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Responses to canopy loss and debris deposition in a tropical forest ecosystem: Synthesis from an experimental manipulation simulating effects of hurricane disturbance

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ABSTRACT

Hurricanes, cyclones, or typhoons are intense and broad-scale disturbances that affect many island and coastal ecosystems throughout the world. We summarize the findings of the articles that compose this special issue of *Forest Ecology and Management*, which focuses on a manipulative experiment (the Canopy Trimming Experiment, CTE) that simulates two key aspects of hurricane effects in a wet tropical forest. Although previous studies of tropical and subtropical forests have documented changes resulting from hurricanes, it is not clear which of the two simultaneously occurring direct effects of hurricanes—canopy openness or debris deposition—most influence responses. In the Luquillo Experimental Forest (LEF) of Puerto Rico, a multi-disciplinary team of scientists used replicated factorial manipulations to determine the independent and interactive effects of canopy openness and debris deposition on structural and functional characteristics of the forest. The majority of responses were primarily driven by canopy openness rather than by debris deposition. Canopy openness resulted in significant increases in densities of and compositional changes in woody plants, ferns, and some litter arthropods, and significant decreases in coqui frog abundances, leaf decomposition, and litterfall. Debris deposition significantly increased tree basal area and microbial diversity on leaf litter, but these increases were relatively small and ephemeral. Several interactive effects of canopy openness and debris addition emerged, including those involving understory herbivory, canopy arthropod structure, terrestrial gastropod abundances and composition, and soil solution chemistry. Arguably, hurricanes are the most important natural disturbance that affect the LEF, and most characteristics that were measured in the CTE showed evidence of resistance or resilience. By identifying the causal factors affecting secondary successional trajectories of diverse taxa ranging from microbes to vertebrates, biogeochemical attributes, microclimatic characteristics, and measures of ecosystem processes following hurricane disturbance, we better understand tropical forest dynamics resulting from past hurricanes and are better able to predict mechanisms of change related to future hurricanes.

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1. Introduction

Hurricanes are broad-scale and intense but relatively infrequent wind and rain storms that affect islands and coastal ecosystems on all continents except Antarctica. There is a long history of interest and study of hurricane effects on forests, in part because of the large-scale nature of the disturbance (local to landscape-level changes) that includes a prominent transfer of biomass from the canopy to the ground. With sustained wind-speeds reaching at least 119 km h^{-1} and covering 1000s of hectares, hurricanes strip most of the leaves and branches from canopy trees, snap stems, uproot trees, and deposit large amounts of biomass (debris) from the canopy onto the forest floor (Walker et al., 1991; Everham and Brokaw, 1996). To better understand how environmental characteristics respond to hurricanes, land managers and scientists have conducted a wealth of studies that have tracked initial and long-term changes to forest ecosystems following hurricanes (Walker, 1995; Burslem et al., 2000; Tanner and Bellingham, 2006; Lugo, 2008; Turton, 2008). A key aspect resulting from these studies is that resistance, the ability of a system to not change substantially in function or structure in response to a disturbance, and

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resilience, the capacity to recover to pre-disturbance conditions after substantial changes have been effected by disturbance (Holling, 1973; Waide and Willig, 2012), are largely dependent on species adaptations to the local disturbance regime, which includes the long-term frequency and intensity of hurricane disturbance. Therefore, forests are typically more resistant and resilient to hurricane effects in regions where these storms have been frequent over millennial timescales, as in the Caribbean or parts of southeast Asia, rather than in areas where they are less frequent (e.g., South America, continental Africa, northern Malaysia; Scatena et al., 2012).

Studies of hurricane effects on forests typically focus on the consequences of a particular disturbance event, not the mechanisms mediating responses. In the Luquillo Experimental Forest (LEF) of Puerto Rico, hurricane studies have been numerous because cyclonic storms are such key components for understanding local and regional forest dynamics. In fact, hurricanes are considered the most important natural disturbance affecting the structure of the LEF (Crow, 1980; Scatena et al., 2012). Major hurricanes (sustained wind speeds of at least 178 km h^{-1}; category 3 or above on Saffir-Simpson Hurricane Wind Scale) pass over the LEF once every 50–60 years, on average (Scatena and Larsen, 1991). Nonetheless, just 9 years separated the last two major hurricanes (Hugo in 1989, Georges in 1998). These two disturbance events had the most severe effects on the LEF relative to all others that have passed through Puerto Rico since 1932, including three category 1 hurricanes (Marilyn in 1995; Bertha in 1996; Hortense in 1996). As evidence of the wide interest in initial and multi-year observations of forest responses to Hurricanes Hugo and Georges in the LEF, two special issues (Walker et al., 1991, 1996a) and >100 additional peer-reviewed journal articles that relate specifically to these hurricanes have been published (http://luq.lternet.edu/publications). The studies contained in the two special issues (both focused on effects of Hurricane Hugo) made clear that many different response trajectories arise after hurricane disturbance; some species populations and biogeochemical attributes increased or decreased immediately after the hurricane, and then returned to pre-hurricane levels (e.g., particular gastropod species and soil nutrients), whereas others experienced rapid decreases and did not recover within a 5 year period (e.g., root biomass, *Lamponius portoricensis* walking sticks; Zimmerman et al., 1996; Willig et al., 2012). Studies after Hurricane Georges highlighted that response trajectories partly reflect disturbance history; that is, responses of Hurricane Georges needed to be interpreted in light of the forest alterations caused by Hurricane Hugo (Boose et al., 2004; Ostertag et al., 2005). Interpreting data from multi-year studies in the LEF following these two major hurricanes has facilitated the development and use of several predictive models relating to the response trajectories of forest attributes and forest dynamics following hurricane disturbance (e.g., Uriarte et al., 2004; Wang and Hall, 2004; Prates et al., 2010). Despite knowledge gained from these observational studies in the LEF and elsewhere, the key factors that modulate response patterns following hurricanes are poorly understood from a mechanistic perspective.

The lack of understanding of key mechanisms driving forest responses following hurricanes is largely the result of the paucity of manipulative studies of hurricane effects. The great value in utilizing experiments to determine mechanistic attributes controlling responses to disturbance has been the primary motivation for the Canopy Trimming Experiment (CTE). The Luquillo Long-Term Ecological Research (LTER) Program in Puerto Rico has undertaken experimental manipulations of two simultaneously occurring direct effects of hurricanes—canopy openness and debris deposition—to evaluate their separate and synergistic effects on forest recovery. Previous research (Walker et al., 1991, 1996a; Zimmerman et al., 1996; Brokaw et al., 2012) identified canopy loss and the accumulation of debris on the forest floor as key factors that govern responses during secondary succession. Although the CTE is the first experimental study of hurricane effects conducted in a tropical forest, there was an experiment in temperate forest at the Harvard Forest LTER site in northeastern USA, where whole trees were pulled down in a single plot to simulate conditions of a previous major hurricane (Bowden et al., 1993; Carlton and Bazzaz, 1998; Cooper-Ellis et al., 1999; Barker Plotkin et al., 2013). The main effects observed in the temperate experiment were reduced basal area of trees due to the physical application of the manipulation, increased light levels, and establishment of pioneer tree species in areas of soil disturbance caused by uprooting (Carlton and Bazzaz, 1998; Cooper-Ellis et al., 1999; Barker Plotkin et al., 2013). In the CTE, we simulated the two key effects of hurricanes 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; see Shiels and González [2014] for details). Moreover, we used a replicated factorial design to evaluate which of these two factors independently or synergistically affected population, community, or biogeochemical dynamics. In this article, we (1) summarize the findings from the CTE that are reported in this special issue, (2) compare the CTE findings to

Fig. 1. A recently trimmed portion of the canopy in a Trim plot in the Canopy Trimming Experiment, Puerto Rico. Note the clean cuts made by the arborist where the branches narrow to 10 cm diameter. Photograph by A.B. Shiels.

Fig. 2. Debris piles (comprising canopy leaves and branches) positioned outside of a 30 × 30 m plot and awaiting deposition into a debris-addition treatment plot in the Canopy Trimming Experiment, Puerto Rico. Contents of debris piles were sorted by category (wood, leaves + twigs, and palm fronds) and placed on sheets of plastic (tarpaulins) until being added to the debris-addition plots as the last activity prior to beginning treatments on a subsequent block. Photograph by A.B. Shiels.

results obtained from observational studies of hurricanes in the LEF and from the experimental study at the Harvard Forest LTER site, (3) identify the causal factors associated with response trajectories following major hurricanes in the LEF, and (4) identify future research opportunities.

2. Methodology

2.1. Study site

This study took place in the LEF of Puerto Rico, near El Verde Field Station (EVFS; 18°20′N, 65°49′W; see map in Shiels and González, 2014). The LEF is a 11,000 ha tropical (18°N latitude) evergreen wet forest that spans elevations from approximately 100 m to 1075 m. The LEF is the primary study area of the Luquillo LTER Program. Mean annual rainfall at EVFS is 3592 mm (*SD* = 829; LTER climate data: http://luq.lternet.edu/data/), and mean annual air temperature is 21–25 °C (Odum et al., 1970; McDowell et al., 2012). The study site for the CTE is in tabonuco forest (subtropical wet forest in the Holdridge System; Ewel and Whitmore, 1973), which is the lowermost and dominant vegetation zone along the elevational gradient of the LEF. The most common trees at the study site (see Shiels et al., 2010) are *Dacryodes excelsa* (Burseraceae), *Prestoea acuminata* var. *montana* (syn. *Prestoea montana*; Arecaceae), *Sloanea berteroana* (Elaeocarpaceaea), and *Manilkara bidentata* (Sapotaceae). In 2003, prior to application of experimental treatments, the 135 tallest canopy trees at the site averaged 18.1 ± 0.3 m (range: 13–30 m; A. Shiels, unpublished data).

2.2. Experimental design

The CTE incorporated a 2-factor, randomized block design with canopy trimming and debris addition as main effects. Each of three blocks (A, B, and C) were established in tabonuco forest with similar land-use history (>80% forest cover in 1936), soils (Zarzal clay series), slope (<35%; average 24%), and elevation (340–485 m) in an area of approximately 50 ha near EVFS (see Shiels et al., 2010). In each block, four 30 × 30 m plots were established (12 plots total). Plot size was chosen after considering the patchiness of altered forest canopies in the LEF following Hurricane Hugo (Brokaw and Grear, 1991). Plots within each block were located at least 20 m from the edge of adjacent plots. To minimize edge effects, a 20 × 20 m interior measurement area was established in each 30 × 30 m plot. The 20 × 20 m measurement area was divided into a grid of 16 quadrats (each ca. 4.7 × 4.7 m), and walking trails were established between adjacent quadrats to minimize disturbance associated with sampling (see Shiels and González, 2014).

Two manipulations were performed: (1) branches and leaves were removed from the canopy (trimmed; Fig. 1), and (2) branch segments and leaves were deposited on the forest floor (debris; Fig. 2). 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; (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 deposited on the forest floor; and (4) Trim + debris, which most closely simulated conditions of a hurricane, in which the canopy was trimmed and debris from the trimming was distributed on the forest floor. Each block was completed before beginning treatments on a subsequent block. Treatment application extended from October 2004 to June 2005. The area trimmed included the vertical projection of the 30 × 30 m plot in the canopy. All non-palm trees ⩾15 cm diameter at 1.3 m height (DBH) within the 30 × 30 m area had branches removed that were less than 10 cm diameter. For 10–15 cm DBH trees other than palms, each tree was trimmed at 3 m height. For palms, fronds extending 3 m above ground were trimmed at the connection with the main stem and the apical meristem was not removed. Therefore, except for some palms that had fronds attached to their stem below 3 m height, no vegetation of any type was trimmed below 3 m height. The trimmed debris was sorted into three categories: wood (branches ⩾1.5 cm diameter), leaves and twigs (branches <1.5 cm diameter and all non-palm foliar material), and palm fronds. All debris was then stored by category outside respective treatment plots until trimming was completed within a block (Fig. 2). Debris was added to plots by distributing it evenly across each 30 × 30 m area. This was done to minimize heterogeneity of debris additions among plots. All plots subject to debris addition within a block had equal amounts of debris added. Similarly, the amounts of each category of debris (kg) that were added to plots were matched as closely as possible among blocks. In total, the amount of debris added to each of the six detritus addition plots was 5408 ± 143 kg (dry-mass basis; or 6 kg m^{-2}), representing 67% wood, 29% leaves and twigs, and 4% palm fronds (Shiels et al., 2010). On average, all treatments within a block were completed within 75 days.

The response characteristics that were considered in contributions to this special issue included population and community characteristics of diverse taxa ranging from microbes to vertebrates, biogeochemical attributes, microclimatic characteristics, and measures of ecosystem processes (Table 1).

2.3. Overcoming barriers of scale, debris deposition simulation, and forest variability

The establishment of treatments within the CTE revealed the challenges associated with simulating hurricane effects at an appropriate scale and in a heterogeneous forest. 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 (0.01–0.05 ha, estimated from Fig. 2 in Brokaw and Grear, 1991; 0.10 ha, Zimmerman et al., 2010) guided our choice of plot size (0.09 ha). Although the size of the plots were equivalent to a canopy patch produced by a hurricane, our study did not reproduce the landscape-level patchwork that is generated from hurricanes in this forest (see Boose et al., 2004) because the CTE plots were embedded in an intact forest matrix. To reproduce the landscape conditions of a hurricane would have required a much larger treatment plot containing a fuller range of patches of canopy loss. After considering such an option, we chose to balance the trade-off between scale of treatment by choosing 0.09 ha plots rather than being faced with the difficulties of interpreting an unreplicated experiment (Barker Plotkin et al., 2013).

Rather than attempting to simulate a hurricane *per se*, our project simulated branch and leaf loss, as well as the open canopy conditions that occur in association with a natural hurricane. To more accurately measure the consequences of decomposing debris at a scale of 4.7 × 4.7 m subplots, we ameliorated the patchy spatial heterogeneity in debris deposition that occurs during a natural hurricane by evenly spreading the debris on plots. Prior to beginning our study, 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 did not attempt to replicate these effects of a natural hurricane. Furthermore, the LEF does not experience a high frequency of whole tree blowdowns during natural hurricanes. For example, Hurricane Hugo was a category 4 storm that passed over our study site in 1989 and with the majority of tree structural effects manifesting as branch and leaf loss; only 9% of trees were uprooted and 11% had snapped trunks (Walker, 1991). In contrast, the experimental blow-down study at the Harvard Forest LTER site uprooted whole

Table 1
A summary of the contributions to the special issue, classifying articles by the subject areas, approximate pre- and post-treatment sampling duration, and sampling frequency within the Canopy Trimming Experiment, Luquillo Experimental Forest, Puerto Rico.

Contributors	Page Nos.	Subject area(s)	Pre-treatment sampling (yrs.)	Post-treatment sampling (yrs.)	Sampling frequency
Shiels and González	1–10	Abiotic and methods	1.0–1.5	1.5–7.0	Monthly, annually
Lodge et al.	11–21	Fungi, phosphorus, and mass loss	0	1.0	Every 7–14 weeks
Cantrell et al.	22–31	Soil and litter bacteria and fungi	2.0	1.0	Every 14 weeks
González et al.	32–46	Decomposition and nutrients	0	1.5	Every 2–3 months
Silver et al.	47–55	Litterfall mass and nutrients	2.0	2.5	Quarterly
McDowell and Liptzin	56–63	Soil solution chemistry	1.5	5.0	Monthly
Zimmerman et al.	64–74	Trees	1.5	7.0	Annually
Sharpe and Shiels	75–86	Ferns	2.0	5.0	Annually
Prather	87–92	Understory herbivory	1.0	3.0	Annually
Schowalter et al.	93–102	Canopy arthropods	1.0	5.0	Annually
Willig et al.	103–117	Gastropods	1.0	7.0	Annually
Klawinski et al.	118–123	Frogs	1.5	1.0	Quarterly

trees to simulate the predominant effects of natural hurricane effects in New England (Cooper-Ellis et al., 1999).

Spatial and temporal variability of the plot locations, and plot sampling, respectively, created a challenging environment from which to interpret responses to canopy removal or debris deposition. Although we carefully selected plots with similar land-use history, soils, slope, and elevation, many of response characteristics differed greatly among plots even prior to treatment (Shiels et al., 2010; Shiels and González, 2014). Before treatment application began in October 2004, all of the plots were monitored and measured for at least 1 year for most biotic variables (e.g., population and community measures of microbes, plants, and animals) and many abiotic variables (e.g., light, throughfall). Willig et al. (2014) dealt with prominent plot variability of the studied characteristics by adjusting all post-treatment sampling values by their initial (pre-treatment) values. Challenges with temporal variation were also apparent for many variables; such variation was largely attributed to the great length of time necessary to complete the treatments, and in particular the labor and logistics required to remove and deposit large amounts of trimmed material in a timely manner. Because treatments within a block were completed prior to beginning treatments of a subsequent block, each treatment replicate was staggered by approximately 75 days (147 days from first to last). Therefore, two strategies were used for measuring forest responses to the CTE treatments. The most common strategy for post-treatment sampling was to sample all plots simultaneously, thereby referencing a single date (June 16, 2005) as the completion date of all treatment replicates. A second strategy was to conduct post-treatment sampling by block such that an equal number of days had passed since a block's completion and its subsequent sampling (e.g., Klawinski et al., 2014). This second strategy was more reflective of "time since treatment", but it meant that the post-treatment sampling crossed seasons. Regardless of strategy, it was impossible to account for all temporal variation that resulted from performing our experimental tests of hurricane effects.

3. Results and discussion

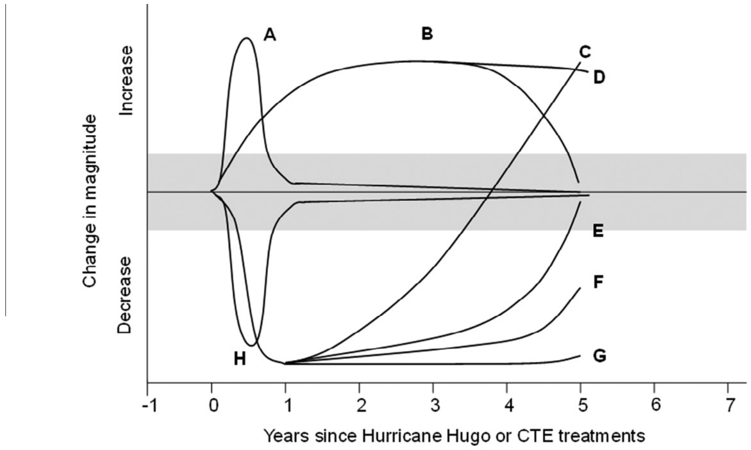
3.1. Key findings and comparisons with past hurricanes

Using a diversity of research methods and sampling frequencies (Table 1), authors in this special issue studied abiotic, biotic, and structural responses of wet tropical forest to the separate and synergistic effects of canopy openness and debris deposition that typically result from a major hurricane. Relative to all other recent hurricanes in the LEF, the physical setting created by the CTE was most similar to that which resulted from Hurricane Hugo (see Shiels et al., 2010). Additionally, there was an abundance of observational studies following Hurricane Hugo that allow for comparison to the CTE (Walker et al., 1991, 1996a; Zimmerman et al., 1996). Therefore, in addition to comparisons with hurricanes that occurred outside of Puerto Rico, we have mostly focused our comparisons of response trajectories from the CTE to those that arose from Hurricane Hugo in the LEF (Fig. 3). Comparisons between the CTE and the Harvard Forest blow-down experiment are also included, and focus specifically on the key findings regarding physical and biogeochemical effects that were documented from the blow-down experiment.

3.1.1. Microclimatic attributes (light, moisture, debris)

The key abiotic responses to treatments in the CTE are summarized by Shiels and González (2014). Canopy trimming caused a twofold increase in light (canopy openness) and a 7–14% decrease in litter moisture that lasted approximately 18 months post-treatment. Plots subject to canopy trimming also experienced increased soil moisture and throughfall that lasted about 3 months post-treatment (Richardson et al., 2010; Shiels and González, 2014). Additionally, in plots where the canopy was trimmed and debris ($6\ \mathrm{kg\ m^{-2}}$) was added to the forest floor, the debris persisted for at least 4 years; debris decomposed more quickly in plots with intact canopies (Shiels and González, 2014). These changes in physical and microclimatic characteristics following the CTE treatments were similar to those measured after the passage of category $\geqslant 3$ hurricanes through similar wet tropical forest, including Hurricane Hugo in the LEF. For example, understory light and canopy openness in the CTE returned to pre-hurricane conditions within about 18 months (curve A in Fig. 3), which was similar to that of this same forest after Hurricane Hugo (14 months; curve A in Fig. 3; Fernández and Fetcher, 1991). After Hurricane Gilbert passed through Jamaican montane forest (1600 m a.s.l.), it took ca. 24–28 months for understory light to recover to pre-hurricane levels (Bellingham et al., 1996). Although a pre-disturbance reference measurement of canopy openness or understory light did not occur in the LEF just prior to Hurricane Georges in 1998, understory light availability was estimated to increase nearly fourfold in the LEF following Hurricane Georges (Comita et al., 2009). Similarly, light levels increased two- to threefold after Cyclone Winifred passed through an Australian rainforest (Turton, 1992). Trimming the canopy in CTE probably created slightly less diffuse light than did a natural hurricane because the surrounding trees and canopy outside each 30 × 30 m plot remained intact.

Forest floor litter mass in tabonuco forest nearly doubled after Hurricane Hugo (based on litter depth; Guzmán-Grajales and Walker, 1991), after Hurricane Georges (Ostertag et al., 2003), and after the debris addition treatments in the CTE (based on litter



Hurricane Hugo	CTE
A: Light, forest floor mass, stream nitrate, some soil nutrients	A: Light (T), leaf microbe diversity (D), soil water nitrate (T+D)
B: NPP, abundances of adult coqui frogs and the snail *Cepolis*	B: Forest floor wood (D), some litterfall nutrients (T)
C: Some species of terrestrial snails, above-ground nutrients	C: *Psychotria* seedlings (T)
D: N/A	D: Tree density (T), tree basal area (D), non-native ferns (T)
E: Tree biomass, tree density	E: Fern density (T)
F: Litterfall	F: Litterfall (T)
G: Fine root biomass, *Lamponius* (walking stick) abundance	G: N/A
H: N/A	H: Frog density (T), litter moisture, inverts, decomposition, and fungi (T)

Fig. 3. Responses of some biotic, abiotic, biogeochemical, and ecosystem processes following either Hurricane Hugo (September 1989) or the experimental hurricane manipulations performed during the Canopy Trimming Experiment (CTE), in the Luquillo Experimental Forest, Puerto Rico. The shaded portion of the graph represents values that are indistinguishable from pre-hurricane (or pre-treatment) values. The CTE response curves are associated with trimming trees and branches to open the canopy (T), or the addition of canopy debris to the forest floor (D). Curve A: transient (ca. 1 yr) increase. Curve B: slow increase and return to pre-hurricane levels. Curve C: rapid decrease and subsequent rise above pre-hurricane levels. Curve D: slow increase and maintained levels outside the range of pre-disturbance conditions. Curve E: rapid decrease and return to near pre-hurricane levels. Curve F: rapid decline and steady increase, but not to pre-disturbance levels. Curve G: rapid decline and little recovery until 5 yr post-hurricane. Curve H: transient (ca. 1 yr) decrease. N/A signifies the absence of a measured variable that followed the specific response curve after Hurricane Hugo or the CTE. Figure modified from Zimmerman et al. (1996).

depth; Shiels et al., 2010). Unlike Hurricane Hugo (ca. 40% leaves, 60% wood) and the CTE (ca. 33% leaves, 67% wood; reviewed in Shiels et al., 2010), the majority of the litter mass on the forest floor after Hurricane Georges was leaf material (50–60%) rather than wood (30–40%; Ostertag et al., 2003). Fine litter (leaves + twigs and palm fronds) that was deposited on the forest floor debris addition plots of the CTE (1989 ± 26 g m^{-2}; Shiels et al., 2010) was nearly identical to that in the same section of the LEF following Hurricane Hugo (1934 ± 26 g m^{-2}, debris suspended and deposited on the ground; Lodge et al., 1991); yet the amount of wood deposited into each debris addition plot within the CTE was slightly greater (4020 ± 139 g m^{-2}; Shiels et al., 2010) than that deposited by Hurricane Hugo in the same section of the LEF (ca. 3000 g m^{-2}; Zimmerman et al., 1995). Because Hurricane Georges was a less intense storm than Hurricane Hugo, and it followed Hurricane Hugo by just 9 years, there was less structural change and much less debris deposited on the forest floor (ca. 500 g m^{-2} fine litter and ca. 250 g m^{-2} wood in the Bisley section of the LEF; Ostertag et al., 2003) than after Hurricane Hugo or in the CTE.

3.1.2. Microbes, decomposition, and biogeochemical attributes

Soil and litter microbial communities were evaluated post-treatment from the standpoint of community change and potential for influencing decomposition and nutrient dynamics resulting from CTE treatments (Cantrell et al., 2014; González et al., 2014; Lodge et al., 2014). Litter decomposition is mainly driven by microbial activity, but litter substrate, microclimate, and litter arthropods also play an important role (González and Seastedt, 2001; Coleman et al., 2004). In the CTE, there were few significant treatment effects detected for soil and leaf microbial communities during the 1 year post-treatment monitoring period (Cantrell et al., 2014). However, fungal and bacterial diversity in the leaf litter increased when debris was added to plots, indicating the importance of this resource to microbial communities (curve A in Fig. 3). Furthermore, Cantrell et al. (2014) found that microbial succession was arrested in plots where the canopy was trimmed and debris was not added.

Basidiomycete fungi in the Agaricaceae play a key role in the decomposition process in wet tropical forests like the LEF because these fungi colonize multiple pieces of litter with their mycelia, degrade lignin, and readily translocate nutrients such as phosphorus (Lodge et al., 2014). By observing different cohorts of leaves, including nonsenescent (green) and senescent, Lodge et al. (2014) determined that agaric fungi connectivity (an estimate of density) increased with litter moisture and phosphorus concentration, and elevated levels of fungi connectivity was also associated with increased mass loss. In trimmed plots, agaric fungi conserved some phosphorus but much phosphorus from green leaves was leached (Lodge et al., 2014). Many agaric decomposer species are sensitive to litter moisture, and the dominant closed canopy species in the LEF (*Gymnopus johnstonii*) disappeared from litter on exposed ridges after the canopy was opened by Hurricane Hugo (Lodge and Cantrell, 1995). Similarly, Lodge et al. (2014) found that in the treatment plots from the CTE, abundances of *G. johnstonii* in leaf litter differed in the following pattern (most abundant to least abundant): No trim > Trim + debris > Trim + no debris. Very high rates of phosphorus translocation by *G. johnstonii* (Lodge, 1993), and its great sensitivity to low moisture, suggests that the reduction or loss of this important agaric species from Trim plots is probably at least partly responsible for the increased loss (lack of translocation) of phosphorus from the leaf litter (Lodge et al., 2014). Lodge et al. (2014) also suggest that fungal dominance shifts under open canopy conditions, whereby agaric macrofungi decrease and microfungi increase. The increase in microfungi in canopy trimmed plots correlates with increases in Trim plots of groups of litter arthropods that consume microfungi (e.g., mites, collembolans, Psocoptera; Richardson et al., 2010). Such fungal and microarthropod shifts associated with canopy loss can have significant effects on rates of decomposition (González et al., 2014).

Leaf decomposition in the CTE was slowed by canopy opening (curve H in Fig. 3), and accelerated by debris addition (Lodge et al., 2014); a similar finding was observed by González et al. (2014) using litter bags, although debris addition only accelerated decomposition in the intact canopy plots and not the Trim + debris plots. A slightly different experimental design used by Lodge et al. (2014) relative to that used by González et al. (2014) could have accounted for the different decomposition results in the Trim + debris plots; green leaves were placed on top of senesced leaves in the study by Lodge et al. (2014) but not in the study by González et al. (2014). As expected, decomposition rates were greater for green leaves relative to senescent leaves, and nitrogen and phosphorus concentrations in green leaves were also greater than concentrations in senesced leaves (González et al., 2014). Debris addition in the CTE plots facilitated the retention of foliar nitrogen at 0.2 years post-treatment (González et al., 2014). Canopy trimming led to a significant increase in concentrations of leaf litterfall nitrogen, phosphorus, and iron (Silver et al., 2014), which are nutrients that appeared important in microbially-mediated movements from the soil to litter (iron; González et al., 2014; nitrogen; Zimmerman et al., 1995), and also among litter cohorts via agaric fungi and from litter to the soil via leaching (phosphorus; Lodge et al., 2014). Therefore, canopy loss and forest floor debris deposition are two key aspects of hurricanes that alter decomposition rates and associated nutrient dynamics across the below- and above-ground continuum that includes the forest litter layer.

Debris additions from hurricane treatments release carbon, nitrogen, and other nutrients during decomposition, potentially contributing to plant growth but also to soil solution chemistry and stream runoff. Additionally, canopy opening from disturbance can decrease nutrient uptake by plants and increase nutrient leaching from increased throughfall (McDowell et al., 2013; Lodge et al., 2014). Dissolved carbon and nutrients in soil solution (groundwater) were reported monthly in all CTE plots (McDowell and Liptzin, 2014). Groundwater nitrate increased in the Trim + debris plots over an 18 month period (curve A in Fig. 3; McDowell and Liptzin, 2014), which was identical to the nitrate pulse in groundwater and streams in the LEF after Hurricane Hugo (curve A in Fig. 3; McDowell et al., 1996) and to the nitrate pulse in the nearest stream to the CTE plots after Hurricane Georges (McDowell et al., 2013). The independent effects of canopy opening or debris addition did not have any significant effects on groundwater chemistry (McDowell and Liptzin, 2014). Furthermore, the CTE treatments did not reflect additional groundwater responses to past hurricanes because there were no increases in dissolved organic nitrogen, ammonium, or potassium concentrations associated with canopy opening or debris deposition (McDowell and Liptzin, 2014). Similarly, in the Harvard LTER blowdown study there were small, if any, changes to soil nutrients, including nitrogen (Bowden et al., 1993). Therefore, nitrate appears to be the most responsive nutrient to hurricane disturbance in the LEF, and its increase is generated by the opening of the canopy occurring simultaneously with the deposition of nutrient-rich debris on the forest floor.

3.1.3. Forest productivity

Changes in plant productivity during the first years after hurricanes (e.g., curve B in Fig. 3) can be attributed to the influence of canopy openness and debris deposition. Basal area increase was one measure of primary productivity included in the CTE. Although the large increase in small stems in the canopy trimmed plots was correlated with increased basal area (see Fig. 1 in Zimmerman et al., 2014), there was no significant effect of trimming on plot-level basal area. Instead, debris deposition resulted in a small but significant increase in basal area (ca. 10% increase) relative to plots where debris was not added (Shiels et al., 2010; Zimmerman et al., 2014). The positive effects of debris deposition on primary productivity were also evident in plots near our study site (Walker et al., 1996b); the removal of debris generated by Hurricane Hugo caused a significant decrease in tree diameter increment relative to control plots. The increase in basal area in the CTE debris deposition plots indicates the potential importance of debris as a fertilizer or soil moisture enhancement that can facilitate stand-level basal area increase for 2 years post-treatment (Shiels et al., 2010). Although debris deposition resulted in subtle increases in basal area and litterfall, which is another surrogate for primary productivity, litterfall did not show any significant response in the CTE to enhanced debris on the forest floor (Silver et al., 2014). Due to branch and leaf loss, litterfall decreased significantly and had not returned to pre-disturbance levels for at least 2.5 years in the CTE trim plots (Silver et al., 2014) and for at least 5 years after Hurricane Hugo (curve F in Fig. 3). While understory and mid-story productivity may be enhanced by canopy opening conditions stimulating the recruitment and growth of small stemmed pioneer species, productivity (basal area or litterfall) on the plot or stand level is not enhanced through experimental canopy disturbance.

3.1.4. Population and community attributes

Woody vegetation is the most common forest attribute measured after hurricane occurrence (Everham and Brokaw, 1996; Burslem et al., 2000; Tanner and Bellingham, 2006; Zimmerman et al., 2010), and therefore many generalizations such as the degree to which a forest is considered resistant or resilient, are based on the responses of woody vegetation to disturbance. Findings from the CTE indicate that following a hurricane, the increase in stem abundance, and the shift in composition to dominance by early successional species, can be largely explained by the increase in light produced by canopy openness rather than by the increase in debris on the forest floor (Shiels et al., 2010; Zimmerman et al., 2014). The increase in woody plant abundance in the trim plots was almost entirely due to recruitment by the smallest size class (1.0–2.5 cm DBH), which remained at elevated densities in trim plots relative to intact canopy plots for at least 7 years (curve D in Fig. 3). A similar result was found in the Harvard Forest blowdown study, where saplings and sprouts increased fourfold, including early successional species such as *Betula* spp. (Carlton and Bazzaz, 1998; Cooper-Ellis et al., 1999). Community analysis in the CTE demonstrated that the dominant individuals in the small size classes of the trimmed plots were pioneer species, and the establishment of pioneers in the canopy trimmed plots (3–6 new species on average) resulted in significant increases in woody plant species richness relative to intact canopy plots (Zimmerman et al., 2014). Therefore, following a natural hurricane, it is the effects of canopy opening that stimulate the rapid increase in stems of pioneer species, thereby increasing the species richness of forest stands, and after 2–3 years the same small size classes of pioneers begin thinning in the understory and mid-story as a result of the canopy closure. Forest thinning of the smallest size classes (up to 5 cm DBH) was also evident in the unmanipulated and intact canopy plots, a pattern most likely explained by continued forest thinning from the last severe hurricane (Georges) that occurred 7 years prior to the CTE treatments (Shiels et al., 2010). Therefore, canopy disturbance from major hurricanes result in relatively long periods (at least 7 years) of forest change (curve D in Fig. 3).

Removing much of the forest canopy above 3 m height, which is a common occurrence following hurricanes as well as the methodology used in the CTE, resulted in a downward shift of the functional forest canopy to the level of the understory herbaceous layer (Willig et al., 2012). The understory fern communities in the CTE plots were highly resistant and resilient to disturbance. Although the density of ferns, including the dominant fern species in the plots, *Thelypteris deltoidea* and *Cyathea borinquena*, decreased initially following Trim + debris treatment, densities recovered to pre-disturbance conditions within 3 years (Sharpe and Shiels, 2014; curve E in Fig. 3). Leaf and spore production increased following canopy trimming, and particularly so in plots where the canopy was removed and debris was added to the forest floor. In contrast, *T. deltoidea* leaf length showed high resistance to canopy loss, particularly in the absence of debris addition to the forest floor (Sharpe and Shiels, 2014). Similar to woody plant changes, four new fern species of early successional status recruited into the open canopy treatment plots; one of the four species was the non-native pioneer fern *Nephrolepis brownii* (curve D in Fig. 3; Sharpe and Shiels, 2014). However, fern compositional dynamics in the CTE were unlike those of woody plant species that resulted from treatments in the CTE (Shiels et al., 2010; Zimmerman et al., 2014) or in other tropical hurricane studies (Walker et al., 1996b; Murphy et al., 2008; Comita et al., 2009) in that there were (1) no resident fern species lost under simulated hurricane treatments (open canopy with debris deposition), and (2) resident (non-pioneer) species instead of pioneer species dominated the understory during the 5 years after the experimental hurricane disturbance (Sharpe and Shiels, 2014). Thus, the understory fern community in the LEF is more resistant and resilient to hurricane effects than is the woody plant community. Although future research is needed, the high resilience of the understory fern community may enact some inhibitory effects on the recruitment and establishment of woody plant species (Royo and Carson, 2006), as previously observed with the temperate fern, *Dennstaedtia punctilobula*, that increased 100% in cover after the experimental blowdown study at the Harvard Forest LTER site (Cooper-Ellis et al., 1999), and with the tree fern *Cyathea arborea*, and scrambling ferns in the Gleicheniaceae on landslide scars in the LEF (Walker et al., 2010).

Pioneer and non-pioneer plants in the understory were differentially affected by invertebrate herbivory in CTE treatment plots. Herbivory was generally higher on pioneer plants in plots where the canopy had been trimmed but the debris had not been added to the forest floor, whereas herbivory was generally higher for non-pioneer plants in plots with both intact forest canopies and debris added to the forest floor (Prather, 2014). Surprisingly, the combination of canopy trimming and debris addition had no significant effect on herbivory of pioneer or non-pioneer plants (Prather, 2014). Thus, understory herbivory follows either curve B or D in Fig. 3 for Trim + no debris (pioneers) and No trim + debris (non-pioneers) because after 2 years post-treatment the herbivory rates did not return to pre-treatment levels (Prather, 2014). These herbivory results from the CTE were unlike those documented after Hurricane Georges because herbivory rates declined from 16% (prior to the hurricane) to just 2% after Georges (Angulo-Sandoval et al., 2004); neither the study by Angulo-Sandoval et al. (2004) nor Prather (2014) measured arthropod abundance.

For pioneer plants, Prather (2014) hypothesized that the increase in herbivory in the Trim + no debris plots was due to the increased density of pioneer plants and a reduction in predators that subsequently caused an increase in abundance of herbivore species that eat pioneer plants (i.e., trophic cascades). Trimming the forest canopy increased densities of seedlings (stems <1 cm DBH) of pioneer species in the CTE, particularly in Trim + no debris plots (Shiels et al., 2010). A flush of new foliar material of woody pioneer species in the understory is often preferred by understory herbivores in tropical forests (Coley and Barone, 1996), and herbivory rates are often elevated on plant species that are locally more abundant (Schowalter and Ganio, 1999; Angulo-Sandoval and Aide, 2000). Additionally, a reduction in populations of coqui frog (an insect predator) was evident in the Trim plots (Klawinski et al., 2014), and Richardson et al. (2010) hypothesized that a reduction in litter arthropod predators may have accounted for the increased abundance of particular groups of litter arthropods in Trim plots.

Prather (2014) further hypothesized that the attributes affecting elevated herbivory of non-pioneer species were different than those for pioneer species, and suggested that the elevated herbivory in No trim + debris plots was probably due to the unmeasured increase in foliar quality and increases in abundance of certain herbivores that feed on non-pioneer plants. In a simultaneous study in the CTE plots, Schowalter et al. (2014) determined that debris deposition increased the diversity of canopy arthropods on plants, and these effects were more pronounced on non-pioneer plant species than on pioneer plant species. Schowalter et al. (2014) suggested that the increases in canopy arthropods in debris-addition plots were probably due to unmeasured increased foliar quality resulting from a fertilizer effect of the debris-addition. However, debris addition in the CTE did not affect leaf litterfall chemistry during the first 2.5 years post-treatment, and it was the trimming of the canopy that instead increased foliar nitrogen and phosphorus in leaf litterfall (Silver et al., 2014). Another possibility for increased herbivory of non-pioneer plants in debris-addition plots is that the debris provides favorable habitat for certain herbivores that feed on non-pioneer plants. Similar to the findings of ferns (Sharpe and Shiels, 2014) and those of seedling and adult woody plants (Shiels et al., 2010; Zimmerman et al., 2014) in the CTE, the levels of herbivory following hurricane effects largely depend on the life-history characteristics of the plant species (i.e., whether it is pioneer or non-pioneer).

Animal responses reported here for the CTE include litter invertebrates, canopy arthropods, gastropods, and coqui frogs (*Eleutherodactylus coqui*). Animals typically responded significantly to canopy trimming, although Schowalter et al. (2014) found that debris-addition caused the greatest responses in canopy arthropod populations and community indices, and Willig et al. (2014) found some significant population and community responses to debris-addition that supplemented the majority of the effects generated by canopy trimming. Coqui frogs (Klawinski et al., 2014) and litter invertebrate diversity and biomass (Richardson et al., 2010) immediately decreased after canopy trimming (curve H in Fig. 3), and the responses of these two groups of animals may be directly related because the majority of the coqui diet is understory invertebrates (Stewart and Woolbright, 1996). Because of the mobility of animals relative to plants, the patch sizes (plots) created by the CTE are particularly important for interpreting responses to natural and simulated hurricane effects involving animals. Immediate and rapid decreases in some terrestrial gastropod and understory invertebrate populations followed Hurricane Hugo (curve C and H in Fig. 3); however some gastropod populations increased following Hurricane Hugo, either immediately or after several years (curve B and C in Fig. 3). From measurements after Hurricanes Hugo and Georges, Bloch et al. (2007) determined that the patchiness of canopy structure produced by hurricanes is particularly important for predicting sites occupied by snails. In general, it was surprising to find that the canopy trimming (including Trim + debris plots) had such a large effect on decreasing populations of litter arthropods (Richardson et al., 2010), gastropods (Willig et al., 2014), and coqui frogs (Klawinski et al., 2014), whereas debris addition had (in most cases) little to no effect on these populations.

Debris addition in the CTE did not have any effect on coqui populations (Klawinski et al., 2014), which was surprising given that adult coqui densities increased sixfold beginning 1 year after Hurricane Hugo (Woolbright, 1996). Woolbright (1991, 1996) attributed the increase in coqui density following Hurricane Hugo to the increase in forest floor habitat structure and humidity that benefited nesting and reproduction (curve B in Fig. 3). Compared to intact canopy plots, litter moisture was 12–15% lower during the first 4 months post-treatment in the Trim plots, and 6–8%

lower during the next 6 months (Richardson et al., 2010; Shiels and González, 2014). Such reductions in litter moisture levels in the Trim plots could have influenced densities of coqui, litter arthropods, and terrestrial gastropods. As discussed in Section 2.3, there were a number of methodological challenges associated with simulating hurricane effects on an appropriate scale and in a heterogeneous forest in this study; some of these challenges may partly explain the differences between responses to Hurricane Hugo and various CTE treatments (Fig. 3).

3.2. CTE conclusions

Following Hurricane Hugo, Zimmerman et al. (1996) summarized many of the key biotic, biogeochemical, and ecosystem responses that occurred in the LEF (Fig. 3). From such a synthesis, it became clear that mechanisms that control hurricanes responses were elusive. The studies summarized here partially fill that gap in understanding. Results from the CTE demonstrate that the majority of responses to hurricane disturbance in the LEF are likely driven by canopy openness rather than by debris deposition (Fig. 3). Canopy openness resulted in significant increases in densities and compositional changes in woody plants, ferns, and some litter arthropods, and significant decreases in coqui abundances, leaf decomposition, and litterfall. Debris deposition significantly increased tree basal area and microbial diversity on leaf litter, but these increases were relatively small and ephemeral. Although interactive effects of canopy openness and debris addition played some role in most of the studies included in this special issue, the most significant interactions involved understory herbivory, canopy arthropod structure, gastropod composition, and soil solution chemistry. The degree to which herbivory influences understory plants after hurricanes largely depends on the life-history status (pioneer versus non-pioneer) of the plant species. Life-history changes in woody plants and litter arthropods were also among the most important changes resulting from canopy treatments. Canopy arthropods and terrestrial gastropods were relatively resistant to hurricane treatments on the plot-size scale, and their adaptations favoring drought tolerance as well as the mobility of these animals, including possible movements between adjacent intact forest and the CTE plots, may have partially enabled their apparent high resistance to disturbance.

Several forest attributes evinced different responses when measured in the CTE versus after Hurricane Hugo (e.g., coqui frogs, some gastropods; Fig. 3). Some of the discrepancy between responses to Hurricane Hugo and the CTE treatments probably stem from variation in the setting at the time of each disturbance, including the physical characteristics of the disturbance and the period between hurricane impacts (Everham and Brokaw, 1996; Ostertag et al., 2005; Lugo, 2008), and logistical and methodological challenges associated with simulating hurricane effects in the LEF (see Section 2.3). An additional challenge with making comparisons between the CTE and Hurricane Hugo was that the same suite of characteristics were not readily comparable either because they were unavailable at the time of the Zimmerman et al. (1996) synthesis (e.g., microbial diversity, decomposition, fern density), or were unavailable for the CTE at this time (e.g., root biomass, soil nutrients, walking stick abundances). Although ongoing measurements for this experiment will further identify the mechanisms of long-term forest change resulting from hurricanes, we have included findings up to the first seven years post-treatment. Understanding the key factors that control forest responses following hurricane disturbance leads to a greater understanding of how population, community, biogeochemical, and ecosystem characteristics contribute to dynamic forest structure and function, and enables improved predictions about what will inevitably result from large-scale disturbances such as hurricanes in the future.

4. Future research directions

The last 25 years has provided a wealth of studies of the effects of hurricanes on tropical and subtropical forests, and more recent studies have built upon several decades of prior observations of hurricane effects (Darling, 1842; Bates, 1930; Webb, 1958; Conway, 1959; Wadsworth and Englerth, 1959). Several future research needs were identified in past syntheses involving the LEF (Tanner et al., 1991; Zimmerman et al., 1996), many of which have been addressed as part of the CTE or in recent observational studies (e.g., Willig et al., 2011). The need for long-term studies (>5 years), studies of interactions among disturbances, and more manipulative studies to determine mechanistic bases of response were identified as some of the priorities (Tanner et al., 1991; Zimmerman et al., 1996). However, these needs have begun to be addressed by studies like Tanner and Bellingham (2006), Heartsill Scalley et al. (2010), and Willig et al. (2011) where 15 years of forest responses to major hurricanes were examined; Beard et al. (2005), which assessed 10 years of hurricanes and droughts in the LEF; and the experimental nature of the CTE. An additional gap in knowledge (Tanner et al., 1991) was the relative importance of new germinates and seedlings, versus previously established seedlings and saplings (residents), in influencing plant communities following a hurricane. The CTE has shed new light on this issue by showing that pioneer woody species recruit from the seed bank immediately after canopy opening, overtaking existing non-pioneer residents, and numerically dominating the adult community for the next several years (Shiels et al., 2010). What still remains unknown is whether recruitment following a hurricane can be predicted according to species presence or their longevity in the seed bank. Additionally, long-term observations are necessary to determine the lasting effects of the pioneer community on forest composition and structure (e.g., Barker Plotkin et al., 2013).

The paucity of information on plant-animal interactions following hurricanes was identified as a future research need by Tanner et al. (1991) and Zimmerman et al. (1996). Although some studies of herbivory have occurred following hurricanes (Torres, 1992; Schowalter, 1994; Angulo-Sandoval et al., 2004; Prather, 2014), much remains unknown and the study by Prather (2014) in the CTE highlighted the greater need for herbivore monitoring concomitantly with herbivory assessments of pioneer and non-pioneer plant species. Predator–prey relationships need further examination following hurricane passages to better determine drivers of changes and cascading trophic effects (e.g., Richardson et al., 2010; Schowalter et al., 2014). Movement dynamics appear critical to better understand both the importance of patch size effects on animal populations (e.g., Bloch et al., 2007) and the extent to which predators (e.g., coqui frogs, some arthropods) track prey after hurricanes. Diet shifts in predators may also be expected with the hypothesized changes in available habitat and prey that result from hurricanes (Waide, 1991).

Future research should also focus on the post-hurricane shifts in microbial communities, and identify the extent to which such shifts affect decomposition and nutrient cycling. Lodge et al. (2014) hypothesized that there is an important microbial shift from macrofungi to microfungi during open canopy conditions, and future experimental manipulations could focus on the extent and effects of such a shift on forest nutrient cycling. Moreover, including bacteria in such an assessment of the relative roles of different microbial groups after canopy and understory disturbance is also recommended. The long-term influence of coarse woody debris on forest change following hurricanes was identified by

Zimmerman et al. (1996) as an important future research direction. Zimmerman et al. (1995) reported the apparent immobilization of nutrients in the presence of coarse woody debris in the LEF, and such immobilization had important effects on reducing litterfall; yet the mechanism remain poorly understood. In contrast, Beard et al. (2005) found that coarse woody debris increased nitrogen and plant growth, but only in high productivity forest in the LEF. A long-term hypothesis established prior to initiation of the CTE was that canopy debris deposited during a hurricane significantly influences long-term (>5 years) forest changes; on-going CTE sampling should help determine if this hypothesis is viable.

Recent interest in hurricane effects to tropical forests has also stemmed from models that predict an increased frequency or intensity of such storms in association with global climate change (Emmanuel, 2005; Nyberg et al., 2007; Bender et al., 2010). In addition to determining the mechanisms driving forest responses to hurricane disturbances, a second phase of the CTE has been planned to experimentally test the effects of repeated hurricanes on abiotic, biotic, and structural characteristics of the LEF. Forest responses from multiple hurricanes at a site over a relatively short period (e.g., weeks to <10 years) are influenced by preceding hurricanes (Burslem et al., 2000; Ostertag et al., 2003, 2005; Bloch et al., 2007), and therefore forest attributes may respond differently given the hurricane history. For example, *Cecropia schreberiana*, which is the co-dominant tree after hurricanes in the LEF (Brokaw, 1998; Shiels et al., 2010), first flowers and fruits at 6 years of age (Silander, 1979; Brokaw, 1998); thus, reduced intervals between major hurricanes (e.g., <6 years) will probably have significant effects on post-hurricane plant community structure and ecosystem processes.

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