Short-term response to Hurricane Disturbance: Impacts of Hurricane Maria onLitter Debris in Puerto Rico

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ABSTRACT

Tropical wet forests play a critical role in the atmospheric carbon cycle (C) and are vulnerable due to climate change causing an increase in the frequency of hurricanes. In the Caribbean, hurricanes are important disturbances that structure tropical ecosystems by triggering regeneration cycles during forest recovery. In Puerto Rico, the Canopy Trimming Experiment (CTE), was established in 2002 with the Luquillo Long-Term Ecological Research Program (LTER) in the Luquillo Ecological Forest (LEF). The experiment was designed to investigate the impact of disturbance by separating the two principal interacting responses: canopy opening and litter deposition. In 2004 and 2014, CTE treatments were applied to simulate an increase in hurricane frequency. After Hurricane Maria, a Category 4 storm, hit landfall in the LEF in October 2017, litter was collected from all plots in November 2017, March 2018, June 2018, and October 2018. To determine how hurricane disturbance affects short-term litter-derived nutrients in a tropical forest, I compared patterns in nutrient mineralization and litter decomposition between hurricane manipulation and control plots. For nutrient concentration, time period, rather than disturbance legacy of treatment, was significant. Leaf and palm C concentrations was significant across the trim + debris and no trim + debris plot, indicating the relative importance of canopy opening. Decomposition occurred most rapidly in the first month after the hurricane. By the end of my study, 63.4% of necromass had been decomposed. These results indicate that short term biogeochemical response is driven by the severity and impact of the most recent disturbance.

KEYWORDS

forest regeneration, canopy opening, litter deposition, microbial decomposition, mineralization

INTRODUCTION

Hurricanes are important climate disturbances in tropical forests in the hurricane belt, altering both biogeochemistry and productivity (Vitousek and Sanford 1986). The damage resulting from hurricanes, including tree mortality and changes in short-term litter dynamics can result in nutrient pulses and microenviornmental changes that affect the activity and composition of food webs and ecosystems processes for years to decades or longer. (Scatena 1989, Lugo 2000). Hurricane return intervals often exceed the tree replacement rates in tropical forests and thus previous hurricane disturbances impact the successional forest recovery; consequentially, hurricane disturbances are not independent events (Tanner et al. 1991). Forest response and recovery varies as a function of topography, species composition, and storm intensity, as well as previous disturbance legacy (Herbert et al. 1999). Hurricanes in Puerto Rico have historically occurred every 60 years, influenced by global atmospheric and oceanic temperatures (Shiels et al. 2010). This pattern has been altered amidst climate change, with trends suggesting increasing hurricane intensity and/or frequency (Emanuel and Mann 2006). In the past three decades, the island of Puerto Rico has experienced a series of intense hurricanes: Hurricane Hugo in 1989, Hurricane Georges in 1998, and Hurricane Maria in 2017 (Elsner et al. 2010). Therefore, studies aimed at understanding the biogeochemical effects of Hurricane Maria must be analyzed within a context of a more frequent hurricane disturbance regime.

The release of nutrients from decomposing litter, or small dead plant material lying on the forest floor, is an important nutrient flux in tropical forest material cycling and regeneration (Vitousek and Sanford 1986). After a hurricane disturbance, the rapid release of nutrients from leaves and debris can create short term nutrient pulses that affect biogeochemical cycling (Ostertag et al. 2003). The rate of decay and subsequent recycling of nutrients from the hurricane-deposited litter are driven by interactions between the litter quality, decomposers, and the physical and chemical environment. These interactions depend on the original nutrients present in the litter, the microbial demand for the nutrient, the availability of exogenous nutrients, and soil and forest floor biotic community composition. In tropical forests, litter quality is assessed through carbon to nitrogen (C:N) ratio, lignin and polyphenol concentrations, and physical characteristics of the material with the highest quality generally indicating higher nutrient concentration and faster decomposition (Tian et al. 2007). Fungi are thought to be primarily responsible for most litter decomposition. (Lodge et al. 2014). The physical and chemical environment is a function of both the climate and soil parent material (González et al. 2014).

Hurricanes can lead to extensive canopy defoliation and organic debris deposition on the forest floor, producing cascading effects in the soil profile. Mature leaves tend to have low nutrient to carbon ratios of mobile elements because of high nutrient resorption before leaf abscission (Lodge et al. 2014). Therefore, normal leaf litter has lower quality than fresh tissues for mobile elements. When a hurricane defoliates a tree, however, a large amount of nutrient rich green leaves is transferred to the forest floor, causing a nutrient influx (Fig. 1). Decaying nutrient-rich leaves supplement old leaf litter and woody debris, increasing forest floor nutrient stocks (Lin et al. 2011). After Hurricane Hugo in Puerto Rico in 1989, total nutrient transfer was 1.3 to 3 times greater than background rates; nitrogen concentration was 1.3 times and P concentration was 2.4 times normal litterfall (Lodge et al. 1991). Moreover, hurricane disturbances exacerbate seasonal drying and wetting cycles that can accelerate the replenishment of nutrient stocks (Lodge et al. 1994). The defoliation additionally increases canopy openings and therefore sunlight reaching the floor, modifying the physical and chemical environment (Fernández and Fetcher 1991). Depending on microbial response and resistance to change, this may increase nutrient mineralization and microbial immobilization that decrease the stock of surface and subsurface nutrient pools (Gavito et al. 2017). While labile carbon, nitrogen, and phosphorus, or the fraction of nutrient stocks with the most rapid turnover times, from soil organic matter redistribution can increase plant and microbial activity, the addition of woody debris with high C:N and C:P ratios can increase microbial immobilization and decrease nutrient availability (Gutiérrez del Arroyo 2018, Sanford et al. 1991, Ostertag et al. 2003, Scatena et al. 1996). The high rainfall and earthworm activity in humid tropical forests can lead to downward migration of nutrients; the subsurface soil's higher moisture content, lower redox conditions and lower microbial activity can lead to the persistence of C and nutrients at depth following hurricanes (Gutiérrez del Arroyo and Silver 2018). The drivers determining these differential biogeochemical responses, however, are not well understood.

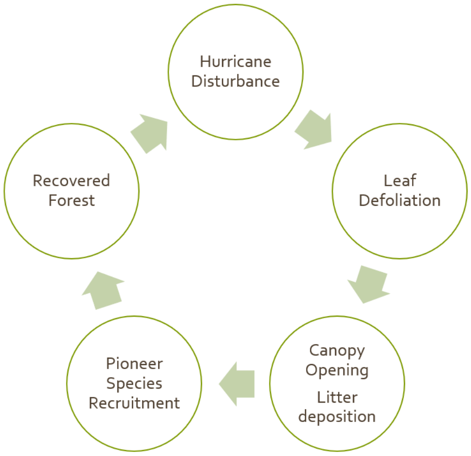

Figure 1. Forest regeneration after disturbance. A hurricane disturbance causes leaf defoliation of trees. The leaf defoliation produces two main effects: canopy opening introducing light into the system and litter deposition introducing nutrient pulses. These two interacting effects facilitate pioneer species recruitment to return to a recovered

Globally, climate is the main driver behind leaf decomposition while litter quality influences local biogeochemical interactions (Lodge et al. 2014). Consequentially, the resulting post-hurricane litter decomposition rates varies not only between hurricane disturbance events, but also across ecosystems. In some studies of northern hardwoods, decomposition rates increased after logging disturbance (Aber et al. 1978, Covington 1981). Yet canopy opening in Costa Rica and Brazil did not lead to an acceleration in decomposition (Denslow et al. 1998, Luizao et al. 1998). Other studies in tropical forests saw that the opening of the canopy dries the litter which could inhibit basidiomycete fungi that contribute to lignin degradation and nutrient conservation (Lodge et al. 2014). The slower decomposition of hurricane generated debris subsequently caused a suppression of forest productivity in a modeling study (Sanford et al. 1991). Forest productivity increased after litter was experimentally removed from sites after Hurricane Hugo, increasing available soil nitrogen (Zimmerman et al. 1995). After Hurricane Georges, while there were short term increases in the nitrogen, phosphorus, calcium, in the litter, nutrient concentrations in palm and tabonuo leaves decomposed at an ambient rate (González et al. 2014). Rapid tropical forest regeneration is therefore typical, and tropical forests can process additional litter inputs on 1-year time scales (Facilli et al. 1991, Ostertag et al. 2003). None of these studies, however, quantified effects mediated by a more intense and frequent disturbance regime, furthering potential differential biogeochemical impacts.

In 2002, the Canopy Trimming Experiment (CTE) in the Luquillo Long-Term Ecological Research (LTER) was established to address this breach in knowledge. The factorial plot design separated the two principal components of hurricane disturbance—canopy opening and litter deposition. Treatments were applied in 2004 and 2014, simulating a more frequent hurricane regime (González et al 2014). Treatments included:

1) no trim + no debris (Control)
2) no trim + debris (Debris Effect)
3) trim + no debris (Light Effect)
4) trim + debris (Simulated Hurricane)

In conjunction with the CTE, the primary objective of this study was to determine how hurricane disturbance affects short-term litter-derived nutrients in a tropical forest. To estimate the relative importance of canopy opening and litter deposition, I compared patterns in litter decomposition and nutrient mineralization between experimental plots that were exposed to the CTE's hurricane manipulation and control plots exposed to the ambient environment. By analyzing changes in percent mass remaining and nutrient concentrations, I explored changes in soil C and N after hurricane disturbance. I predicted that carbon and nutrient mineralization would occur more quickly in the CTE plots compared to the control plots because the control plots without a disturbance legacy would have trees with higher quality litter than hurricane manipulation plots.

METHODS

Study site

I conducted this research using samples from the Luquillo Long-Term Ecological Research Program (LTER) in Puerto Rico and at the University of California Berkeley. The Luquillo Experimental Forest (LEF) is in the Luquillo Mountain range in the northeastern corner of the island (Figure 2). The forest is subtropical and dominated by tabonuco forest type, accounting for approximately 70% of land area trees. The forest has 190 tree species including sierra palm (*Prestoea acuminata*), asubo (*Manikara bidentate*), motillo (*Sloanea berteriana Choisy*), and tabonuco (*Dacryodes excelsa Vahl*) trees (Shiels et al. 2010). Previous land use included selective harvesting and small-scale farming. The dominant large-scale disturbances are hurricanes and droughts (Zalamea and González 2008). The site is at approximately 350 m elevation above sea level. The mean annual air temperature is 24.2 (±0.1) ºC and mean annual precipitation is 3105 (±70) mm (Heartsill-Scalley et al., 2007). Rainfall is weakly seasonal, with the "dryer" season occurring between December and March (González et al. 2014). Litterfall peaks between March and June with a secondary spike in September. Litterfall is lowest from December to February (Zalamea and González 2008). The soils in the LEF are derived from volcanoclastic sediments and are predominantly in the Oxisols complex (Scatena 1989). The study site is a part of the National Science Foundation supported Long-term Ecological Research program (LTER), Critical Zone Observatory program (CZO), and the Department of Energy Next Generation Ecosystem Experiment Tropics program (NGEE) program (Harris et al. 2012).

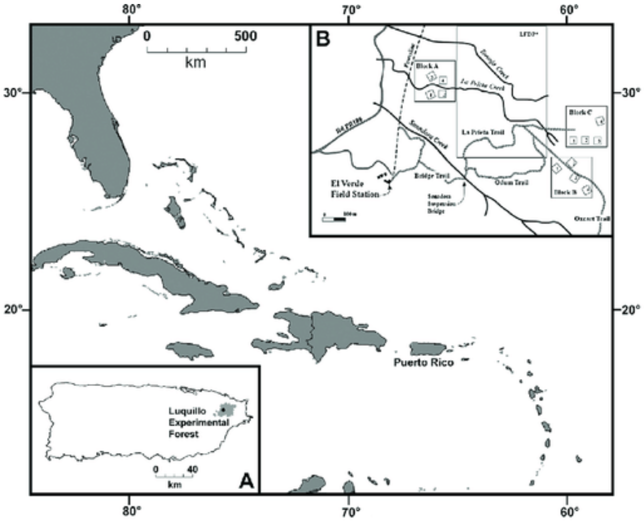

Figure 2. Location of Canopy Trimming Experiment. Map of the Caribbean that shows the location of Puerto Rico. Box A shows the location of the Luquillo Experimental Forest (LEF). Box B shows the location of the Canopy Trimming Experiment. Source: Willig et al. 2014

Canopy Trimming Experiment

The CTE was established at the LEF in 2002 as a long-term manipulative experiment designed to isolate forest responses to hurricanes. Specifically, the CTE analyzed the separate and combined effects of canopy openness and detritus deposition occurring after a hurricane (Shiels et al 2010). The experiment followed a randomized block design with three blocks (A, B, C). Each block contained four 30 m x 30 m plots (12 total plots). To avoid bias due to edge effects of the treatment, the LTER created 20m x 20m measurement areas that were divided into 16 quadrats (4.7m x 4.7m quadrats). Each plot in a block was randomly assigned one of four hurricane manipulation treatments: trim + detritus, trim + removal, no trim + detritus, and control (Figure 2,3). A hurricane was simulated in the trim + detritus plots by cutting branches and leaves from trees (trim) and placing the debris on the forest floor. Similar trimming occurred in the trim + removal plots, with the debris being placed in the untrimmed + detritus plots. The control plots were left in ambient environmental conditions.

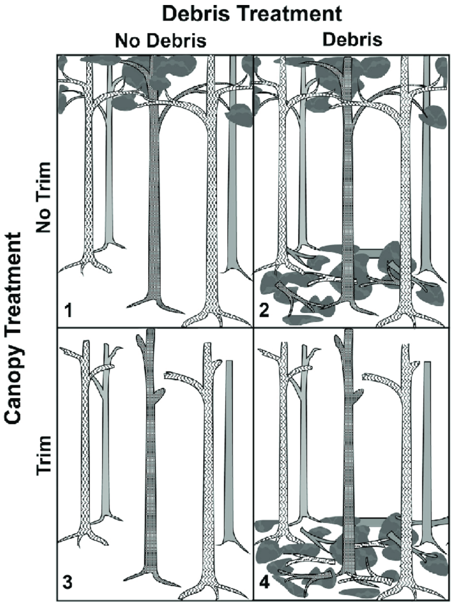

Figure 3. CTE Treatments. The CTE was a factorial designed experiment to separate the interacting effects of light from canopy opening and nutrient inputs from litter deposition: 1. Control (No trim + no debris); 2. Debris added without trim (Debris + no trim); 3. Canopy trimmed with debris removed (Trim + no debris); 4. Canopy trimmed with debris addition (Trim + debris). Source: Willig et al. 2014

After an initial period to collect background measurements, treatments were applied in 2004 and 2014 (Shiels et al. 2010). Monthly measurements and analysis of soil and leaf litter samples are ongoing. When Hurricane Maria, a Category 4 storm, passed through the LEF in September 2017, the experiment was modified to study the impact of frequent disturbance on soil carbon and nutrient biogeochemistry. Plots that received the trim + debris treatments represented forest in a more frequent disturbance regime while the control plot represented forest affected by the Hurricane Maria disturbance. Subsequently, my project addressed plots with the following treatments

1) trim + debris: 2 CTE treatments, Hurricane Maria
2) trim + no debris: 2 CTE treatments, Hurricane Maria
3) no trim + debris: 2 CTE treatments, Hurricane Maria
4) control: Hurricane Maria

Puerto Rico fieldwork

1. Leaf litter collection by the LTER

In November 2017, samples were collected from the trim + detritus and control plots. Within each sublot, a random number generator was used to pick 5 integers between 0-10. Those numbers were then mapped to their position along a 10 m transect. A 50 x 50 cm quadrat was then placed on the ground at each randomly chosen position. The middle of the quadrat's cutout was placed over the meter number which was measured. If more than 30% of the quadrat prevented from getting flush to the ground from big rocks, logs, or other disturbance, the quadrat was moved to the first normal half meter after the unusable area. Then, the field assistants collected the leaf litter. A knife was used to cut large leaves or sticks that were only partially inside the cut out to keep quadrat area consistent. Any fronds were then removed from the quadrat area and placed into a bucket for later analysis. The field assistants weighed the bucket, recorded the weight, and emptied the palm leaves into a paper sandwich bag. They repeated the same process for leaves. At the end of sampling, they then recorded the wet weights of litter subsamples. After they oven dried the subsamples, they recorded the dry weights again. This litter collection process was repeated in January 2018, June 2018, and October 2018.

Berkeley lab work

1. Leaf dry weight

Palm and litter samples were sent to the Silver Lab at UC Berkeley for nutrient analysis. Because the oven used in Puerto Rico was subject to periodic power outages, I oven-dried the palm and litter samples in Berkeley. To prevent loss of sample from fragile or tearing bags, I put the samples into a second brown paper bag. The individual, new bag's weight and the new bag + sample bag weight were recorded. I placed the samples in an oven at 65˚C for 24 hours. Then, I kept the samples in the oven until consecutive weights were within 0.5% of each other.

After drying litter bags to a constant weight, I used a Spex Mill to grind the leaves in each bag until homogenized. I placed the total sample into a crucible and left it to grind for 8 minutes. Then, I transferred the ground sample to a scintillation vial. For sample bags with a large amount of litter (>60 g), I used a larger mill to grind through a 1 mm grate. The bulk sample was then placed in a specimen cup. I then filled a single crucible of the bulk sample and ground it for 8 minutes in the smaller mill. I then transferred the ground sample to a scintillation vial.

2. *Ashing*

To estimate soil contamination, I ashed a subset of samples from each sampling period. I placed 1 g (± 0.1 g) of each ground sample place in a ceramic crucible and heated it in a muffle furnace at 500 °C overnight to determine the proportion of minerals (% weight) in the sample. This process corrects the dry weight of the harvested leaves for any added soils that may have penetrated the litterbags while they were out in the field by comparing mineral content of the initial litter to the litter from later time points.

3. *Carbon and nitrogen*

I estimated total carbon and nitrogen concentration using an elemental analyzer (EA Flash 2000—Thermo Fisher Scientific, Waltham, MA). I measured 10-15 mg of the ground litter samples into aluminum capsules. Each sample had two replicates run through the EA. I then averaged the C and N concentrations for each litter sample.

Data analysis

1. *Carbon and nitrogen*

I calculated the C:N ratio by dividing the average C concentration at each time point for each sample by the average N concentration. For each litter type (leaf or palm), I ran a one-way ANOVA and Tukey test to test the significance of time and treatment. I also ran a two-way ANOVA testing for any interaction between time and treatment. All statistical tests were performed using R.

2. *Decomposition*

I calculated changes in forest floor litter biomass over time by using the ash-corrected mass from each sampling period. For each time period, the average days since hurricane was calculated. Time points from November 2017 were broken into two sections to illustrate the rapid decomposition that occurred within a week (40 days after hurricane to 49 days after hurricane). For each litter type (leaf or palm frond), I then ran a one-way ANOVA and Tukey test to test the significance of time and treatment. I also ran a two-way ANOVA testing for any interaction between time and treatment. All statistical tests were performed using R.

RESULTS

Carbon and nitrogen

1. *Leaf litter*

Leaf litterfall nutrient N concentrations varied over the four time periods. Leaf litter N (%) was significant across time ($p < 0.0001$), but not across treatment. Percent N peaked in March 2018 (Fig. 4) and then subsequently decreased throughout June 2018 and October 2018. A Tukey test revealed that all time period pairings except November 2017 and June 2018 were significant. There was an interaction between time period and treatment for percent N ($p= 0.0324$).

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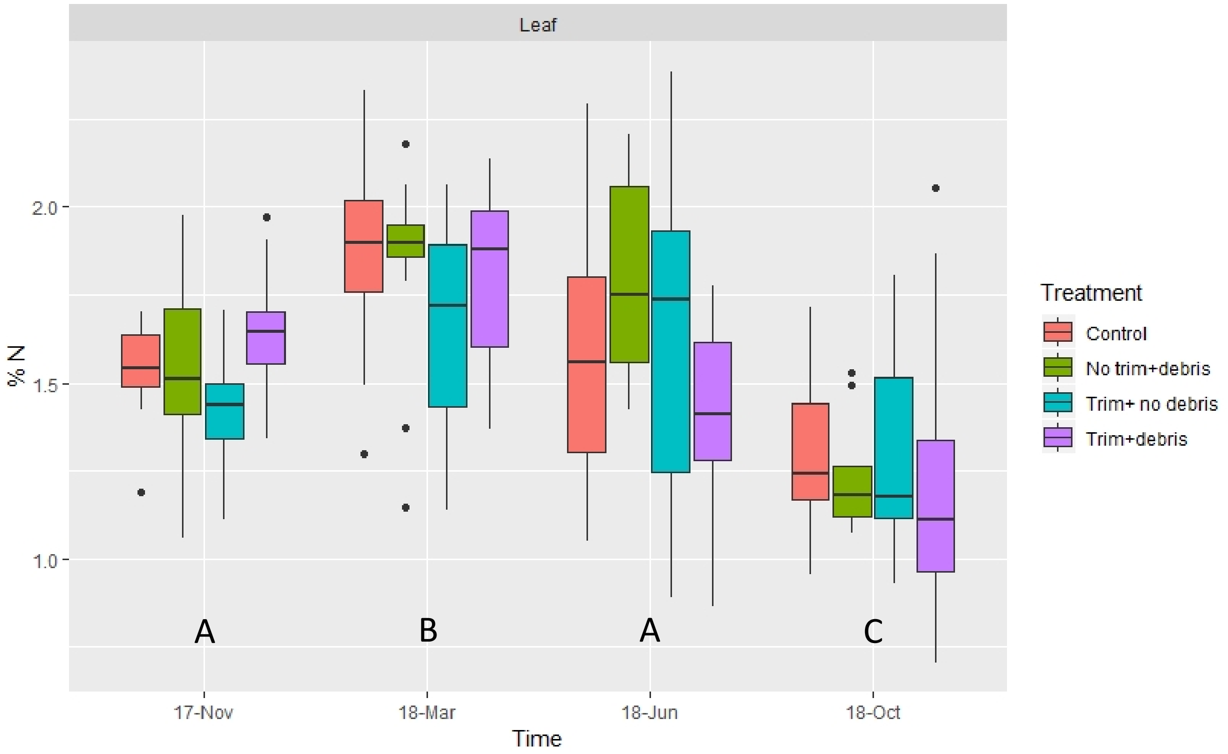

Figure 4. Distribution of leaf litterfall %N across time periods. %N peaked in March 2018 and then declined throughout June 2018 and October 2018. %N was significant across time ($p<0.0001$), but not across treatment.

Leaf litter C (%) concentrations were less variable and were significantly different between November 2017 and June 2018 ($p=0.0331$). Leaf litter C concentrations were also significantly different (to the $p<0.1$ level) between the trim + debris and no trim + debris plots ($p=0.0524$, Fig. 5). There was no interaction between time period and treatment.

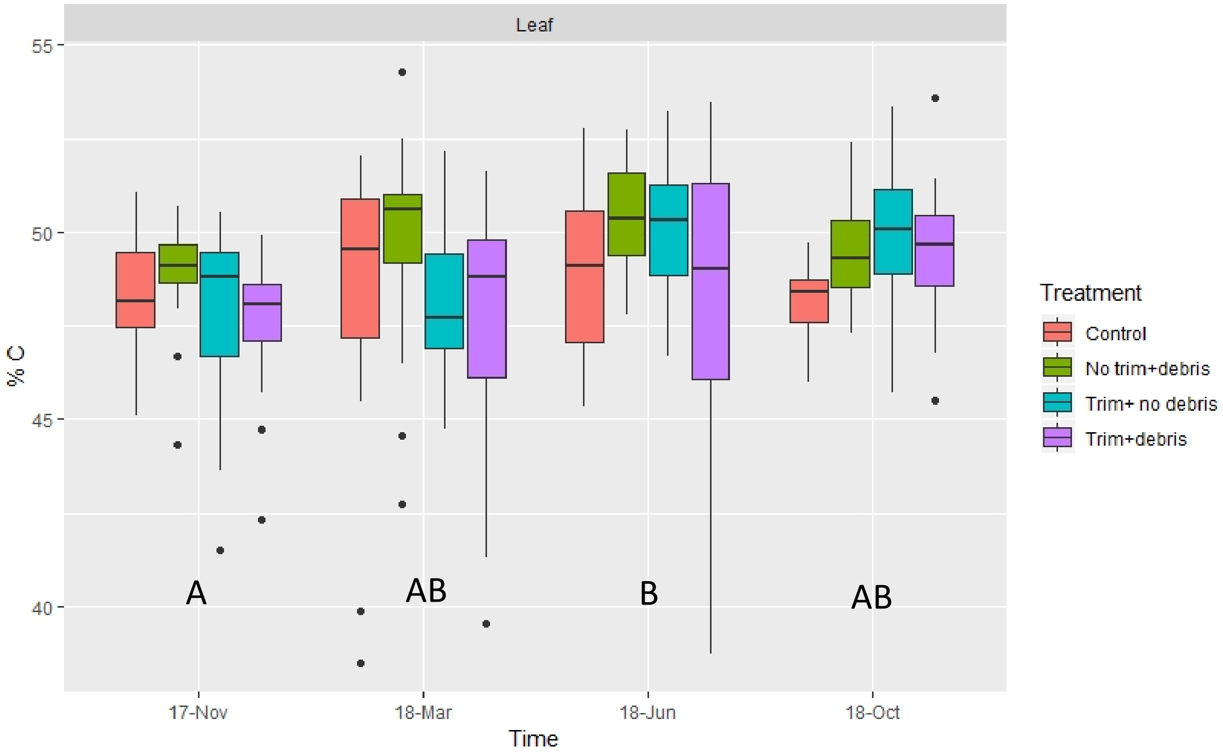

Figure 5. Distribution of leaf litterfall %C across time periods. %C was significant across time ($p<0.0331$) between November 2017 and June 2018 ($p=0.0524$). %C was also significant between the Trim + debris and No trim + debris treatments ($p= 0.015$).

Leaf C:N ratios were lowest during the March 2018 time period and subsequently increased throughout June 2018 and October 2018 time periods (Fig. 6). Leaf C:N ratios were varied significant across time ($p<0.0001$) for all time period pairings except November 2017 and June 2018. C:N declined for the first 6 months, but then was increased from June 2018 and October 2018 (Fig. 7). Leaf C:N ratios were not significantly different across treatment. There was no interaction between time and treatment.

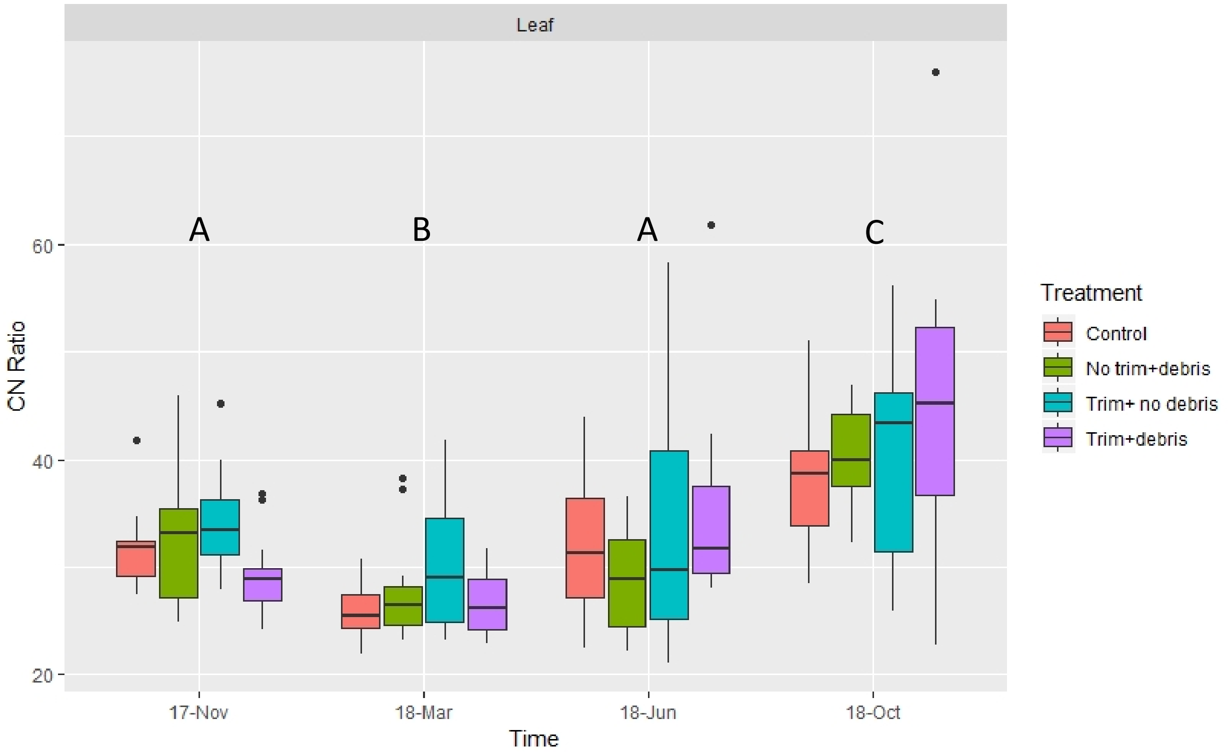

Figure 6. Distribution of leaf litterfall C:N ratio across time points. C:N ratio was significant across time ($p<0.0001$) for all time pairings except November 2017 and June 2018. C:N ratio was not significant not across treatment.

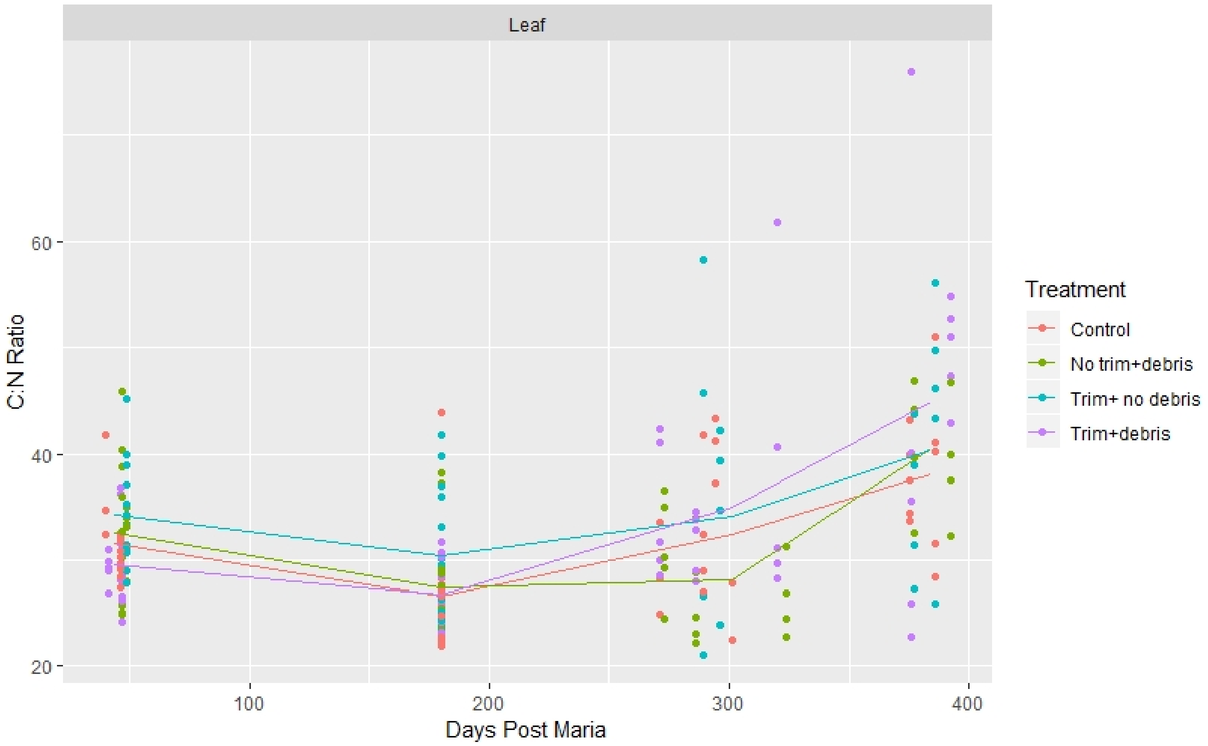

Figure 7. Leaf C:N ratios as a function of time. The points represent individual C:N ratios while the lines represent mean C:N ratios for each time point. The C:N ratio initially decreases, and then increases.

2. Palm litter

Palm litterfall nitrogen concentrations varied less over the four time periods. Palm litter N varied significantly across time (p = 0.004), but not across treatments. Percent N decreased slightly over time(Fig. 8). A Tukey test revealed that time period pairings November 2017 and March 2018 and November 2017 and October 2018 were significant. There were no interactions between time period and treatment.

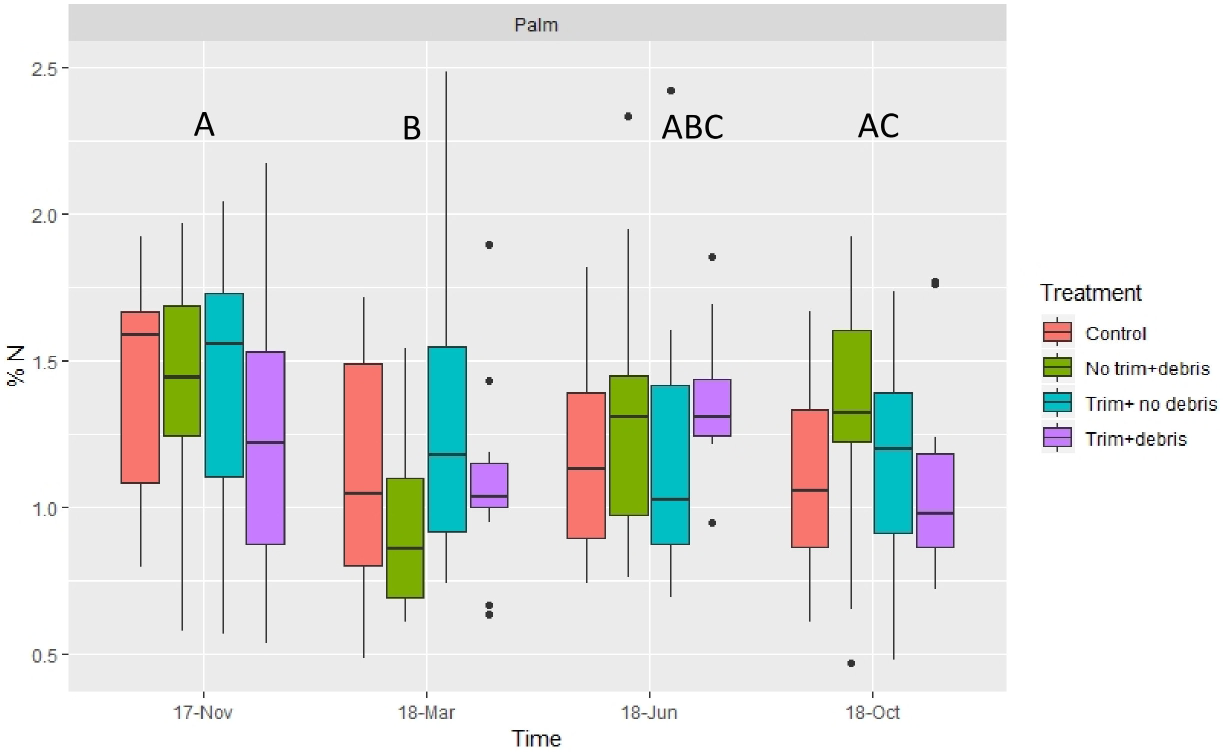

Figure 8. Distribution of palm litterfall %N across time periods. %N was significant across time (p=0.004) between November 2017 and March 2018 and November 2017 and October 2018. %C was not significant across treatment.

Palm litter C concentrations varied significantly between November 2017 and June 2018 and March 2018 and June 2018 (p<0.001). Palm litter C concentrations gradually increased over time. Palm litter C was generally lower in the trim + debris than in the no trim + debris plots (p=0.024, Fig. 9). There was no interaction between time period and treatment.

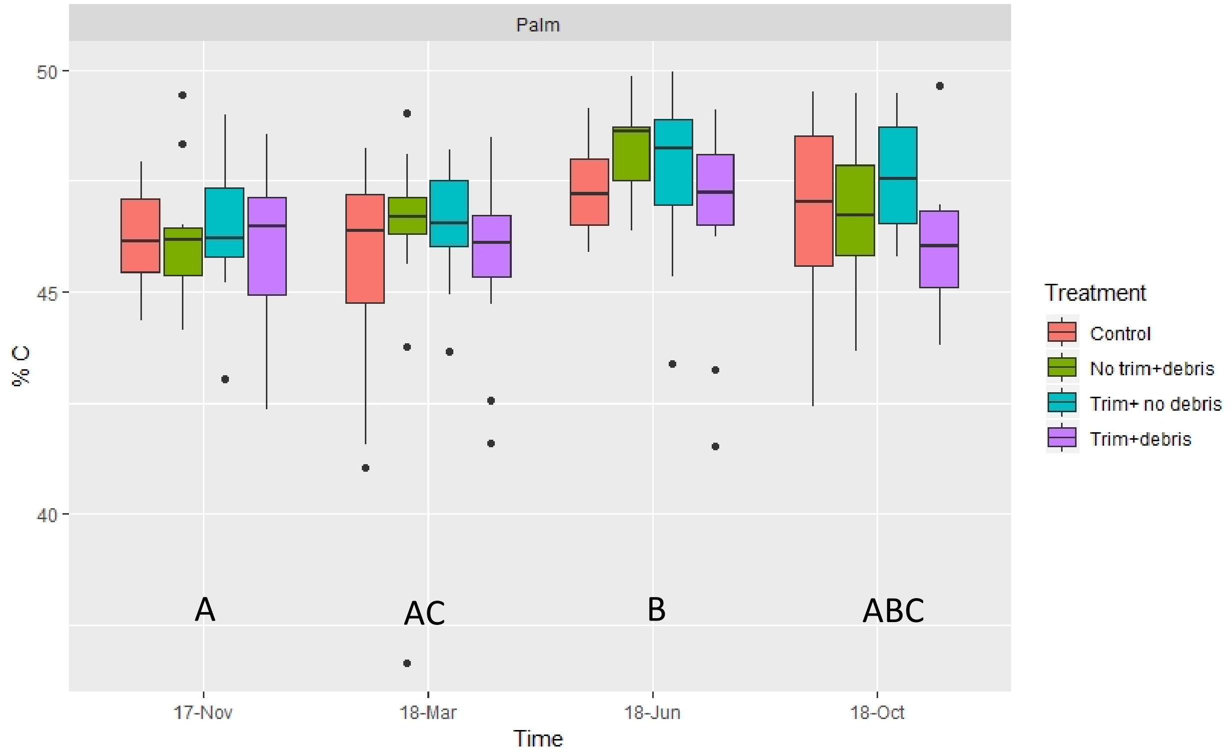

Figure 9. Distribution of palm litterfall %C across time periods. %C was significant across time periods November 2017 and June 2018 and March 2018 and June 2018 ($p<0.001$). %C was significant across the Trim + debris and No trim + debris treatments ($p=0.024$).

C:N ratios increased slightly over time, reflecting the increase in C from November 2017 to October 2018 (Fig. 10). Palm C:N ratios were significantly different across time between November 2017 and March 2018 ($p<0.0001$). Palm C:N did not vary significantly across treatment (Fig. 11). There was no interaction between time and treatment.

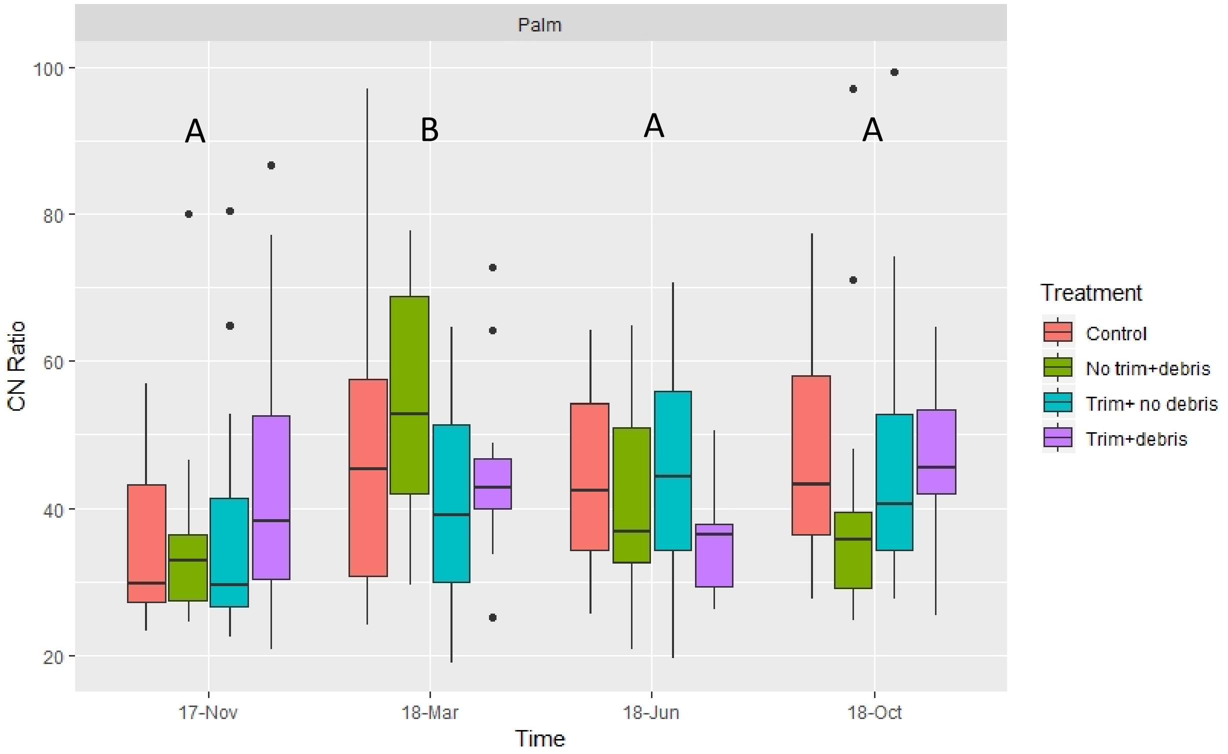

Figure 10. Distribution of palm litterfall C:N ratio across time points. C:N ratio was significant across time between November 2017 and March 2018 (p<0.0001). C:N ratio was not significant not across treatment.

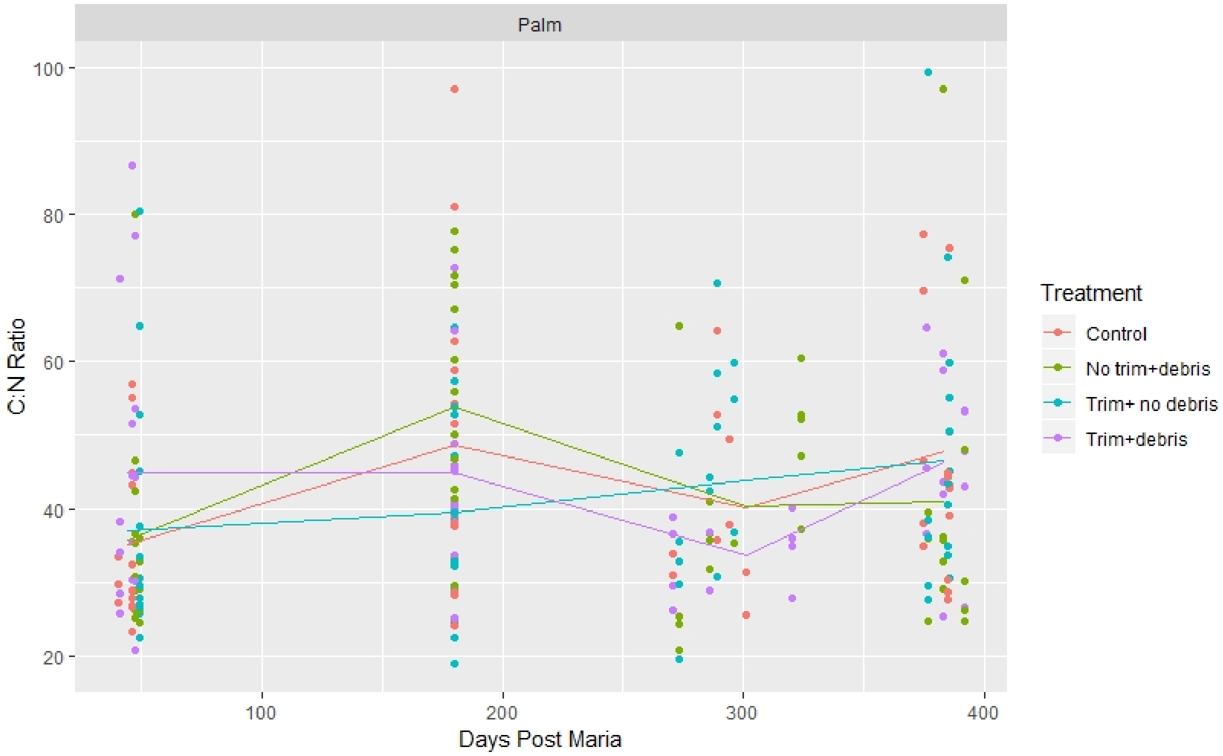

Figure 11. Palm C:N ratios as a function of time. The points represent individual C:N ratios while the lines represent mean C:N ratios for each time point.

Decomposition

The forest floor mass decreased from November 2017, about 1-month post Hurricane Maria, to October 2018, a little over a year post Hurricane Maria (Fig. 12). The most rapid decomposition took place within the first week of sampling, between 41 and 49 days after Hurricane Maria hit. The decomposition rate during that initial period was 51.051 ± 25.207 g/m^2. Necromass observations were not normally distributed, but a log transformation produced a valid QQ plot. A one-way ANOVA test revealed that mass and average days since hurricane were significant. After around 380 days after the hurricane in October 2018, 63.4% of necromass present in November 2017 had been decomposed.

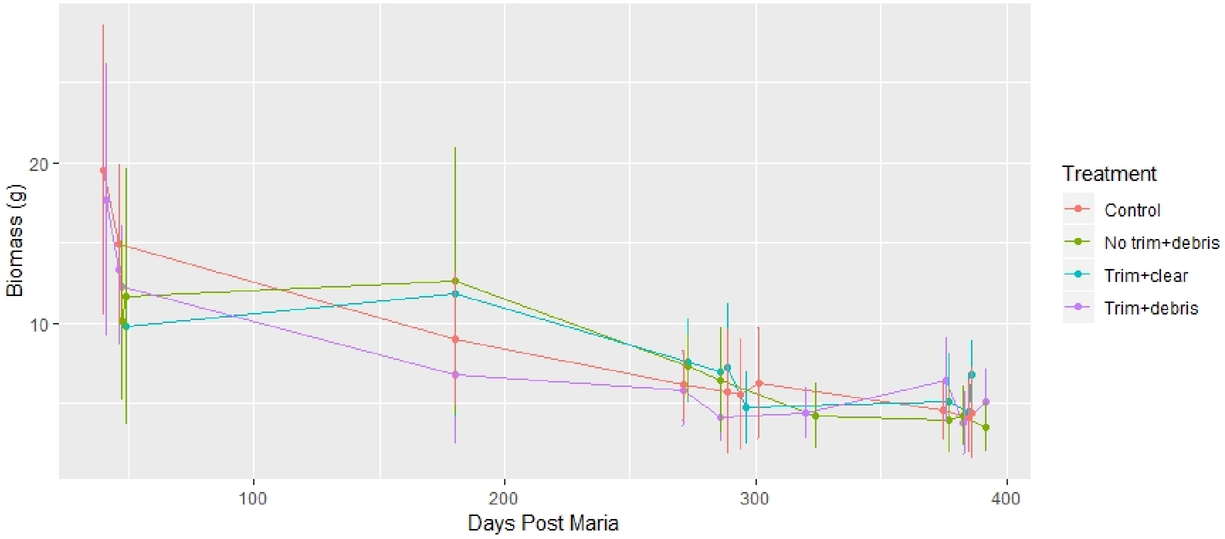

Figure 12. Litter decomposition over time. Shows decomposition as a function of days after Hurricane Maria. The most rapid decomposition took place in the first 45 days after the hurricane and then gradually declined.

DISCUSSION

The short-term impact of hurricane disturbance on ecosystem structure and process results from simultaneous canopy opening and debris deposition. Hurricane nutrient pulses were derived from the large input of biomass. Average necromass at the beginning of the study was more than three times greater than necromass remaining at the end, suggesting that decomposition was linked to pulses in N and C. For N concentration, time was the dominant factor driving litter nutrient concentrations, indicating that the impact of Hurricane Maria overshadowed the impact of disturbance legacy on CTE manipulation plots. For C concentration, however, the difference between the trim + debris and no trim+ debris treatments suggest that light plays a strong role in altering the microenvironment and subsequently contributing to microbial shifts that alter biogeochemical pathways. These results suggest that immediate biogeochemical response within a more frequent hurricane regime is predominantly influenced by the most recent disturbance.

Carbon and nitrogen

I found that the input of debris post-hurricane translated to pulses in nitrogen and carbon stocks to the forest floor. My results demonstrate that the input of debris was translated to pulses in N and C stocks on the forest floor. Silver et al. 2014 reported a similar trend as litterfall was the predominant factor controlling nutrient fluxes through forest reorganization after a canopy trimming debris deposition. Forest recovery through reorganization was quantified by Scatena et al. 1996. They determined that during the 1st year of recovery, natural processes prioritized re-leafing trees that survived the hurricane. Senesced litterfall was consequentially decreased as canopy opening caused the rainfall reaching the forest floor to increase. Most nutrient uptake from the litter input occurred in the aboveground biomass. Correspondingly, the leaf and palm litter collected in my study in November 2017 had greater nutrient concentrations than litter collected at the end of the study October 2018. These trends can be expected to be propagated, as Gutierrez del Arroyo and Silver 2018 predicted that the additional aboveground C input would take at least 5 years to recover to a pre-disturbance level.

Leaf C:N ratios decreased in the first 6 months after the hurricane, indicating that forest floor debris lost C relatively faster than N. One mechanism explaining this trend is the potential for microbes to break down and subsequently take up litter-derived C faster than litter-derived N. This trend accounts for both N being abundant in tropical forest and thus in less microbial demand than C and for organic forms of N to be substantially less available to the microbial community than inorganic N (Vitousek and Sanford 1986, Chapin et al. 2002). An alternative mechanism explaining the trend in leaf C:N ratios over time can be found by considering leaf litter % N trends over time. Leaf litter N concentration increased significantly within the first 6 months after Hurricane Maria. This can be attributed to immobilization of soil inorganic N from the forest floor as microbes grow on and decompose the newly-deposited litter. Twigs and branches (generally with large C:N ratios) were transported to the forest floor via debris deposition, resulting in microbes not being able to meet N requirements from the lower-quality litter. Therefore, microbes may have had to increase exogenous N from the plant available litter pool to convert to microbial biomass. The decrease in N mineralization is consistent with estimated effects from Sanford et al. 1991 that predicted an immobilization of N in the first year after a hurricane. Unlike leaf C:N ratios, palm C:N ratios increased slightly over time, suggesting an increase in carbon input from debris deposition. Palm C:N ratios were less variable than leaf C:N ratios, suggesting that palm, containing a higher concentration of lignin in their petioles, is of lower litter quality, a finding consistent with other studies (Ewel 1976, Tomlinson 1990).

Treatment was only significant for leaf and palm C concentration between the trim + debris and no trim + debris treatment, suggesting that light alters the microenvironment, potentially causing a microbial shift. Light penetration can be assumed to have significantly increased after Hurricane Maria; after Hurricane Georges light was estimated to be 4 times greater and after each CTE treatment was predicted to be about twice as high as in areas with an intact canopy (Shiels et al. 2014). Soils with canopy opening have been demonstrated to retain 10% greater soil moisture from the increased rainfall penetration and decreased transpiration (Shiels et al. 2014). Silver et al. 2014 additionally found that the abiotic shift could last up to 18 months. While the soil retains more moisture, conversely the litter is drier (Lodge et al. 2014). Richardson et al. 2010 detailed how the increased light penetration caused a microbial shift from agaric fungi (Basidiomycota) to micro fungi by regardless of litter deposition. Larger arthropods prefer the exposed, dry litter which subsequently caused decreases in the fungal connections (Shiels et al. 2015, Lodge et al. 2014). Rivera-Figuerora 2008 also found that trimmed plots had lower basidiomycete white rot activity, causing a microbial shift toward micro fungi. Thus, within microbial communities, canopy opening has numerous pathways by which it can drive microbial community change. My results can also be linked to hypotheses associated with microbial shifts: palm litter C was generally lower in the trim + debris than in the no trim + debris plots while leaf litter C in the trim + debris plots was additionally lower than the no trim + debris plots in in November 2017 and March 2018. These differences can be potentially explained by trimmed plots having lower basidiomycete white rot activity that are responsible for lignin (C) breakdown (Rivera-Figuerora 2008).

I hypothesized that debris deposition and light would be dominant drivers of nutrient mineralization, yet, with the exception of limited and subtle differences in litter C across treatment, found mostly no significant differences across treatment. Wood et al. 2009 described a similar situation with a 4-fold increase in litter biomass that remained for 1.5 years after an El Niño event in a tropical forest, but found no significant effect of the debris addition on nutrient concentrations. However, persisting legacies of disturbance may play out over longer timescales. For instance, Pinage et al. 2019 quantified lasting detrimental effects in tropical forests in the Amazon subject to repeated logging, another form of frequent disturbance. They found that there were new gaps, or low growth areas, in spaces in or adjacent to old logged areas compared to undisturbed forest, suggesting that previous disturbance jeopardizes future recovery and resilience.

Decomposition

I saw that forest floor biomass was dramatically increased after Hurricane Maria. After Hurricane Hugo and Hurricane Georges, forest floor litter mass doubled. Following the CTE treatments, biomass was additionally doubled (Guzman-Grajales and Walker 1991, Ostertag et al. 2003). Therefore, it can be assumed that the amount of necromass found on the forest floor in November 2017 was at least 2 times the ambient mass. Decomposition occurred most rapidly during the November 2017 time period and then gradually decreased over time. Slowing decay could be attributed to the decrease in litter moisture, microbial shift, or changes in aboveground faunal community (González et al. 2014). Total decomposition is consistent with results found in Ostertag et al. 2003 as tropical forests are capable of processing hurricane litter on time scales of less than 1 year. There was additionally no significant effect of hurricane manipulation treatment on percent mass remaining of litter, consistent with results found in González et al. 2014.

Decomposition of C and N can have important global change biology impacts by contributing to greenhouse gas production and ecosystem N losses through streams. The N cycle can be disrupted in several key ways after hurricane disturbance and debris deposition. As decomposition of litter proceeds, litter N can be incorporated into the soil, can be lost to streams via soil water flow or to the atmosphere as microbially-emitted gases, or can be incorporated into microbial or plant biomass (Campbell et al. 2016). González et al. 2014 found that debris addition increased the percent of initial nitrogen in soils. Hurricane disturbance has also been shown to stimulate nitrification and NO_3^- leaching, which can lower pH and increase nitrogen concentrations in runoff and streams (Silver and Vogt 1993, McDowell and Liptzin 2014). Excess N has also been correlated to additional N_2O emissions. Tropical forests are phosphorus limited, and thus more sensitive to nitrogen inputs (Hall and Matson 1999). In a tropical rainforest in southwest China, researchers found that removing litter from plots compared to control plots subject to ambient environment, N_2O emissions decreased by 33% (Gao et al. 2018). The carbon cycle also has the potential to be disrupted by hurricanes and associated debris deposition. Gutiérrez del Arroyo and Silver 2018 found that debris deposition alone resulted in higher soil C and N concentrations, suggesting that soil has the potential to increase nutrient and C storage. Excess carbon can also enter the atmosphere as CO_2, with higher soil CO_2 flux rates observed for two years following hurricane disturbance (Shiels et al. 2015). Within a more frequent hurricane regime, these additional greenhouse gas spikes will be important to understand when working towards solutions to manage and mitigate climate change.

Limitations and further directions

My results demonstrated that short term biogeochemical response is mediated by canopy opening and litter deposition that activate cascading effects in nutrient cycling and forest regeneration. Within my study, it would have been interesting to have decomposition rates prior to Hurricane Maria to compare with the decomposition I found over time to address whether hurricane disturbance increases or decreases decomposition. Additionally, it would have been interesting to have another time point between November 2017 and March 2018 to further show how decomposition changed over time. While my results demonstrate that short term response is predominantly driven by the most recent disturbance, future studies should continue nutrient cycling and decomposition measurements over a longer time scale to see if the interacting effects of canopy opening and litter deposition decouple. Studies should also address the partitioning of excess nutrients to greenhouse gases to understand impact on climate change. Consequentially further studies of forest regeneration and recovery will inform forest management practices to adjust for excess debris and light penetration, carbon and nutrient storage, forest productivity, and greenhouse gas production.

Conclusion

Climate change increases the frequency of hurricane disturbance regimes in the Caribbean and threatens the viability of tropical forest recovery and function (Emmanuel and Mann 2006, Holland and Bruyere 2014). These ecosystem functions play critical roles in shaping the carbon cycle through, for instance, sequestering carbon via photosynthesis and emitting carbon through litter decomposition. Tropical forests store 20% of the worlds terrestrial carbon and due to rapid turnover rate, these systems are highly sensitive to disturbance (Brown and Lugo 1982). Previous studies have demonstrated that hurricanes structure tropical forest ecosystems but have not quantified the effect of an increased disturbance regime on the simultaneous and interacting canopy opening and litter deposition that is responsible for nutrient and carbon biogeochemical cycles (Shiels et al. 2010). The short-term biogeochemical response to litter derived inputs measured here indicates that recent, intense disturbance can overshadow differential biogeochemical responses from disturbance legacy. This suggests that biogeochemical effects from an increase in disturbance frequency may propagate over longer timescales and across ecosystem variables such as soil nutrient availability and species composition. Furthermore, this research warrants future studies into consequential greenhouse gas increases from the reported C and N inputs. Understanding these dynamic regeneration processes will help forest managers design landscape management plans that accommodate various environmental goals. Furthering our knowledge of the interaction between biogeochemical impacts and ecosystem response to disturbance is crucial to maintaining healthy tropical forests amidst climate change.

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