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Understanding the key mechanisms of tropical forest responses to canopy loss and biomass deposition from experimental hurricane effects

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ABSTRACT

To date, it is not clear which are the factors that most influence tropical forest recovery from hurricanes. Increased canopy openness and increased detritus (debris) deposition are two of the most likely factors, but due to their simultaneous occurrence during a hurricane, their relative effects cannot be separated without a manipulative experiment. Hence, in the Luquillo Experimental Forest (LEF) of Puerto Rico, the Luquillo Long-Term Ecological Research Program (LTER) has undertaken experimental manipulations in replicated 30×30 m plots to simulate the major effects of hurricane disturbance–increased canopy openness and debris addition to the forest floor. Using a factorial experiment enabled investigation of the separate and combined effects of canopy opening and debris on this wet tropical forest; the experimental outcomes may help direct forest management decisions in similar disturbance-prone environments. In this first article of the special issue, we (1) provide details of the design and methodology for this manipulative experiment (the Canopy Trimming Experiment, CTE), (2) report some principal abiotic responses to treatments, and (3) introduce the subject areas of the 12 additional CTE manuscripts in this special issue. The physical conditions created by canopy and understory treatment and the amounts of debris added to CTE plots were similar to the LEF's conditions following Hurricane Hugo (a category 4 storm) in 1989; although more wood and a 37% (1.5 cm) deeper litter layer was present in the CTE. Our selective cutting and removal of the forest canopy above 3 m, which included trimming 234 palm trees and 342 non-palm trees, greatly altered the understory micro-environment by increasing light levels and decreasing litter moisture for 18 months; throughfall and soil moisture were elevated in trim plots for 3 months. In plots where the canopy was trimmed and the debris (6 kg m^{-2}) was added to the forest floor, the canopy debris persisted on the forest floor for at least 4 years; debris decomposed more quickly in plots with intact canopies. The diverse collection of papers in this special issue provide mechanistic understandings of response patterns of tropical forest biota (microbes, plants, animals) and processes (decomposition, herbivory, nutrient cycling, primary production) to canopy and understory disturbance that resembles a major ($\geqslant$category 3) hurricane. Although measurements for this experiment are ongoing to further identify the mechanisms of long-term forest change resulting from hurricanes, we include findings up to the first seven years post-treatment at this time.

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1. Introduction

Cyclones (called hurricanes in the Atlantic) dominate the disturbance regime experienced by islands, forests, and coastal ecosystems in many parts of the world (Everham and Brokaw, 1996; Whitmore and Burslem, 1998; Lugo, 2008). Each year these large windstorms attract worldwide attention that includes several days of anticipation prior to each storm, and many weeks of recovery from destruction of property, disrupted infrastructure, and in some cases the loss of human lives following the storms. For humans and other biota, hurricanes cause losses across a wide range of spatial and temporal scales (Lugo, 2000). For centuries, forest managers and scientists have been intrigued by how forest ecosystems are altered by hurricanes. With sustained wind-speeds reaching at least 119 km h^{-1} over tens of consecutive kilometers in breadth, hurricanes strip most of the leaves and branches from canopy species, snap stems and uproot trees, and deposit large amounts of canopy biomass (debris) onto the forest floor (Walker et al., 1991; Everham and Brokaw, 1996). The absence of an intact canopy alters understory light, temperature, and moisture; the deposited canopy debris may provide resources for some

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organisms but may deter or delay colonization by others (Richardson et al., 2010; Shiels et al., 2010). The post-hurricane conditions often leave forest managers and scientists wondering if the forest will recover to pre-hurricane status; how long it will take for such recovery to be completed; to what extent species composition, diversity, and ecosystem processes are altered; and what the key factors are that drive forest recovery (Stanturf et al., 2007; Turton, 2012). This special issue of Forest Ecology and Management brings together findings from a large-scale hurricane experiment in a tropical wet forest in Puerto Rico. The goal of our experiment was to understand the key mechanisms driving forest responses following a hurricane by determining the independent and interactive effects of increased canopy openness and deposition of canopy debris onto the forest floor.

Hurricanes can cause long-term changes to forest structure and composition (Foster, 1988; Burslem et al., 2000; Lugo et al., 2000; Chazdon, 2003; Weishampel et al., 2007). The number of studies that describe the effects of hurricanes on tropical and subtropical forests has increased in the past three decades, as evidenced by many publications, including several special issues of ecological journals covering hurricane effects in the South Pacific (Turton, 2008) and the Caribbean (Finkl and Pilkey, 1991; Walker et al., 1991, 1996; Stone and Finkl, 1995; Middleton and Smith, 2009). Most of these past studies reflect "major" hurricanes, or those with sustained wind speeds of at least 178 km h^{-1} (category 3 or above on Saffir–Simpson Hurricane Wind Scale). Tree structural effects following major hurricanes are commonly documented (Foster, 1988; Brokaw and Walker, 1991; Putz and Sharitz, 1991; Bellingham et al., 1995; Imbert et al., 1996; Mabry et al., 1998; Franklin et al., 2004; Van Bloem et al., 2005; Lee et al., 2008; Metcalfe et al., 2008; Lewis and Banner-Martin, 2012; McGroddy et al., 2013; Webb et al., 2014), as are incidences of sprouting and tree recovery (Walker, 1991; Merrens and Peart, 1992; Bellingham et al., 1994; Zimmerman et al., 1994; Bellingham et al., 1996; Everham and Brokaw, 1996; Batista et al., 1998; Burslem et al., 2000; Uriarte et al., 2004). Fewer plant studies have described hurricane effects on woody seedlings (Guzmán-Grajales and Walker, 1991; Walker et al., 2003; Murphy et al., 2008; Comita et al., 2009) or the herbaceous layer of the forest understory (Chinea, 1999; Meléndez-Ackerman et al., 2003; Halleck et al., 2004; Sharpe, 2010; Royo et al., 2011). Studies of animals in terrestrial ecosystems following major hurricanes have largely focused on birds (Askins and Ewert, 1991; Lynch, 1991; Waide, 1991; Wunderle et al., 1992; Wunderle, 1996; Freeman et al., 2008), bats (Gannon and Willig, 1994; Grant et al., 1997), lizards (Reagan, 1991), frogs (Woolbright, 1991; Vilella and Fogarty, 2005), and invertebrates (Willig and Camilo, 1991; Schowalter, 1994; Schowalter and Ganio, 1999). Microbial responses to hurricanes (Lodge and Cantrell, 1995; Willig et al., 1996; Vargas et al., 2010) are not well studied relative to plants and animals, yet several studies have documented ecosystem processes that in part involve microbes after these storms, such as decomposition (Herbert et al., 1999; Sullivan et al., 1999; Ostertag et al., 2003), greenhouse gas flux (Erickson and Ayala, 2004), and changes in terrestrial nutrient status (Blood et al., 1991; Lodge et al., 1991; McDowell et al., 1996; Scatena et al., 1996; Silver et al., 1996; Herbert et al., 1999; Xu et al., 2004; Heartsill Scalley et al., 2010). Recent interest in hurricane effects to tropical forests has also stemmed from models that predict an increased frequency and/or intensity of these storms associated with global climate change (Emmanuel, 2005; Nyberg et al., 2007; Bender et al., 2010).

Despite the large number of studies that have documented the effects of hurricanes on forests, there is an absence of understanding of the key factors that govern forest responses to hurricanes. Such lack of understanding is primarily due to the paucity of experimental hurricane studies. In fact, prior to our study, the only experiment simulating hurricane effects was conducted at Harvard Forest, a temperate forest in north-eastern USA, where whole trees were pulled down to simulate conditions of a previous major hurricane (Bowden et al., 1993; Carlton and Bazzaz, 1998; Cooper-Ellis et al., 1999). The main effects from this temperate hurricane experiment were increased light levels, reduced basal area due to the physical application of the manipulation, and establishment of pioneer tree species in areas of soil disturbance from tree uprooting (Carlton and Bazzaz, 1998; Cooper-Ellis et al., 1999). Studies of forest responses to experimental hurricane effects not only reveal the key factors responsible for changes resulting from natural hurricanes, but may help direct forest management decisions following non-hurricane disturbances where conditions of canopy loss or forest floor debris modifications result (e.g., logging, wind storms, fire). For example, forest management practices may be altered based upon their understanding of how excess debris on the forest floor may alter subsequent plant recruitment rates, carbon storage, or stand productivity following wind storms or logging practices. Thus, examination of experimental hurricane effects can provide insights into adaptations of species, recruitment processes, successional dynamics, competition, resistance and resilience, carbon and nutrient cycling, and legacy effects. It is currently unclear what the key factors are that determine tropical forest recovery from hurricane effects. Increased canopy openness and increased debris deposition are two of the most likely factors, but due to their simultaneous occurrence during a hurricane, their relative effects cannot be separated without a manipulative experiment. Thus, the Luquillo Long-Term Ecological Research Program (LTER) in Puerto Rico has undertaken experimental manipulations of key aspects of hurricane effects to separate and evaluate the confounding effects of canopy opening and debris deposition on forest recovery. We simulated these two aspects of major hurricane effects in the LEF by selectively cutting and partially removing the forest canopy (Fig. 1), and by modifying the deposition of canopy debris on the forest floor (Fig. 2). Using a factorial experiment allowed us to investigate the separate and combined effects of canopy opening and debris on this forest. In this introductory manuscript, we (1) describe the study site, (2) detail the methodology employed in our experiment, (3) report some of the principal abiotic responses to treatments, and (4) introduce the subject areas of the 12 additional manuscripts included in this special issue.

2. Methodology

2.1. Study site

The island of Puerto Rico is located in the Caribbean, Western Atlantic, which is a region that experiences an average of 5.9 hurricanes annually (based on years 1950–1982; Gray, 1984). The Luquillo Experimental Forest (LEF) in northeastern Puerto Rico is a 11,000 ha tropical (18° N latitude) evergreen forest that spans elevations of approximately 100–1075 m (Fig. 3). The LEF is the primary study site of the Luquillo LTER. Major hurricanes pass over the LEF once every 50–60 years, on average (Scatena and Larsen, 1991); yet just 9 years separated the last two major hurricanes (Hugo in 1989, Georges in 1998). The Canopy Trimming Experiment (CTE) occurred in the northwestern portion of the LEF near El Verde Field Station (EVFS) in tabonuco forest (subtropical wet forest in the Holdridge System; Ewel and Whitmore, 1973), which is the forest type that comprises the majority of the LEF and is dominated by the trees *Dacryodes excelsa* (tabonuco; Burseraceae), *Prestoea acuminata* var. *montana* (syn. *Prestoea montana*; sierra palm; Arecaceae), *Sloanea berteroana* (motillo; Elaeocarpaceaea), and *Manilkara bidentata* (ausubo; Sapotaceae). Mean annual rainfall at EVFS is 3592 mm (SD = 829; LTER climate data:

Fig. 1. Photographs from the initiation of canopy trimming treatments (Trim) within the Canopy Trimming Experiment in Puerto Rico wet forest, showing (a) an arborist ("Jesus") reaching for a recently cut branch in the canopy, and (b) a portion of a completed Trim treatment plot (30 × 30 m) where all tree branches ⩽10 cm diameter were cut and removed from the canopy. Photographs by A.B. Shiels.

Fig. 2. Photographs from the initiation of debris addition treatments (Debris) within the Canopy Trimming Experiment in Puerto Rico wet forest, where (a) two researchers (P. Klawinski and M. Strickland) stand at the edge of a measurement plot and deposit canopy debris, and (b) twigs + leaves, palm fronds, and wood (up to 10 cm diameter) cover the forest floor in a completed debris-addition plot (30 × 30 m), where debris was added at a rate of approximately 6 kg m^{-2} (dry mass basis). Photographs by A.B. Shiels.

http://luq.lternet.edu/data/). Rainfall is weakly seasonal, with relatively less rain falling between January and March than the rest of the year; monthly rainfall rarely averages < 200 mm (Zimmerman et al., 2007; McDowell et al., 2012). The wettest periods are April–May and September–November (McDowell et al., 2012). Diurnal and mean annual air temperatures above the canopy are 21–25 °C (Odum et al., 1970; McDowell et al., 2012). There are two main peaks of leaf fall observed in this forest (April–May and August–September), which coincide with the periods of major solar radiation at this latitude (Zalamea and González, 2008). Soils are a complex of well and poorly drained Ultisols and Oxisols with a clay and silty clay loam texture (Soil Survey Staff, 1995). The average tree canopy heights were 20.4 ± 0.3 m (mean ± SE) before Hurricane Hugo (Brokaw et al., 2004), yet in the CTE plots in 2003 prior to treatments the 135 tallest canopy trees averaged 18.1 ± 0.3 m (range: 13–30 m; A. Shiels, unpublished data). The sizes of forest patches (i.e., patches of nearly complete canopy loss) near EVFS that were created by the two most recent major hurricanes were 0.01–0.05 ha based on canopy structure following Hurricane Hugo (estimation based on Fig. 2 in Brokaw and Grear, 1991), and 0.10 ha based on plant community change of canopy trees following Hurricane Hugo and Georges (Zimmerman et al., 2010). These canopy gaps created by recent hurricanes guided our choice of plot size (0.09 ha) for our experiment. For comparison, treefalls near EVFS that are unrelated to hurricanes typically create canopy gaps of ⩽30 m^2 (0.003 ha), where the largest gap encountered in the forest survey was 117 m^2 (Brokaw et al., 2004).

2.2. Experimental design and treatments

The CTE incorporated a 2 × 2 factorial randomized block design where each of three blocks (A, B, and C) had four 30 × 30 m plots (each 0.09 ha; 12 plots in total; Fig. 3). Each block had similar land-use history (>80% forest cover in 1936), soils (Zarzal clay series), slope (<35%; average 24%), and elevation (340–485 m; Shiels et al., 2010). Two manipulations were performed: (1) branches and leaves were removed from the canopy (trimmed), and (2) branch segments and leaves were deposited on the forest floor (debris). Each plot within a block was randomly assigned to one of the four treatments (n = 3 for each treatment): (1) No trim + no debris, in which neither the canopy nor the forest floor were altered (Fig. 4); (2) Trim + no debris, in which the canopy was trimmed and the debris from the trimming was removed from the plot; (3) No trim + debris, in which the canopy was unaltered, but debris from the Trim + no debris treatment was weighed and deposited on the forest floor; and (4) Trim + debris, which simulated the conditions of a natural hurricane, in which the canopy was trimmed and debris from the trimming was weighed and then distributed on the forest floor below. Each plot was no closer than 20 m from the edge of an adjacent plot. Each block was completed prior to beginning treatments on a subsequent block.

In total, six plots had their canopies trimmed (two per block: one Trim + debris and one Trim + no debris treatment). The area trimmed included the vertical projection of the 30 × 30 m plot,

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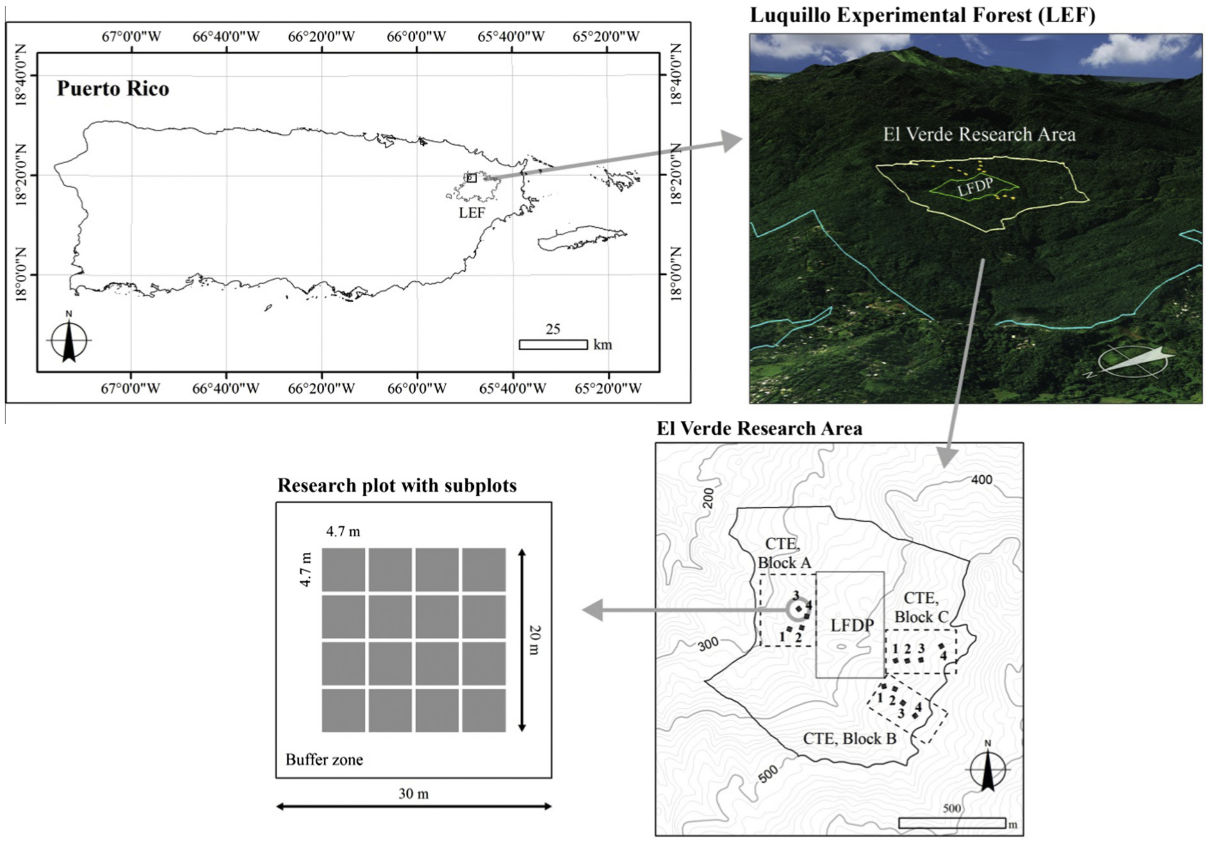

Fig. 3. Location of the Canopy Trimming Experiment (CTE) in El Verde research area within the Luquillo Experimental Forest (LEF), northeastern Puerto Rico. CTE blocks are adjacent to the Luquillo Forest Dynamic Plots (LFDP), and inferred area covered by each block (broken lines) is 40,000 m^2. Treatment plots (square plots, numbered 1–4 within each block) are each 30 × 30 m. Within each plot, a 5 m buffer area surrounds a 20 × 20 m core measurement area where 16 subplots (quadrats, each 4.7 × 4.7 m) are separated by trails (white lines) to minimize observer impacts. Figure modified from Zalamea et al. (2012).

Fig. 4. Photograph of a No trim + no debris plot within the Canopy Trimming Experiment in Puerto Rico wet forest; the No trim + no debris plots ($n = 3$) serve as reference comparisons for forest responses to canopy trimming and debris addition treatments. Walking paths (ca. 0.4 m wide, delineated by the cords visible in lower center of the photograph) separated the subplots where plant, animal, microbial, and abiotic sampling occurred. Within the sampling subplot in the lower left of the photograph, plastic flags mark where soil cores were removed from the plot or where soil gas measurements occur; also visible is a lysimeter for measuring soil water chemistry (lower right, below striped flagging), a plant tag (shiny metal; lower right), a litterfall basket positioned at 1 m height (center), a throughfall collector attached to the outside of the litterfall basket (not clearly visible), and a 30 cm diameter plastic ring used for soil gas sampling (on ground in center). Photograph by A.B. Shiels.

utilizing the following methods. All non-palm trees ⩾15 cm DBH (diameter at 1.3 m height) within the 30 × 30 m plot had branches that were less than 10 cm diameter removed. For non-palm trees 10–15 cm DBH, each tree was trimmed at 3 m height. For palms ⩾3 m tall (at the highest part of the leaf), all leaves were trimmed at the connection with the main stem, and the apical meristem was preserved. Therefore, except for some palms that had leaves attached to their stem below 3 m height, no vegetation of any type was trimmed below 3 m height. These trimming procedures reflected tree conditions resulting from major hurricanes that had previously passed through this forest (e.g., Brokaw and Grear, 1991). In each of the six 30 × 30 m plots where the canopy was trimmed, there were approximately 57 non-palm trees trimmed (16 trees 10–15 cm DBH, 41 trees ⩾15 cm DBH) and 39 palm trees removed of their fronds. Thus, the total number of trees trimmed in our experiment was 576 (342 non-palm trees, 234 palm trees), which was represented by 28 species including the five most abundant species trimmed (in descending order): *D. excelsa*, *P. montana*, *M. bidentata*, *Matayba domingensis* (Sapindaceae), and *Micropholis garciniifolia* (Sapotaceae). *Prestoea montana* was the only species of palm in the CTE plots.

Six plots had canopy debris added to the forest floor (two per block: one No trim + debris and on Trim + debris). As canopy debris was obtained from a Trim plot, it was moved outside of the plot, cut into manageable sized lengths (e.g., 0.5–1.0 m woody sections), sorted into three categories that included wood (branches ⩾1.5 cm diameter), twigs + leaves (branches <1.5 cm diameter and all non-palm foliar material), and palm fronds; debris was then weighed and piled on plastic sheets (tarpaulins) by category outside of the respective debris-addition plot (Shiels et al., 2010). Subsamples of each debris category were weighed, dried at 45 °C, and reweighed to establish wet/dry weight ratios. Subsamples of debris

were also analyzed for carbon and nutrients during the period that the debris was piled outside of the plots (Table 1). All debris was obtained from, and distributed within, the same block. The amounts of each debris category (kg) added to treatments among blocks were matched as closely as possible; therefore, for block A, it was necessary to trim additional debris from a nearby location (60 m outside the nearest plot) to more closely match the total debris added to debris-addition plots in the other two blocks (Shiels et al., 2010). Approximately 11,157 ± 362 kg (mean ± SE) of wet mass debris (6530 ± 186 kg dry mass) was removed from each of the six trim plots, and 5408 ± 143 kg (dry mass) per plot (or 6 kg m^{-2}) was added into the Trim + debris and No trim + debris plots by spreading it evenly across each plot (Fig. 2) in the following proportions: 67% wood, 29% twigs + leaves, and 4% palm fronds (Shiels et al., 2010). In addition to weighing debris removed from each Trim plot, subsamples of debris were weighed just prior to addition to determine the mass lost since the trimming occurred. The net loss of approximately 1100 kg (or 17%) of debris per plot was largely due to natural decomposition (primarily foliar material) as the piles of debris at plot edges were added into the two debris-addition plots as the final activity that completed treatment of an individual block. On average, it took approximately 75 days to complete all treatments within a block, and the specific treatment periods were: Block B: 26 October 2004–20 January 2005; Block C: 24 January-17 March 2005; Block A: 22 March-16 June 2005. When averaged across plots, the amount of mass lost due to natural decomposition as the debris piles remained at the plot edges was 11.6% for wood, 27.5% for twigs + leaves, and 16.1% for palm fronds (Shiels et al., 2010). The initial ratios of carbon to nitrogen concentrations of trimmed debris were 208:1, 40:1, 32:1 for wood, twigs + leaves, and palm fronds, respectively (Table 1). During the maximum period that debris was piled outside of the plots (i.e., ca. 10 weeks), wood and twigs + leaves tended to gain nitrogen (decreasing the carbon: nitrogen by 10–35%) and calcium, whereas palm fronds tended to lose nitrogen, phosphorus, and potassium (increasing the carbon: nitrogen ratio by 9%; Table 1).

To minimize the influence of edge effects associated with the treatments, the core 20 × 20 m area in each 30 × 30 m plot was used for all of the CTE measurements (Fig. 3). Furthermore, the 20 × 20 m interior measurement area was divided into 16 quadrats (each ca. 4.7 × 4.7 m; also referred to as subplots) with walking trails (ca. 0.4 m wide) established between adjacent quadrats to minimize disturbance (Fig. 3). Due to the large number of measurements planned for this long-term experiment, the 16 quadrats were randomly assigned to soil-related measurements (e.g., soil nutrient and gas sampling) or surface sampling (e.g., woody seedlings and herbaceous plants, litter arthropods, decomposition). Many of these measurements were also restricted to boulder-free areas, and boulders and stones covered approximately 25% of the surface (Shiels et al., 2010). The walking trails provided access to sampling locations and were used as transects for conducting some density estimates (e.g., ferns, frogs, lizards, spiders; Klawinski et al., 2014; Sharpe and Shiels, 2014). Prior to treatment application beginning in October 2004, all of the plots were monitored and measured for at least 1 year for all CTE biotic variables (e.g., population and community measures of microbes, plants, and animals) and all abiotic variables (e.g., light, throughfall) except for litter moisture.

2.3. Abiotic measurements

Due to canopy and understory disturbance associated with the CTE treatments, we focused our measurements of abiotic conditions within each plot on the following variables: understory light (assessed via canopy openness), throughfall, litter and soil moisture, and debris depth and cover on the forest floor. Here we review or expand upon some of the abiotic measures that appear in the two previous CTE publications (Richardson et al., 2010; Shiels et al., 2010).

In each plot, and beginning in December 2003 (approximately 1 year before CTE treatments began), hemispherical canopy photos were taken using a fisheye lens at 1 m height above the center of five random quadrats (subplots) and at the corners and center of the 20 × 20 m measurement area (i.e., $n = 10$ photos per plot per sampling period). In addition to the single pre-treatment photo period, canopy photos were taken and analyzed for light transmission (canopy openness) 2–3 times each year post-treatment (2005–2008; Shiels et al., 2010). Funnels attached to bottles were placed at 1 m height in three random locations in the measurement area of each plot to collect rainfall (throughfall) at 2-week intervals (Richardson et al., 2010). Quarterly measures of soil moisture and litter moisture were determined by calculating wet/dry ratios for samples (soil cores or leaf litter) collected from five

Table 1
Mean ± SE elemental concentrations (dry mass basis) of different aged debris piles (0, 1, 2, 4, and 10 week old) that resulted from canopy trimming in the Canopy Trimming Experiment (CTE), Luquillo Experimental Forest, Puerto Rico. Once debris was trimmed from the canopy (initial debris), it was sorted into three categories that included wood (branches 1.5–10 cm diameter), twigs + leaves (branches < 1.5 cm diameter and all non-palm foliar material), and palm fronds; debris was then piled outside of the debris-addition plots until redistributed into the plots. A combination of all aged debris listed was added into the debris addition plots at a rate of approximately 6 kg m^{-2}. Debris pile samples were usually obtained from all six canopy trimmed plots in the CTE.

Debris pile category and age	Carbon (%)	Nitrogen (%)	Phosphorus (mg/g)	Calcium (mg/g)	Potassium (mg/g)	Sodium (mg/g)	Iron (mg/g)	Aluminum (mg/g)
Wood								
Initial ($n = 8$)	50.91 ± 0.24	0.25 ± 0.04	0.18 ± 0.05	1.93 ± 0.56	1.63 ± 0.20	0.40 ± 0.09	0.11 ± 0.05	0.12 ± 0.06
Week 1 ($n = 8$)	51.65 ± 0.10	0.37 ± 0.04	0.21 ± 0.03	2.90 ± 0.28	1.61 ± 0.11	0.71 ± 0.23	0.14 ± 0.05	0.17 ± 0.05
Week 2 ($n = 3$)	51.31 ± 0.20	0.35 ± 0.08	0.28 ± 0.11	2.36 ± 0.39	2.30 ± 0.81	0.53 ± 0.05	0.11 ± 0.02	0.06 ± 0.02
Week 4 ($n = 11$)	51.48 ± 0.17	0.37 ± 0.05	0.24 ± 0.04	3.11 ± 0.57	1.83 ± 0.21	0.32 ± 0.05	0.16 ± 0.04	0.10 ± 0.03
Week 10 ($n = 4$)	51.65 ± 0.14	0.38 ± 0.07	0.18 ± 0.05	3.33 ± 1.02	1.33 ± 0.19	0.65 ± 0.09	0.16 ± 0.09	0.14 ± 0.08
Twigs + leaves								
Initial ($n = 25$)	50.03 ± 0.30	1.24 ± 0.04	0.63 ± 0.02	7.73 ± 0.52	4.63 ± 0.22	2.35 ± 0.21	0.35 ± 0.07	0.67 ± 0.36
Week 1 ($n = 31$)	50.68 ± 0.29	1.22 ± 0.03	0.65 ± 0.02	6.53 ± 0.19	4.92 ± 0.27	2.34 ± 0.12	0.75 ± 0.14	0.72 ± 0.14
Week 2 ($n = 36$)	50.83 ± 0.31	1.23 ± 0.03	0.62 ± 0.02	7.33 ± 0.36	4.23 ± 0.24	1.97 ± 0.14	1.25 ± 0.27	1.06 ± 0.22
Week 4 ($n = 35$)	50.80 ± 0.36	1.17 ± 0.03	0.56 ± 0.02	8.92 ± 0.35	3.79 ± 0.22	1.73 ± 0.12	1.06 ± 0.27	0.93 ± 0.22
Week 10 ($n = 10$)	51.71 ± 0.73	1.44 ± 0.04	0.71 ± 0.04	10.30 ± 0.08	3.46 ± 0.44	1.54 ± 0.28	0.28 ± 0.06	0.25 ± 0.05
Palm fronds								
Initial ($n = 19$)	47.71 ± 0.37	1.48 ± 0.05	0.92 ± 0.03	5.26 ± 0.26	7.33 ± 0.46	1.13 ± 0.15	0.70 ± 0.30	0.76 ± 0.33
Week 1 ($n = 9$)	47.78 ± 0.36	1.35 ± 0.08	0.87 ± 0.06	4.88 ± 0.34	7.03 ± 0.93	1.64 ± 0.30	0.54 ± 0.25	0.58 ± 0.27
Week 2 ($n = 5$)	41.11 ± 0.31	1.20 ± 0.11	0.79 ± 0.11	3.54 ± 0.39	6.37 ± 2.24	1.72 ± 0.72	1.11 ± 0.70	1.42 ± 0.69
Week 4 ($n = 9$)	48.20 ± 0.27	1.31 ± 0.07	0.79 ± 0.05	4.17 ± 0.33	6.23 ± 1.23	1.85 ± 0.32	1.21 ± 0.56	1.19 ± 0.51
Week 10 ($n = 3$)	48.12 ± 0.76	1.36 ± 0.08	0.71 ± 0.07	5.53 ± 0.49	4.37 ± 0.79	1.31 ± 0.53	0.65 ± 0.51	0.53 ± 0.40

random quadrats per plot (Richardson et al., 2010). In each plot, debris was measured on the forest floor on an annual basis in each of five subplots by estimating the percentage cover of dead wood and leaf litter, as well as by measuring the depth of the debris at 12 standardized points within each subplot (Shiels et al., 2010).

3. Results and discussion

3.1. Post-treatment abiotic conditions and comparisons to natural hurricanes

The physical conditions created by canopy treatment (Trim + debris, and Trim + no debris) and understory treatment of debris deposition (Trim + debris, and No trim + debris) were similar to those resulting from past major hurricanes (⩾category 3) that passed through the LEF (see review in Shiels et al., 2010). Immediately following our canopy trimming treatments, understory light availability (calculated by measurements of canopy openness from 1 m height) was about twice as high as the light conditions when the canopy was intact (Fig. 5a; Shiels et al., 2010). Following Hurricane Georges in 1998, understory light availability in this same forest was nearly 4-fold greater than the estimated pre-hurricane levels (Comita et al., 2009). Similarly, after Cyclone Winifred passed through an Australian rainforest, light levels increased 2- to 3-fold (Turton, 1992). Our study probably created slightly less diffuse light than a natural hurricane simply because the surrounding trees and canopy outside each 30 × 30 m plot remained intact. Understory light and canopy openness in our study returned to pre-hurricane conditions within about 18 months (Fig. 5a; Richardson et al., 2010; Shiels et al., 2010), which was similar to that of this same forest after Hurricane Hugo in 1989 (14 months; Fernández and Fetcher, 1991). An additional pattern of interest was the apparent reduction in canopy openness in the plots where the canopy was unaltered (i.e., No trim plots; Fig. 5a), which is a pattern probably attributable to prolonged forest recovery from the last major hurricane (Georges) that occurred about 7 years prior to the completion of the CTE treatments in June 2005 (Shiels et al., 2010).

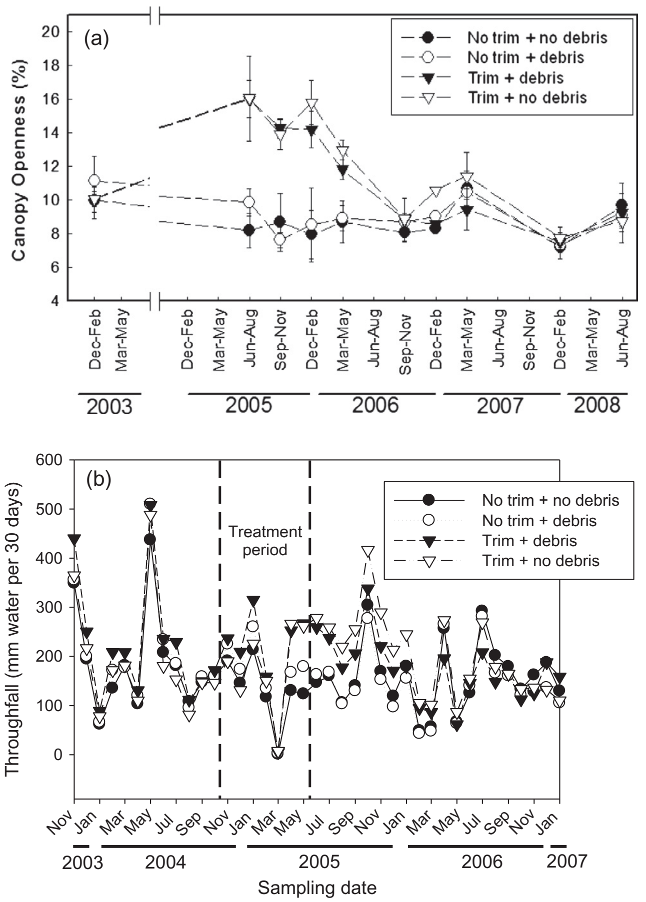

Fig. 5. Mean (SE) (a) canopy openness, and (b) throughfall, measured at 1 m height in the four treatments ($n = 3$ plots per treatment) within the Canopy Trimming Experiment in Puerto Rico wet forest. Treatments were completed prior to June 2005 sampling. Note that some symbols overlap. There were just 4 days of throughfall falling during March 2005, and total average throughfall for March 2005 did not exceed 8 mm for any treatment. (a) is modified from Shiels et al. (2010); (b) is modified from Richardson et al. (2010).

Trim plots received more throughfall than plots with intact canopies (Fig. 5b; Richardson et al., 2010). During the first 3 months post-treatment, the plots with intact canopies (No trim) received approximately 60% of the throughfall that Trim plots received; after 9 months post-treatment, throughfall at 1 m was indistinguishable between Trim and No trim plots. The increase in water penetrating the understory (throughfall) probably benefited soil moisture, and plots with their canopies trimmed had about 10% greater soil moisture (based on soil dry weight) than plots with intact canopies during the first 3 months following completion of the CTE treatments (Richardson et al., 2010). However, the increase in soil moisture in Trim plots could have also resulted from reduced transpiration from major leaf loss associated with canopy trimming. Litter moisture followed the opposite trend as that of soil moisture; during the first year post-treatment the surface litter in plots with intact canopies had 7–14% greater moisture content than plots with trimmed canopies, and litter moisture levels remained higher in the intact canopy plots than trimmed canopy plots for 18 months post-treatment (Richardson et al., 2010). Therefore, the opening of the canopy greatly altered the understory micro-environment by increasing light and decreasing litter moisture for 18 month, and increasing throughfall and soil moisture for 3 months.

The amount of debris deposited onto the forest floor varies greatly between hurricanes (e.g., Lodge et al., 1991 vs. Ostertag et al., 2003) and among locations in the same forest following the same hurricane (e.g., Vogt et al., 1996 vs. Lodge et al., 1991; Zimmerman et al., 1995). However, the amount of canopy debris that was added to the CTE plots was similar to that naturally deposited in this forest from Hurricane Hugo. In fact, Hugo deposited almost identical amounts of leaves, twigs, and palm fronds (1934 g m^{-2}; termed fine litter by Lodge et al., 1991) as we added into each debris addition plot (1989 ± 26 g m^{-2}, mean ± SE; Shiels et al., 2010). The amount of wood deposited on the forest floor following Hugo was estimated at nearly 3000 g m^{-2} (Zimmerman et al., 1995), whereas 4020 ± 139 g m^{-2} of wood was deposited into debris addition plots in our study (Shiels et al., 2010). Shiels et al. (2010) reported several categories of debris that comprised the litter layer of the CTE plots by conducting annual measurements prior to treatment application, as well as for 3 years post-treatment. They found that the percentage of leaf litter cover rapidly declined after treatments in all of the plots except the No trim + no debris plots; the three manipulation treatments did not recover to levels of the No trim + no debris plots for 2 years post-treatment. The leaf litter declines that occurred in the Trim + no debris plots probably resulted from the large reduction in litterfall due to canopy removal (Fig. 1) coupled with decomposition of the leaves in the litter layer that were deposited prior to canopy trimming. In contrast, the leaf litter declines in the debris-addition plots were probably due to the greater proportion of woody material (i.e., twigs and wood) relative to that of leaves. Shiels et al. (2010) also found that the smaller size class of wood (pieces < 5 cm diameter)

appeared to decline to pre-treatment levels within 3 years in debris addition plots, yet the largest size class of wood (pieces ⩾ 5 cm diameter) in debris-addition plots had not returned to levels of the No trim + no debris plots within 3 years (Fig. 6a). Relative to Hurricane Hugo, our study included more wood and a deeper (1.5 cm, or 37% greater) litter layer (Fig. 6b; Shiels et al. 2010). The litter depth following Hurricane Hugo was 4.1 ± 0.9 cm (Guzmán-Grajales and Walker, 1991), and it was 5.6 ± 0.5 cm in our study and persisted in elevated levels in the Trim + debris plots relative to No trim + no debris plots for at least 4 years post-treatment (Fig. 6b). These variable patterns of hurricane-debris disappearance rates are expected to be important for biotic recovery and ecosystem processes that may occur beyond the initial months following treatment applications (Richardson et al., 2010; Shiels et al., 2010).

There are a number of attributes of our experimental debris addition treatments that differed from that of a natural hurricane (see Shiels et al., 2010 for a detailed review), including (1) whole trees and woody material >10 cm diameter were not part of the added debris, (2) debris was cut into pieces and spread evenly across the treatment plots rather than mimicking patchy distributions, and (3) minimal fresh debris (e.g., green foliar material) was part of the debris added because canopy debris had naturally decomposed for several weeks outside of the plots prior to debris addition. Our project was aimed at simulating branch and leaf loss, and ameliorating the patchy spatial heterogeneity in debris deposition that occurs during a natural hurricane by evenly spreading the debris on plots. Spreading the debris evenly allowed us to more accurately measure the ecosystem consequences of decomposing debris at a scale of 4.7 × 4.7 m subplots. We cut the woody debris into ⩽1 m pieces because it was logistically easier to handle and transport. We had recognized the difficulty in uprooting trees and adding large woody debris (>10 cm diameter) in a uniform manner within the scale of our plots, and therefore we did not attempt to replicate these effects of a natural hurricane. The only hurricane study for which we are aware of that simulated the uprooting of large trees was that completed in temperate forest, at the Harvard Forest LTER site, where winches were deployed to pull down whole trees (Bowden et al., 1993; Carlton and Bazzaz, 1998; Cooper-Ellis et al., 1999). Unlike natural hurricane effects at Harvard Forest, the LEF does not experience a high frequency of whole tree blow-downs during natural hurricanes. For example, Hurricane Hugo was a category 4 storm (yet of "moderate intensity" relative to five other previous hurricanes in Puerto Rico; Scatena and Larsen, 1991) that passed over our study site in 1989 and resulted in the majority of tree structural effects as branch and leaf loss, and just 9% of trees were uprooted and 11% had snapped trunks (Walker, 1991). The CTE also differed from the experimental hurricane study at Harvard Forest because the CTE included treatment-plot replication.

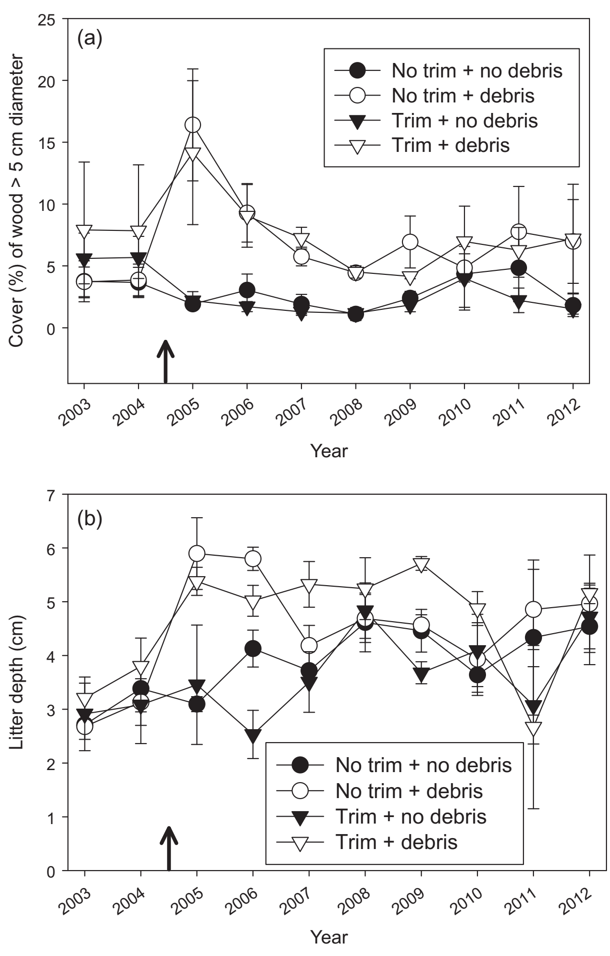

Fig. 6. Mean (SE) physical conditions of (a) percentage wood >5 cm diameter on the forest floor, and (b) litter depth, measured in each of the four treatments (n = 3 plots per treatment) within the Canopy Trimming Experiment in Puerto Rico wet forest. Treatments occurred prior to the 2005 sampling. Note that some symbols overlap.

3.2. Articles within this special issue

Studies that have occurred within the CTE permanent plots are diverse, and the associated findings detailed in this special issue provide mechanistic understandings of response patterns of tropical forest biota (microbes, plants, animals) and processes (decomposition, herbivory, nutrient cycling, primary production) to canopy and understory disturbance that resembles that of a major hurricane. Although measurements for this experiment are ongoing, we include findings for up to the first seven years post-treatment at this time. There are two papers published to date that document the results of this large-scale experiment (see Richardson et al., 2010; Shiels et al., 2010). In addition to some of the abiotic responses to CTE treatments described above, Richardson et al. (2010) focused on the litter invertebrate community responses during the first year post-treatment, and Shiels et al. (2010) focused on the woody seedlings and tree (stems ⩾1 cm DBH) responses during the first 3 years following experimental treatments. In both studies, the majority of the biotic changes (i.e., litter invertebrates and plants) observed were driven by the opening of the canopy, yet there was also evidence that the debris treatments and the synergistic effects (i.e., interactions) of canopy trimming treatments with debris addition treatments had some effect on driving forest change. For example, canopy openness decreased diversity and biomass of litter invertebrates, and shifted species dominance, irrespective of debris deposition (Richardson et al., 2010). Shiels et al. (2010) reported that when the canopy was trimmed the number of stems (indiv. >1 cm DBH) increased 2-fold and rates of recruitment increased >25-fold, whereas debris addition temporarily increased seedling mortality and tree basal area, and plots with trimmed canopies without debris addition had a several hundred-fold increase in seedlings of pioneer species.

The specific subject areas of the 12 additional papers in this special issue are described below. Cantrell et al. (2014) surveyed the bacteria and fungi communities in soil, and on non-senescent (green) and senescent leaves, by using lipid extractions followed by genetic screening to investigate for treatment effects and variation in pre- and post-treatment conditions. Lodge et al. (2014) linked fungi activity and phosphorus dynamics in the green and senescent litter with initial (1 year post-treatment) decomposition rates. González et al. (2014) also conducted a decomposition study

during the initial 1.5 years post-treatment by using green and senescent leaves placed in litterbags of different mesh sizes to examine the influence of different sized litter invertebrates on decomposition and nutrient release processes. Nutrient dynamics were also examined aboveground in the form of litterfall production in the CTE (Silver et al., 2014), and McDowell and Liptzin (2014) measured soil solution chemistry and matched it with stream nutrient dynamics in the period following Hurricane Hugo in 1989. Aside from microbial dynamics, decomposition, litterfall, and nutrient cycling studies within the CTE, there are two studies focused on plant community responses, one on herbivory, and three studies of animal responses in this special issue. Zimmerman et al. (2014) examined tree responses to CTE treatments by expanding on the findings of Shiels et al. (2010) and including an additional 4 years of tree surveys to form long-term (7 years post-treatment) conclusions about tropical tree dynamics following hurricane effects. Ferns are rarely studied following hurricanes, and Sharpe and Shiels (2014) investigated fern community structure, growth, and spore production for the initial 4 years post-treatment. Prather (2014) measured midstory and understory leaf herbivory on five pioneer, and three non-pioneer, plant species. Finally, the three articles that focused on animal responses to canopy and understory disturbance in the CTE included Schowalter et al. (2014) that investigated arthropod community structure in the mid-story and canopy; Willig et al. (2014) that monitored population and community responses of terrestrial gastropods; and the only study involving vertebrate responses to CTE hurricane effects was by Klawinski et al. (2014), where coqui frog (*Eleutherodactylus coqui*) populations dynamics were documented.

This collection of manuscripts highlight how the experimental nature of the CTE hurricane study will benefit those studying other natural and anthropogenic disturbances in forest ecosystems, as well as those managing forests exposed to large-scale canopy disturbance or woody debris deposition. Most forest processes are greatly altered by canopy disturbance and debris addition or removal regardless of whether the disturbance is natural (e.g., hurricanes, Zimmerman et al., 1995) or anthropogenic (logging, Johns et al., 1996; Feldpausch et al., 2005). In addition to establishing the level at which forest properties resist or recover from such disturbances, the experimental nature of the CTE will assist forest managers in mechanistic understanding of changes in productivity, decomposition, nutrient cycling, and population and community dynamics following disturbance. We end our special issue with a synthesis paper (Shiels et al., 2014) that highlights the findings from all of the special issue articles, and further demonstrates how this large-scale experiment has improved our overall understanding of tropical forests of past, present, and future.

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