotic recognition, but from an abiotic point of view the 15% buffer corresponds with visual recovery in the time series. Other studies have defined recovery as the year in which the annual maximum value (of the disturbed area) returns to a previous annual maximum value (assumed representative of undisturbed conditions; Lin et al., 2017). While the method used here is dependent on the size of the smoothing neighborhood; it is able to make use of the parallelly collected control data to calculate more precise recovery lengths than a year. Furthermore, in a frequently disturbed regime such as the LEF, it is difficult to say what year would be representative of undisturbed conditions. Time series were also analyzed to calculate acute change from disturbance. The acute change after the hurricane was defined as the change in the control time series or the satellite time series from right before the hurricane to right after the hurricane, September 20, 2017. The acute change after an experiment disturbance event was defined as the maximum difference between the treated and control time series (in relation to the control time series) on any day between the last day of the canopy trimming (spring 2005, December 2014) and of the next September 20 (year 2005 and 2015, respectively), so that the experimental changes could be compared to the hurricane changes. Sensitivity tests were performed to see how the calculated recovery lengths differed with smaller and larger buffers than the 15%, as well as how the recovery lengths and acute changes differed with smaller and larger smoothing neighborhoods than the one year.

Temperature data were collected after 2015 by a Decagon Devices VP-3 sensor in each plot in the air 2 m up from the ground (which also collected relative humidity in the air) and a 5TM sensor in each plot in the soil 0.05 m down into the ground. Earlier temperature data were collected hourly by a Campbell Scientific 107 sensor in each plot in the air and one in the soil, underneath the canopy. Air temperature above the canopy was calculated with the same instrument the entire time period, so annual patterns of the ratios of above-canopy air temperature to below-canopy air and soil temperature were used to calibrate the 107 data. First, the ratios were calculated for two years of VP-3 data before the hurricane (so excluding the 2015 drought). These annual patterns were averaged and smoothed into one annual ratio pattern for air and one for soil. Then an air and soil annual ratio pattern was calculated for the complete years of the 107 data (so excluding 2005-2007) and the above canopy data, and the difference between the ratios were used to make one annual correction each for air and soil that was applied for every year of the 107 data. The air temperature field data were compared directly to MODIS Aqua and Terra satellite land surface temperature (LST) data at 1 km, 8-day resolution. MODIS LST measures energy balance at the land surface, so is not representative of air temperature under the canopy but it will be affected by changes in air temperature. Annual maximums of

LST and air temperature are highly correlated across the globe with correlation strongest in forested areas (Mildrexler et al., 2011), and LST has been shown to respond to forest cover changes in other areas of the tropics (van Leeuwen et al., 2011).

Soil volumetric water content (VWC) data were collected after 2015 by reflectometers: one Decagon Devices 5TM sensor in each plot shallowly at 5 cm and three Campbell Scientific CS616 sensors in each plot as profiles 0-15 cm. The VWC profile data are comparable to measurements of soil moisture collected by drying out soil samples. Such soil samples were collected for GWCs approximately every 3 months 2003-2006, and in 2015, with 5 in each plot. Some of these soil GWCs have been published previously before this reanalysis (Richardson et al., 2010). Here, soil GWCs were converted to soil VWCs estimates with measurements of soil bulk density recorded at the same time as the GWCs; or, using average values from each plot if direct measurements were not available. The 2015 overlap period between the smoothed data of the sensors and the soil sample data was used to calibrate the converted data. The shallow soil VWC field data were compared directly to AMSR2 descending and ascending track satellite soil VWC data, at 10 km, 1-day resolution.

Leaf saturation data were collected after 2015 by three Decagon Devices dielectric leaf wetness sensors in the canopy leaves in each plot 5 m up from the ground and three in the litter leaf layer in each plot. These sensors have similar thermal mass and radiative properties to real leaves, and wetness is measured by the voltage signal output after voltage excitation, which is higher in proportion to the volume of water on the sensor. This voltage output was then assigned 0% saturation (dry) at the lowest recorded value, and 100% saturation at the highest recorded value. Earlier measurements of litter saturation were made with leaf GWC values from litterbags, 5 in each control plot and 10 in each treated plot. These litterbags were made of air-dried, pre-weighed leaves, placed in the litter layer immediately after the CTE1 trimming and retrieved for collection approximately every 3 months 2005-2006. This data was published previously (Richardson et al., 2010). The litterbag procedure was repeated for the CTE2 trimming, and four litterbag measurements of GWC were made in 2015. Leaf GWC is proportional to leaf VWC if the assumption of constant leaf bulk density across plots is made. Then the early litterbag data could be converted to saturation percentages using the ratio between the data of the 2015 litterbags and the smoothed data of the dielectric leaf wetness sensors collected at the same time.

Solar radiation data were collected after 2015 by a Campbell Scientific LI200X pyranometer in each plot measuring 400-1100 nm light from sun plus sky radiation. Earlier estimates of solar radiation were made with sets of hemispherical canopy photos, ten photos in each set in each plot, which were taken approximately every 4 months 2005-2012. Sets of photos were also taken before the first experiment, and once a year 2015-2017. The solar radiation field data were compared to MODIS Aqua and Terra satellite leaf area index (LAI) data at 500 m, 8-day resolution. The Beer-Lambert law (Monsi, 1953) was used to convert the LAI data into solar radiation estimates. Annual patterns of photosynthetically active radiation (PAR) extinction coefficients needed for the Beer-Lambert law were calculated by solving the Beer-Lambert Law for the coefficients with the field-measured control plot solar radiation, and the field-measured above canopy solar radiation, and the MODIS LAI data. The coefficients were solved for using with all data interpolated or averaged to daily values, and only using the two years of data before the hurricane (so excluding the 2015 drought). These annual patterns were averaged and smoothed into one annual pattern that was applied for every year of the MODIS data.

2.2 Estimating Solar Radiation from Canopy Photos

Canopy photos were converted to global solar radiation data with a modified version of the Hemiphot method (ter Steege, 2018) as follows. Images were converted from color to black and white with a threshold, where the threshold is found iteratively for the best separation of background and foreground using the Ridler and Calvard method (Bachelot, 2016); this method requires calibration. Thresholding was later calibrated to have agreement between annual patterns in the photo solar radiation data and annual patterns in the instrument measured solar radiation data measured in the control plots. Next, the black and white images were converted to canopy openness data by calculating openness on concentric rings of the photo representing sky hemisphere with an arc of 1 degree.

Then, PAR was calculated under the canopy for every day of the year before and after each photo, assuming a constant canopy cover for those time periods. The PAR was then made into one daily time series at each photo site by linearly interpolating PAR each day as a fraction of the previous and the next photo's calculated PAR on that day. This roughly interpolated the canopy cover changes due to recovery from the trimming, and interpolated seasonal changes in canopy cover as long as the photos were repeated every winter and summer.

The PAR is the sum of direct and indirect light. The direct light was calculated from the path length of the sun's light through the atmosphere to the forest and the atmospheric transmissivity. Atmospheric transmissivity was given variability around the standard tropical value assuming a linear relationship with relative humidity in the air (Winslow et al., 2001) (as measured above canopy). Path length was calculated from the sun's orbital position on each day of the year relative to the forest. Diffuse light was calculated assuming each part of the sky is equally bright and thus diffuse light is a fraction of direct light. Underneath the canopy, PAR can be approximated as the sum of the direct light through all open parts of the canopy and the diffuse light multiplied by the uniform overcast sky indirect site factor. Global solar radiation is then approximated as a multiple of PAR (2X; see Escobedo et al., 2009) calibrated to solar radiation measurements from above the canopy.

3 Results

Figures 1 and 2 show all data in daily time series from 2003 to 2019, for field data and satellite data. Data for each day of measurement are plotted, as well as the data smoothed with LOESS. No smoothing was done across any of the event dates, in CTE treated, control, or satellite data, regardless if the data type was affected by each event. These smoothing breaks were used to keep boundary conditions of the LOESS applications more similar. Figure 1 shows primary factors and Figure 2 shows secondary factors. Soil temperatures (Figure 1d) are somewhat between primary and secondary factors, since it is reasonable that they would respond to changes in throughfall at some level; however, based on the data results they are considered primary factors in this study. Table 1 shows recovery time from the canopy trimming experiments and the percent and absolute acute change after a disturbance event, experimental or actual hurricane, as computed on the smoothed data and defined in the methods. The time of recovery from the experiments for each abiotic factor is also marked on Figures 1 and 2, if recovery is seen before the next event. Recovery of throughfall was calculated to be the longest, followed by solar radiation with the temperatures and relative humidity in the air taking less than half the time to recover (Table 1). The most acute change is seen in the solar radiation, followed by throughfall, then soil moisture and leaf saturation, and lastly temperatures (Table 1).

Sensitivity tests were performed using different LOESS smoothing neighborhoods and altering the size of the 15% buffer. The calculated recovery times are very robust to altering in the size of the neighborhood from half as large to twice as large (neighborhoods of 0.5-2 years), with a mean of less than ±0.2 years for any neighborhood size. Larger neighborhoods than the one-year reported in Table 1 disproportionally effect the calculated recovery times of the coarser data, throughfall and CTE1 litter saturation (Figures 1b, 2e). Smaller neighborhoods than the one-year reported in Table 1 disproportionally affect the calculated recovery times of the noisier data and the data with many missing observations, throughfall and CTE1 air and soil temperatures, respectively (Figures 1b-d). Allowing the buffer (inside which the control and treated plots are said to be similar enough to warrant a recovered state) to be from half as large to twice as large (buffers of 7.5-30%) only affects the calculation of the recovery lengths of CTE1 solar radiation, CTE1 throughfall, and CTE1 and CTE2 litter saturation (Figures 1a, 1b, 2e and Table 1). Solar radiation is calculated to recover after CTE1 somewhat quicker, in 5 years (from 6 years) with a larger buffer, and it does not recover in the 7.6 years if the buffer is shrunk to 7.5%. Throughfall recovery calculation does not change if the buffer is larger, but it does not recover in the 9.9 years of CTE1 if the buffer is smaller. Litter saturation is calculated to recover after CTE2 in 0.7 years right after the summer 2015 drought (down from >2.8 years) with a larger buffer (and still in 1.0 years after CTE1, and it does not recover in the 2.1 years after CTE1 if the buffer is shrunk to 7.5% (and still not in the 2.8 years after CTE2). The calculated changes after an experimental disturbance event are fairly robust to altering the size of the neighborhood (absolute changes are on average less than ±15% different), but the calculated changes after the hurricane can be quite affected if the neighborhood is expanded, making the time series smoother at the end points before and after the hurricane (Figures 1, 2).

Daily means of all data (point data in Figures 1 and 2) were prewhitened by filtering with an autoregressive integrated moving average model (ARIMA; (Box et al., 2015) and first-differencing to remove seasonality and trends, and the resulting prewhitened data were examined for correlation between primary and secondary factors for periods with daily data (after CTE2 and after the hurricanes). The prewhitened air relative humidity correlated well with both the prewhitened solar radiation and air temperature (R^2 = -0.67) across all periods and plots. The prewhitened leaf saturation (canopy and litter) correlated somewhat with both the prewhitened solar radiation (R^2 = -0.35) and air temperature (R^2 = -0.49) across all periods and plots.

The prewhitened soil moisture (shallow and profiles) did not correlate consistently well with any of the primary factors. All significant correlations were highest at zero lags.

4 Discussion

The data from after hurricane María were very similar to the data after the two trimming events, which was the aim; however, it is encouraging how well the experiments worked. With only 0.09 ha plots, edge effects of the non-disturbed forest were expected to lessen the effectiveness of the experiments in simulating hurricane disturbance; yet, the solar radiation suggested that CTE2 was the most immediately disruptive event. However, the differences in the seasonal timing of the experiment treatments and hurricane María, as well as sensitivity of the calculations of actual hurricane effects to the data smoothing, make direct comparison of acute changes from the experimental events and actual hurricane disturbances challenging. The quantification of the acute changes in the experimental setup is useful as a measure of the effect of a hurricane on the abiotic environment, while the quantification of the acute changes from the actual hurricane serves best as a comparison between the field and satellite data, and between the relative effects on each abiotic factor for the CTE and the hurricane.

The passage of hurricane María, 2.8 years after the second experiment, showed a smaller effect on the treated plots than the control plots, such that the absolute level of abiotic disturbance on the treated plots was smaller than on the control plots (Figures 1, 2). It is expected that the abiotic fluctuations from the hurricane would be smaller in the unrecovered treated plots than in the control plots since there is less vegetation to disturb. The fluctuation is smaller, but furthermore for most of the abiotic factors, the treated plots are closer to the recovered state after the hurricane than are the control plots. For example, there is more solar radiation reaching the forest floor in the treated plots than in the control plots before hurricane María, but after the hurricane there is less solar radiation reaching the forest floor in the treated plots than in the control plots (Figure 1a). The same scenario can be seen in the throughfall (Figure 1b), the temperatures to a lesser extent (Figures 1c, d), the soil moisture profile (Figure 2c), and the litter saturation (Figure 2e). The air relative humidity has the opposite scenario, showing treated plots closer to the recovery state of less humidity in the air after the hurricane (Figure 2a). This provides evidence that when frequent hurricanes happen, the forests will exhibit abiotic resilience, and thus possibly forests with an intermediate hurricane frequency will have larger abiotic fluctuations due to disturbance than forests with infrequent or frequent hurricanes. Supporting evidence has been found also in the biotic factors of the forest after hurricane María (Hogan et al., 2018), with analysis suggesting tree demographics (the rates of species and stem mortality and growth) were the most dynamic in areas which had the chance to grow some (but not all) trees past the pioneer stage. Intermediate disturbance has long been suggested to keep systems as far from equilibrium states as possible, with the important effect of driving ecosystem diversity (Connell, 1978). Frequent disturbance in the LEF could be regarded as less than a decade (because abiotic factors have not recovered in this time frame), with intermediate frequency longer than a decade but still less than the 60-year long-term return interval for hurricane disturbance in this forest. The 60 year time frame has been estimated to be a long enough period to achieve steady state for time-length of biomass turnover (Scatena, 1995), so disturbances, for this system, might be considered infrequent if they happen less than every 60 years.

Satellite data have similar characteristics to the field data in the control plots (blue vs. black lines in Figures 1a, 1c, 2b) in that the magnitude is similar and the responses to the summer 2015 drought and hurricane María are in the same direction. However, they appear to exhibit spatial smoothing horizontally and vertically across the landscape. The LEF lost 51% of the initial greenness in hurricane María, but the U.S. Caribbean overall lost 31% of its initial greenness (Van Beusekom et al., 2018), so for the hurricane disturbance, including area outside the forest would be expected to smooth the hurricane signal. Before the hurricane, the (MODIS LAI-estimated) solar radiation satellite data look similar to the field data, but the smaller change in the satellite data after the hurricane and faster recovery down to previous values (Figure 1a) suggests that the satellite was measuring an averaged area that contained thin and dense forest, versus the point in the field. Also, LAI may measure some low vegetation that grows back quicker and not recovering canopy, thus vertically averaging the LAI. The (MODIS LST-estimated) temperature satellite data plot between the field air temperature data measured below the canopy and that measured above the canopy at 30 m (black and gray lines respectively, Figure 1c), giving evidence that the satellite measurements were affected by a vertically averaged Earth, as might be expected from a LST representative of surface energy balance. The (AMSR2-estimated) shallow soil moisture satellite data seem strongly affected by their large spatial smoothing (10 km resolution), with the 2015 drought and the hurricane effects appearing in the data but the soil moisture recovery of the intact forest after the drought is not seen in the satellite data as it is in the field data (Figure 2b).

Two of the primary factors, light and water, changed dramatically after the disturbance events (Table 1, Figures 1a, 1b). Across the three events, the range of the percentage change in understory solar radiation after disturbance was quite large; it is likely that a sizeable portion of the range is due to the different seasonal timing of the events. The 1998 Hurricane Georges was estimated to have changed the forest light by almost 400% (Comita et al., 2009), which is within the range seen here. The response of reduced understory light and throughfall (Table 1) was found here to last much longer than the 18 months concluded in previously (Richardson et al., 2010). However, it was noted in a related study (Shiels et al., 2010) that the control plot understory solar radiation appeared to be still recovering from the 1998 Hurricane Georges in the early measurements. The time series here support a continuing recovery from Georges; see the decreasing solar radiation trend 2004-2008 in control CTE data, and also in the satellite data 2003-2008 (Figure 1a). This 9 to 10-year understory light recovery time after Hurricane Georges is compatible with the new CTE1 estimate of 8.9 years to recovery (Table 1). This study had additional information from the second experimental trimming, as well as a longer record of analyzed data from the first trimming and new methods to make a more-continuous record from the intermittent field data. The response may appear in the drier darker season as being recovered (e.g., January 2008, 3 years post-trimming), but it is clear with the longer record that the response is slower to recover. Temperatures of air and soil were much more robust in respect to the changes from the events versus their annual seasonal cycle changes, with approximately 3% air and 6% soil acute increases, or +0.7 °C air and +1.4 °C soil, recovered by

2-2.5 years (Table 1, Figures 1c, 1d). But these changes may still be significant to biotic factors. Other studies show that gross primary productivity of the forest is highly sensitive to small increases in temperature greatly increasing canopy temperature (Pau et al., 2018), so this change that is exemplified in the hottest parts of the year (Figures 1c, 1d) should not be discounted.

Abiotic factors that change because of primary factor changes, or secondary factors, have more complicated recovery paths than the primary factors. Specific timelines for recovery would be expected to be highly influenced by the tree species and soil types, and the rates seen here for all abiotic factors would not necessarily apply to all hurricane-effected tropical forests. Nevertheless, general patterns might be expected to hold. All of the secondary factors were clearly affected by the summer 2015 drought and subsequent long-term rainfall levels, as seen by the large magnitude decreases in summer 2015 and the recovery afterwards in all plots of Figure 2. However, daily patterns of the relative humidity in the air and leaf saturation under the canopy were significantly influenced by the temperature and light inputs (based on the results of the residual correlations), while soil moisture may not be influenced much by these inputs. Relative humidity (Table 1, Figure 2a) recovered from a 5% decrease after CTE2 in 2.7 years (right before hurricane María) according to the defined recovery criteria, but it seems conceivable that it had only temporarily recovered in the autumn season, and the treated plots would not have reached the same maximum seasonal relative humidity in the air as the control plots in the winter. The soil moisture and litter saturation responses from the first trimming present different conclusions when analyzed along with the nearly continuous in situ measurements after the second trimming. Previous studies found very quick recovery of these factors, 3 months and 18 months, respectively (Richardson et al., 2010). However, re-analysis of the data after the first experimental trimming: separating the data into control and treated plots; calculating volume-based percentages of water in the soil and litter instead of mass-based percentages; and most significantly, looking at the trimonthly collected data from CTE1 in light of the nearly continuously collected data from CTE2, led this study to draw different conclusions.

The soil moisture increases in all three trimming events (including the hurricane) but the magnitude of the acute change and the time till recovery appears highly dependent on the amount of rainfall (Table 1, Figure 2b, 2c). Differences between treated and control sites appear pronounced in dry periods (e.g., spring 2006 and summer 2015), with wet periods obscuring the differences in the sites when the soil may be approaching saturation (e.g., summer 2006). However, the recovery process happens mostly monotonically (in the smoothed time series) and looks close to the 15% buffer by 2.8 years. Soil moisture is higher after disturbance because there is more throughfall and less transpiration (no leaves), but once the leaf area starts to recover the soil moisture recovers quickly.

Conversely, during the dry periods the differences between treated and control sites are obscured for the leaf saturation data. The litter leaves in the second trimming were measured to be wetter and drier following the trim, and not uniformly drier as concluded previously (Figures 2d, 2e). Data from the second trimming and hurricane María shows that the litter was more saturated immediately following the events, and the canopy leaves were drier. During periods of low rainfall, the treated plots dry out faster than the control plots, in both litter and canopy leaves. Sometimes this results in the leaf saturation being lower in the treated plots than the control plots (e.g., summer 2015 and spring 2017). When the rainfall increases after a dry period, during the late-summer rainfall, the treated plot leaf saturation increases much faster than the control plots, suggesting the long-term effect of disturbance on leaf saturation is a more dramatic modulation in saturation by rainfall. Other studies in completely different ecosystems, southeastern United States, have seen that litter is able to become more saturated after large storms than before the storms, and they attribute this to the addition of new debris being able to hold on to more water (Van Stan et al., 2017). The litter saturation data from the first experimental trimming (data from 2005-2007) do not contradict this conclusion, but due to their record length and collection interval (trimonthly) they are not overly conclusive.

The results do not support a longer or shorter recovery time interval for the second treatment, ten years after the first (Table 1). The results in the sensitivity tests showed that quantifying recovery times using smoothed time series to homogenize data from several sources was a worthwhile effort, in that the abiotic factors can be sorted into quicker and slower recoveries, with results robust to the smoothing method. However, the definition of the ‘recovered point’ in time will be dependent on what biotic life considers ‘normal’, necessarily different for every organism. Across all abiotic factors, this study used a uniform buffer metric of ‘within 15% agreement between control and treated plots’ once the experimental response is finished, in order to quantify the length of abiotic recovery as a starting point to for other researchers to frame the changes found in biotic factors post-hurricane. The percentage of the buffer did not matter to the results in most cases, as shown in the sensitivity tests. However, the percentage did alter the results on factors with more complicated recovery paths, such as litter saturation (Figure 2e), and factors with more data variance, such as solar radiation and throughfall (Figures 1a, b). This points to the difficulty of quantifying recovery in an environmental system.

Climate projections predict Puerto Rico air temperature will be +2 °C warmer in the coming century and rainfall will be -20 to -30% smaller in the fall and summer wet seasons (Hall et al., 2013; Karmalkar et al., 2013). Effects from future hurricanes on the abiotic factors will be on top of this background change. This means a hurricane could add an acute effect of almost 50% more to the temperature increase, with a recovery of over 2 years (Table 1). The throughfall after a hurricane was found to increase >100% with a long recovery of almost 9 years (Table 1). But, given the climate projections of more events like the summer 2015 drought, the more noteworthy effect of future hurricanes may be the litter and canopy leaves drying out much faster in the drought and saturating faster with rain after the drought. This will creating a much more dynamic environment of leaf wetness, which may have implications for biotic factors.

5 Conclusions

The manner in which abiotic characteristics are disturbed and the speed at which they recover will be key to the continued existence of tropical forests under a climate with more intense hurricane activity. Climate projections predict changes that will exacerbate the effects of hurricanes of increasing temperature and dynamically changing leaf wetness. There is evidence here that intermediate hurricane frequency will have the most extreme abiotic response (with evidence on almost all abiotic factors tested) versus infrequent or frequent hurricanes, and that satellite data may show a faster recovery than field data looking at canopy response and soil moisture. Caution must be exercised when declaring the recovered point of a forest, as canopy closing may take a decade and not all abiotic factors recover monotonically. Abiotic factor responses to hurricanes are not included in current climate projections. Results from detailed manipulative experiments such as this study are needed in order to begin to quantify abiotic factor responses to hurricanes to add to the climate projections.

Data Availability

The CTE data are hosted on the USDA Forest Service Research Data Archive at https://doi.org/10.2737/RDS-2019-0051 (González et al., 2019).

Author Contribution

AEVB designed and carried out the mathematical analysis. GG, SS, JKZ, and AR designed, supervised, and carried out the experiment. GG installed sensors and oversaw data collection of solar radiation, temperature, relative humidity, soil moisture, and leaf saturation after CTE2. AEVB prepared the manuscript with contributions from GG and AR.

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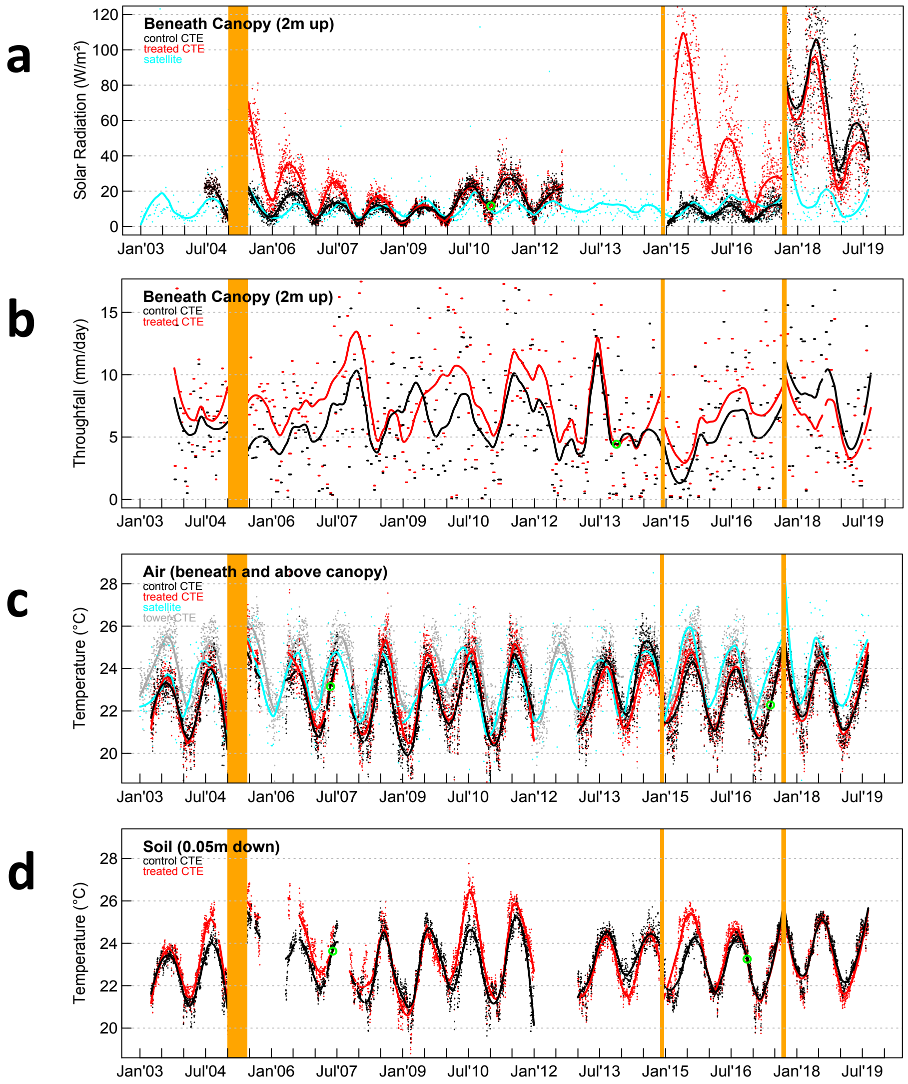

Figure 1: Primary factor time series, or factors that change due to the initial disturbance changes. Orange vertical lines are the periods of canopy trimming experiment (CTE) 1, CTE2, and hurricanes Irma and María (appear as one line), sequentially. Points are data values on a day and lines are smoothed data. Red points and lines are from treated areas and black points and lines are from control areas (until the hurricanes) beneath the canopy. Gray points and lines are from a 30 m tower above the whole area and cyan points and lines are from satellite data estimates of some of the variables. The time of recovery from each experiment (if seen) is marked with a green circle, Plots show a) solar radiation beneath the canopy; b) throughfall; c) air temperature; and d) soil temperature.

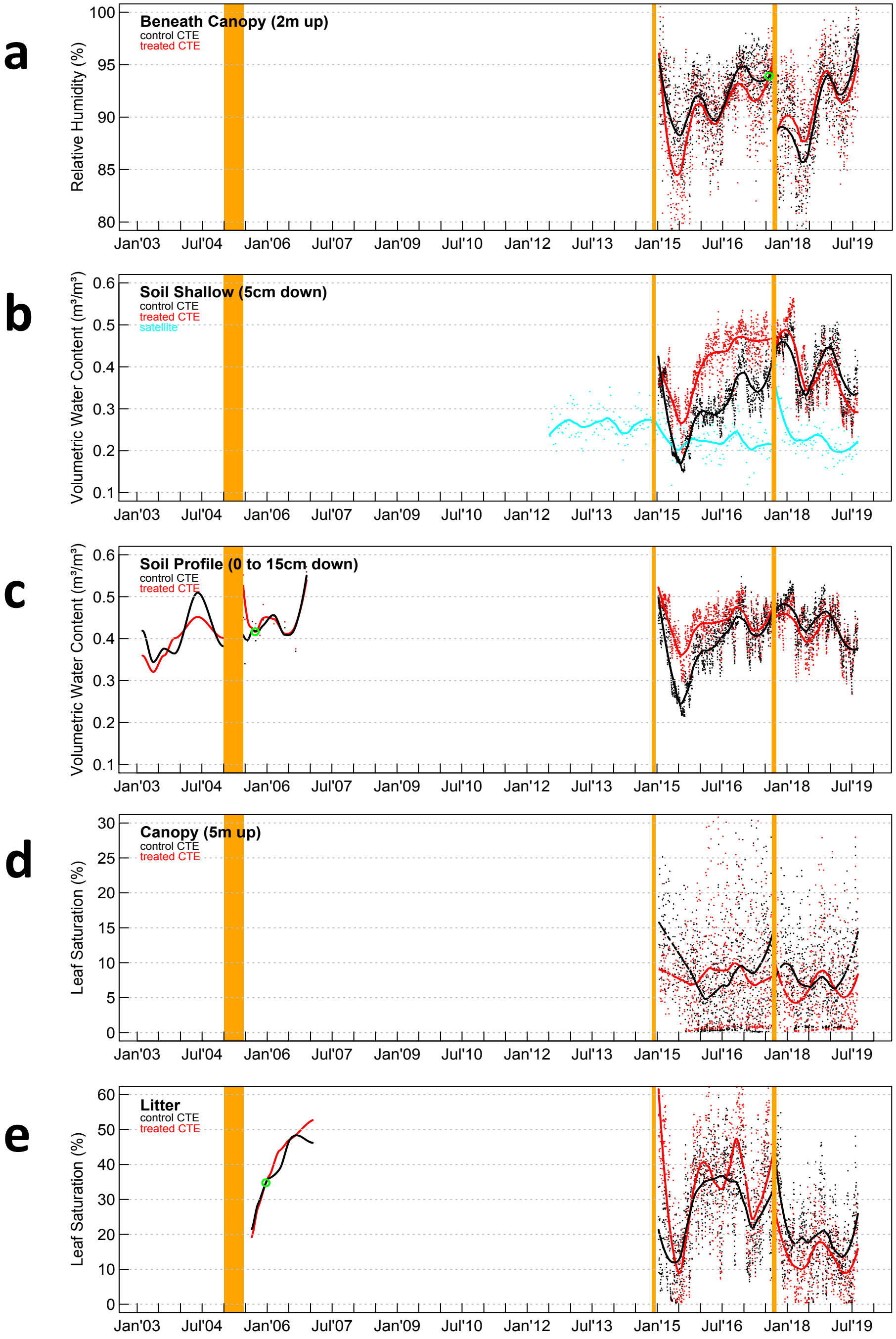

Figure 2: Secondary factor time series, or factors that change because of primary factor changes. Orange vertical lines are the periods of canopy trimming experiment (CTE) 1, CTE2, and hurricanes Irma and María (appear as one line), sequentially. Points are data values on a day and lines are smoothed data. Red points and lines are from treated areas and black points and lines are from control areas (until the hurricanes) beneath the canopy. Cyan points and lines are from satellite data of some of the variables.

The time of recovery from each experiment (if seen) is marked with a green circle, Plots show a) air relative humidity; b) soil moisture shallow; c) soil moisture profile; d) canopy leaf saturation; and e) litter leaf saturation.

	Recovery Time		Change from CTE				Change from Hurricane			
	CTE1	CTE2	CTE1*		CTE2*		Instruments**		Satellite**	
Solar Radiation	6.0 yrs	>2.8 yrs	214 %	*48 W/m^2*	919 %	*99 W/m^2*	666 %	*74 W/m^2*	234 %	*40 W/m^2*
Throughfall	8.9 yrs	>2.8 yrs	100 %	*4 mm/day*	119 %	*2 mm/day*	46 %	*4 mm/day*		
Temperature Air	2.4 yrs	2.5 yrs	3 %	*0.6 °C*	3 %	*0.7 °C*	2 %	*0.4 °C*	12 %	*3.1 °C*
Temperature Soil	2.4 yrs	2.0 yrs	3 %	*0.9 °C*	8 %	*1.8 °C*	0 %	*0.05 °C*		
Relative Humidity		2.7 yrs			-5 %	*-4 %*	-6 %	*-6 %*		
Shallow Soil Vol. Water Content		>2.8 yrs			58 %	*0.1 m^3/m^3*	5 %	*0.02 m^3/m^3*	67 %	*0.1 m^3/m^3*
Soil Profile Vol. Water Content	0.7 yrs	>2.8 yrs	29 %	*0.1 m^3/m^3*	48 %	*0.1 m^3/m^3*	0 %	*-0.002 m^3/m^3*		
Saturation Canopy		>2.8 yrs			-42 %	*-7 %*	-46 %	*-7 %*		
Saturation Litter	1.0 yrs	>2.8 yrs	-11%	*-2 %*	189 %	*-40 %*	30 %	*-10 %*		

* First column is percentage change from control; second column in italics is absolute change from control

** First column is percentage change from before hurricane María; second column italics is absolute change from before hurricane María

Table 1: Recovery time from the canopy trimming experiments (CTE1 and 2) and the change after each disturbance event as seen by field instruments and satellites.