

Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico

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Summary

1. We simulated two key components of severe hurricane disturbance, canopy openness and detritus deposition, to determine the independent and interactive effects of these components on woody plant recruitment and forest structure.
2. We increased canopy openness by trimming branches and added or subtracted canopy detritus in a factorial design. Plant responses were measured during the 4-year study, which followed at least 1 year of pre-manipulation monitoring.
3. The physical conditions of canopy openness and detritus deposition in our experiment resembled the responses to Hurricane Hugo, a severe category 4 hurricane that struck this forest in 1989.
4. Canopy detritus deposition killed existing woody seedlings and provided a mechanical barrier that suppressed seedling recruitment. The increase in understorey light caused by canopy trimming stimulated germination from the seed bank and increased seedling recruitment and density of pioneer species several hundred-fold when hurricane debris was absent. Many significant interactions between trimming and detritus deposition were evident from the manner in which seedling density, recruitment and mortality changed over time, and subsequently influenced the composition of woody stems (individuals ≥ 1 cm d.b.h.).
5. When the canopy was trimmed, stem densities increased > 2 -fold and rates of recruitment into the stem size class increased > 25 -fold. Trimming had no significant effect on stem mortality. The two dominant species that flourished following canopy trimming were the pioneer species *Cecropia schreberiana* and *Psychotria berteriana*. Deposition of canopy detritus had little effect on stems, although basal area increased slightly when detritus was added. There were no evident effects of the interactions between canopy trimming and detritus deposition on stems.
6. *Synthesis.* The separate and interactive effects of canopy openness and detritus deposition result in variable short-term trajectories of forest recovery. However, the short interval of increased canopy openness due to hurricane impacts and its influence on the recruitment of pioneer trees is the dominant factor that drives short-term recovery and may alter long-term structure and composition of the forest.

Key-words: *Cecropia*, competition, detritus, disturbance, light, *Psychotria*, seedlings, succession, understorey, wind

Introduction

Hurricanes dominate the disturbance regime experienced by forested ecosystems in many parts of the world (Everham &

Brokaw 1996; Whitmore & Burslem 1998; Lugo 2008). How ecosystems are altered by hurricanes has long intrigued ecologists, as hurricanes represent large-scale, natural disturbances that can result in long-term changes to forest structure and composition (Foster 1988; Burslem, Whitmore & Brown 2000; Lugo, Figueroa Colon & Scatena 2000; Chazdon 2003; Weishampel *et al.* 2007). The number of studies that describe the impacts of hurricanes on tropical and subtropical forests has

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increased in the past two decades, as evident from several special issues of ecological journals encompassing hurricane effects in the South Pacific (Turton 2008a) and the Caribbean (Finkl & Pilkey 1991; Walker *et al.* 1991, 1996a; Stone & Finkl 1995; Middleton & Smith 2009). Hurricanes recur at a given site in the Caribbean every 9–60 years (Scatena & Larsen 1991; Lugo 2008), depending, in part, on long-term cycles in hurricane activity (Goldenberg *et al.* 2001; Nyberg *et al.* 2007; Uriarte *et al.* 2009) and possibly global temperature changes (Emmanuel 2005; Bender *et al.* 2010). These numerous studies make clear that tropical forests in the Caribbean recover quickly from even the most severe hurricanes (Scatena *et al.* 1996; Imbert & Portecop 2008), probably because the species which compose them are adapted to a disturbance regime that has prevailed in the region for millions of years (Brokaw *et al.* 2004). While studies of the impacts of hurricanes on forests have been plentiful, an understanding of the key factors that govern responses to hurricanes are lacking but could be determined by large-scale experiments similar to that conducted at Harvard Forest in north-eastern USA (Bowden *et al.* 1993; Carlton & Bazzaz 1998; Cooper-Ellis *et al.* 1999). Such experiments may provide insights into adaptations of species, recruitment processes, successional dynamics, competition and legacy effects.

To date, it is not clear which are the key factors that determine the rapid recovery of Caribbean forests from hurricane damage. One factor identified early on, however, is that while the physical damage to forest canopies caused by a severe hurricane is often very great, the amount of tree mortality is often relatively low, and the surviving trees are able to resprout after the storm (Bellingham, Tanner & Healey 1994; Zimmerman *et al.* 1994; Van Bloem, Lugo & Murphy 2006) and begin directly the re-establishment of the forest canopy (Brokaw *et al.* 2004). In addition to low tree mortality, we hypothesize that two factors – increased canopy openness and increased detritus deposition – will drive forest recovery following hurricane impacts. Because these two factors occur simultaneously during a storm, their relative effects cannot be separated without a manipulative experiment.

Hurricanes are one of several natural disturbances that alter successional dynamics by creating canopy gaps of varying sizes and by increasing understorey light (Garwood, Janos & Brokaw 1979; Fernández & Fetcher 1991; Bellingham *et al.* 1996; Denslow, Ellison & Sanford 1998). Light is one of the most limiting resources for plant growth in wet tropical forests (reviewed in Denslow 1987). The rapid closure of the overstorey by canopy trees creates a limited window of opportunity for increased rates of recruitment and growth in the understorey (Walker *et al.* 2003; Angulo-Sandoval *et al.* 2004; Uriarte *et al.* 2004, 2005), especially for light-demanding pioneer species with life-history characteristics of rapid germination and growth (Guzmán-Grajales & Walker 1991; Merrens & Peart 1992; Imbert & Portecop 2008). Also following hurricanes, density-dependent mortality results in self-thinning of new seedlings in the understorey (Scatena *et al.* 1996; Walker *et al.* 1996b; Comita *et al.*

2009). Such changes in species composition and abundance immediately following hurricane disturbance may be partially responsible for the legacy effects that are observed decades after hurricanes pass through temperate and tropical forests (Foster 1988; Whitmore & Burslem 1998; Weishampel *et al.* 2007).

Canopy detritus deposition may influence plant establishment and growth through its physical and nutritional effects (Guzmán-Grajales & Walker 1991; Denslow, Ellison & Sanford 1998; Murphy *et al.* 2008). Because soil nutrients often limit plant growth in wet tropical forests (reviewed in Vitousek & Sanford 1986), fresh canopy litter may increase nutrients and organic matter at the forest floor and benefit colonizing plants (Lodge *et al.* 1991; Denslow, Ellison & Sanford 1998). Alternatively, additions of coarse-woody debris (branches and tree trunks) following a hurricane may result in reduced plant growth because of nutrient immobilization. Nutrient immobilization occurs when microbial decomposers draw upon plant-available soil nutrients to compensate for poor-quality woody debris (e.g. high carbon:nitrogen ratios) by raising the nutrient content of the debris to that of their own biomass (Zimmerman *et al.* 1995). The deposition of hurricane debris in the understorey can also bury or physically impede seedlings, particularly pioneer species (Guzmán-Grajales & Walker 1991; Murphy *et al.* 2008). Therefore, canopy detritus generated from hurricane impacts may have positive or negative effects on plants and may alter the species composition and structure of the forest.

Many other aspects of ecosystem responses to hurricane disturbance revolve around understanding the interactive effects of hurricanes on forest canopies and the forest floor (Lodge & McDowell 1991; Zimmerman *et al.* 1994; Schaefer *et al.* 2000; Lugo 2008). The spatial patchiness in both the damage to the forest canopy (Brokaw & Grear 1991; Metcalfe, Bradford & Ford 2008) and the deposition of hurricane debris (Lodge *et al.* 1991) provides an additional component of variation which strongly influences plant establishment and growth. To understand fully the effects of a hurricane on a forested ecosystem, the Luquillo Long-Term Ecological Research Program has undertaken experimental manipulations of key aspects of hurricane impacts to disentangle and evaluate the confounding effects of canopy opening and detritus deposition on forest recovery. Working in subtropical wet forest in the Luquillo Experimental Forest (LEF) in eastern Puerto Rico, we simulated severe hurricane damage by selectively cutting the forest canopy and by modifying the deposition of canopy debris on the forest floor. Using a factorial experiment allowed us to investigate the separate and combined effects of canopy opening and detritus on this ecosystem. Here, we focus on the plant responses to manipulations that mimic the most prominent physical aspects of a severe hurricane as we address the following questions:

- 1 How do plants respond to factorial variation in canopy openness and detritus deposition?
- 2 How do plant responses from our experimental hurricane compare to past natural hurricanes at our site and others?

Materials and methods

STUDY SITE

This study took place in the LEF in north-eastern Puerto Rico, near the El Verde Field Station (EVFS; 18°20' N, 65°49' W). Mean annual rainfall at EVFS is 3500 mm, and monthly precipitation is variable, but May to December are usually the wettest months and January to April are typically slightly drier (Zimmerman *et al.* 2007). The study site is in tabonuco forest (subtropical wet forest in the Holdridge System; Ewel & Whitmore 1973), which is the lowermost of four general vegetation zones along an altitudinal gradient across the LEF. Tabonuco forest, representing 70% of the LEF, is dominated by tabonuco (*Dacryodes excelsa* Vahl), sierra palm (*Prestoea acuminata* (Willdenow) H.E. Moore var. *montana* (Graham) Henderson and Galeano; hereafter referred to as *Prestoea acuminata*), asubo (*Manilkara bidentata* (A. DC.) A. Chev.) and motillo (*Sloanea berteriana* Choisy) trees. The terrain at EVFS is steep and rocky, as boulders and stones cover c. 25% of the soil surface (Soil Survey Staff 1995). Soils near EVFS are mostly Zarzal clay series, which are deep Oxisols and Ultisols that were derived from volcanoclastic parent material (Seiders 1971; Johnston 1992; Soil Survey Staff 1995). A 1936 air photo indicated that a large portion of the forest to the north of our study location was clear-cut, and small patches of coffee (*Coffea arabica* L.) were also grown around EVFS (Thompson *et al.* 2002). Most of the forest around EVFS was selectively logged (described as 'light thinning') for stand improvement by the USDA Forest Service from 1937 to 1946 (F. Wadsworth cited by Odum 1970). The two most recent severe hurricanes impacting the LEF and preceding our experimental hurricane manipulation included Hurricane Hugo (a category 4 storm on the Saffir–Simpson hurricane scale) in September 1989, and Hurricane Georges (a category 3 storm) in September 1998.

EXPERIMENTAL DESIGN

Our experiment followed a completely randomized block design. Each of three blocks (A, B and C) were established in tabonuco forest with similar land-use history (> 80% cover in 1936; Foster, Fluet & Boose 1999; Thompson *et al.* 2002), soils (Zarzal clay series; Johnston 1992), slope (< 35°; average: 23.75°) and elevation (340–485 m a.s.l.) in an area of approximately 50 ha near EVFS. In each block, four 30 m × 30 m plots were established (12 plots total). Plot size was chosen after considering the apparent patchiness of damage to forest canopies in the LEF following Hurricane Hugo (Brokaw & Grear 1991); gaps of approximately 100 m² appeared interspersed with relatively undamaged canopy. Plots within blocks were located at least 20 m distant from the edge of adjacent plots; GPS locations (x,y coordinates using Puerto Rico planar NAD27) for each plot are available at <http://luq.lternet.edu>.

To minimize edge effects associated with the treatments, each 30 m × 30 m plot had a 20 m × 20 m interior measurement area. Additionally, the 20 m × 20 m measurement area was divided into a grid of 16 quadrats (each c. 4.7 m × 4.7 m) with walking trails established between adjacent quadrats to minimize disturbance. To plan for the large number of measurements for this long-term experiment, the 16 quadrats were randomly assigned to soil-related measurements (e.g. soil nutrients, soil gas sampling) or surface sampling (e.g. seedlings, litter arthropods, litter decomposition). Plots were monitored for at least 1 year, beginning in 2003, before experimental treatments were applied.

Each plot within a block was randomly assigned one of the four treatments: (i) Trim + Detritus (TD), where the canopy was trimmed

and detritus from the trimming was added to forest floor; (ii) Trim + Removal (TR), where the canopy was trimmed and the detritus from the trimming was removed and added to the Untrimmed + Detritus (UD) plot; (iii) UD, where the canopy was unaltered, but detritus from the TR plot was added to the forest floor; (iv) Control (CN), where neither the canopy nor the detritus were altered. Each of the blocks was treated individually and was completed before beginning treatments on a subsequent block. Treatment application extended from November 2004 to June 2005. In total, six plots had their canopies trimmed (two per block, consisting of one TD and one TR) by professional arborists. The area trimmed included the vertical projection of the 30 m × 30 m plot, utilizing the following methods: All non-palm trees ≥ 15 cm diameter at 1.3 m height (d.b.h.) within the 30 m × 30 m area had their branches that were less than 10 cm diameter removed. For non-palm trees between 10 and 15 cm d.b.h., each tree was trimmed at 3 m height. For palms ≥ 3 m tall (at the highest part of the leaf above ground), all leaves (hereafter referred to as palm fronds) were trimmed at the connection with the main stem and the apical meristem was preserved. 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 detritus 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. The detritus was immediately weighed to establish wet mass, and then subsampled, weighed, dried at 45 °C to constant mass, and reweighed to establish wet-dry mass ratios. All detritus was then piled by category outside respective treatment plots (TD or UD) until trimming and weighing in both plots within a block was completed. Approximately 11 157 ± 362 kg (mean ± SE) of (wet mass) detritus (6530 ± 186 kg dry mass) was removed from each of the six trim plots (TD and TR).

Detritus was added into the TD and UD plots by spreading each category of detritus evenly across each 30 m × 30 m area. This was performed to minimize heterogeneity of detritus additions within plots. Subsamples of detritus were weighed just prior to addition to determine the mass lost since the trimming occurred, and to estimate the total detritus added into each plot. 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 from the detritus piles (resulting from natural decomposition) during the time period from trimming the canopy to the detritus addition was as follows: 11.6% for wood, 27.5% for leaves and twigs, 16.1% for palm fronds. All TD and UD treatment plots within a block had equal portions of detritus added. Similarly, the amounts of each category of detritus (kg) added to treatments among blocks were matched as closely as possible; therefore, it was necessary to trim additional detritus from a nearby location (a telephone line c. 60 m distant outside the nearest plot) for block A to more closely match the total detritus added to TD and UD treatment plots in the other two blocks. In total, the amount of detritus added to each of the six detritus addition plots (TD and UD) was 5408 ± 143 kg (dry-mass basis), represented by 67% wood, 29% leaves and twigs and 4% palm fronds.

MEASUREMENTS

A number of physical characteristics relating to changes in light and detritus were measured in five 1 m × 3.5 m subplots (hereafter called seedling subplots) within each treatment plot. Each of these seedling subplots was randomly located in surface sampling quadrats within

each 20 m × 20 m measurement area that were at least 75% boulder-free. Hemispherical canopy photographs were taken before (December 2003) and after (2–3 times each year, 2005–2008) the treatment application using a fisheye lens (Nikon FC-E8; Nikon Inc., Tokyo, Japan) mounted on a Nikon 4500 camera body (Nikon Inc.) at 1 m height above the centre of each seedling subplot, as well as at the corners and centre of each 20 m × 20 m measurement area (i.e. $n = 10$ photos per 30 m × 30 m plot per sampling period). We analysed the colour hemispherical photos using an automatic thresholding program (Jonckheere *et al.* 2005, 2006) which ensures repeatable and accurate results of the light regime. Following this analysis, the percentage light transmission (canopy openness) was calculated as the weighted proportion of pixels classified as sky, and used as a measure of available light at each location within a plot for each sampling period. On an annual basis and in each seedling subplot, we measured percentage cover of dead wood and leaf litter, as well as litter depth (at 12 standardized points in each seedling subplot). We also quantified graminoid cover and the maximum graminoid height for each seedling subplot.

Woody plants < 1 cm d.b.h. (considered seedlings), which included trees, shrubs and lianas, were measured annually in each seedling subplot. Seedlings ≥ 10 cm tall were identified, permanently tagged and measured for height. Seedlings < 10 cm tall were identified to species but not tagged.

All woody individuals ≥ 1 cm d.b.h., hereafter termed stems, were marked with permanent tags, identified to species (nomenclature follows Liogier 1985, 1988, 1994, 1995, 1997) and measured for d.b.h. in March 2003 and October 2004 (pre-treatment measures) and October 2007 and October 2008 (post-treatment measures). We included in the group 'stems' the small palms in which the bases of the two youngest (unexpanded) leaves were at 1.3 m or higher, measuring the diameter at the top of the woody portion of the palm between the top two exposed leaf scars. All stems were marked with a wax crayon at the point of measurement to minimize measurement error on subsequent samplings.

DATA ANALYSIS

Percentage canopy openness and percentage cover values for dead wood, litter and graminoids were converted to arcsin-square roots prior to analysis of variance (ANOVA). Seedling densities were log-transformed prior to ANOVA. Rates of mortality and recruitment were calculated on a monthly basis to take into account differences in time intervals between measurements using the following equations (Condit, Hubbell & Foster 1995):

$$\text{mortality rate} = [\ln N_t - \ln(N_t - \text{no. dead}_{t+1})] / \text{no. months} \quad \text{eqn 1}$$

and

$$\text{recruitment rate} = [\ln(N_t - \text{no. recruits}_{t+1}) - \ln N_t] / \text{no. months} \quad \text{eqn 2}$$

where N_t is the number of seedlings or stems alive at the beginning of a time interval (t). Stem recruitment occurred when individuals < 1 cm d.b.h. grew to sizes ≥ 1 cm d.b.h.

Repeated-measures ANOVAS (SAS Institute Inc 2004) were utilized to test for treatment differences among sampling periods. For canopy openness, percentage cover, litter depth, graminoid height and seedling measurements, we used subplot values or means [where there were multiple measurements per subplot (cover percentages and litter depth); $n = 60$ subplots], whereas responses of stems were based on the 20 m × 20 m measurement area of each plot ($n = 12$). Detritus additions and trimming were treated as fixed effects while subplots

and blocks were treated as random effects in the ANOVAS. P -values reported here take into account the Greenhouse–Geisser Epsilon adjustment for sphericity (a measure of the variance–covariance structure of the data set; SAS Institute Inc 2004). In most cases, this adjustment had only a minor effect on the reported P -values. Significant differences were based on $P < 0.05$.

Results

LIGHT AND DETRITUS RESPONSES

After treatment application, the percentage canopy openness at 1 m height nearly doubled in plots with trimmed canopies (TR and TD) compared with plots with unaltered canopies (UD and CN). The elevated light levels in the canopy-trimmed plots, relative to untrimmed plots, lasted approximately 18 months (time × treatment: $P < 0.0001$; Fig. 1). Additionally, in untrimmed plots (UD and CN), transmitted light in the understorey decreased from *c.* 10.5% in 2003 to *c.* 8% in 2005–2006 (Fig. 1).

Because TD and UD plots were augmented with canopy detritus, there were large amounts of dead wood cover (< 5 cm and ≥ 5 cm diameters) on the forest floor in 2005 (Fig 2a,b). For dead wood cover < 5 cm, these treatment differences gradually returned to pre-treatment conditions within 3 years (time × detritus: $P < 0.0001$; time × trim: $P = 0.0453$) and there were no further interactions among treatments (time × detritus × trim: $P = 0.3677$). Following treatment applications, dead wood cover ≥ 5 cm in TD and UD plots gradually declined (time × detritus: $P = 0.0314$), yet retained greater dead wood cover ≥ 5 cm through 2008 compared to plots without canopy detritus added (Fig. 2b). The trimming treatments had no influence on this pattern (time × trim: $P = 0.8834$). Leaf litter cover decreased follow-

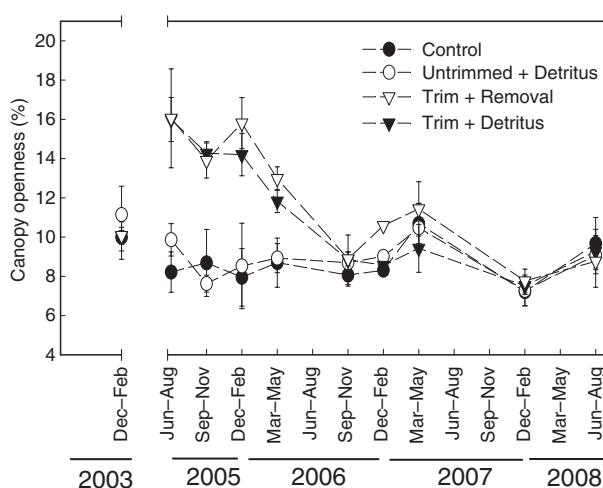


Fig. 1. Mean (± SE) percentage light availability at 3-month intervals for plots with their canopies trimmed and plots with canopies left intact (control and untrimmed) in a wet montane forest, Puerto Rico. Light availability was determined from the analysis of hemispherical (fish-eye) photographs (10 photos per plot per sampling period) at 1 m height. Canopy trimming and detritus treatments were completed in the months prior to the June 2005 census.

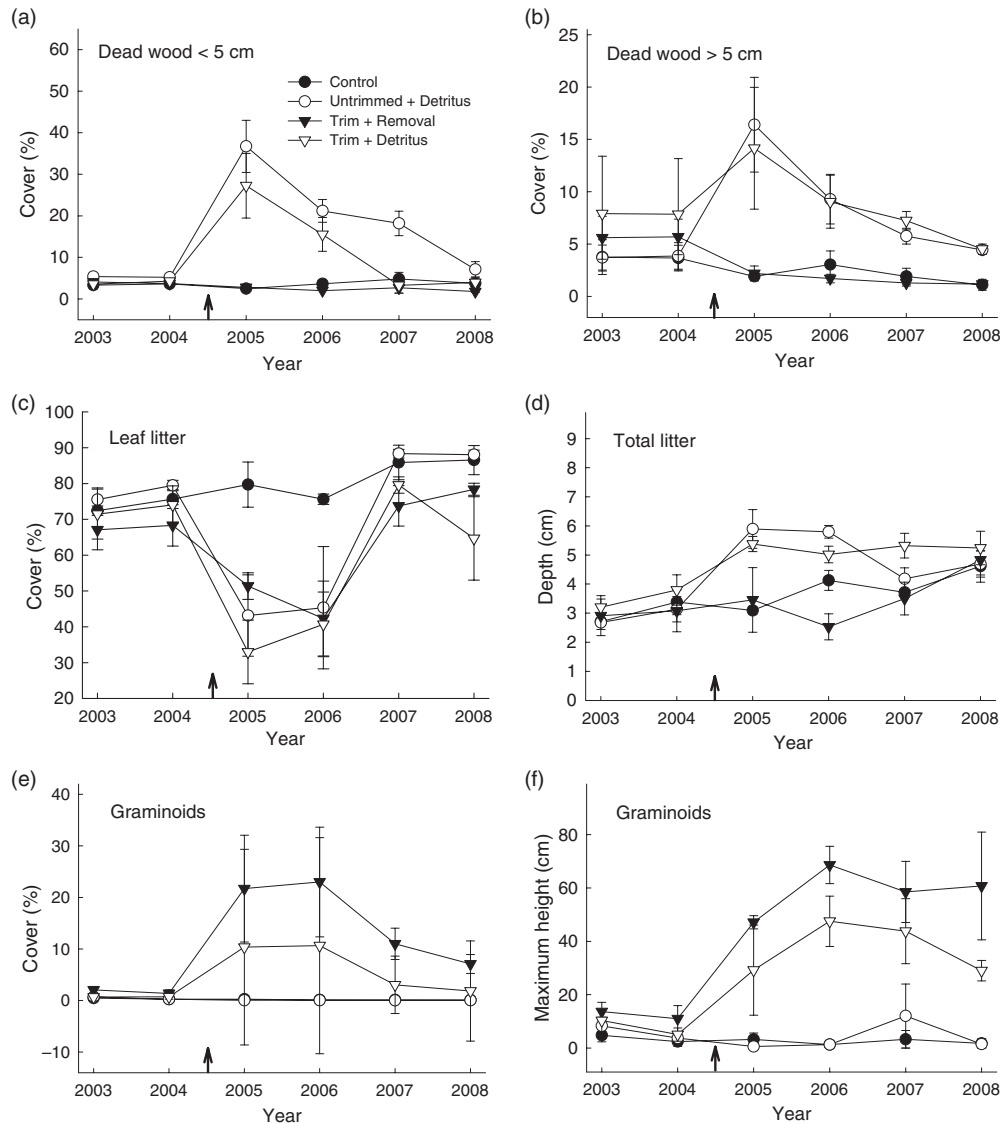


Fig. 2. Mean ($\pm$ SE) changes at the forest floor before and after simulated hurricane treatments in the Luquillo Experimental Forest, Puerto Rico. Measurements at the ground surface included (a) dead wood < 5 cm diameter cover, (b) dead wood $\geq$ 5 cm diameter cover, (c) leaf litter cover, (d) total litter depth, (e) graminoid cover and (f) maximum height of graminoids. Canopy trimming and detritus treatments were completed in the months prior to the 2005 census (marked by an arrow).

ing the manipulations for all treatments except CN (Fig. 2c), which was due, in part, to the dramatic increases described for dead wood cover in the UD and TD plots. The lower leaf litter cover for UD, TD and TR, relative to the CN, lasted 1.5 years after treatment application; leaf litter cover tended to be similar among treatments during 2007 and 2008 (time $\times$ detritus: $P = 0.0016$; time $\times$ trim: $P = 0.5495$; Fig. 2c). Total litter depth was significantly greater in TD and UD plots when compared with TR and CN plots ($P = 0.0002$). In 2005, which was the first sampling after treatment application, the litter layer in TD and UD plots was 1.5–2 times deeper than TR and CN (Fig. 2d). Following the peak litter depth for TD and UD in 2005, treatment plots gradually became more similar in litter depth, such that by 2008 there were no differences among treatments. There was no effect of canopy trimming on total

litter depth ($P = 0.8638$) and there were no other significant interactions.

GRAMINOID RESPONSES

During the study, graminoid cover (Fig. 2e) and maximum height of graminoids (Fig. 2f) increased significantly in TD and TR plots when compared with untrimmed plots ($P < 0.0001$ for each). While this pattern was significant, graminoid cover rarely exceeded 20% in any of the treatments. The increase in graminoid cover and maximum height tended to be highest in the TR plots following treatment application, but were not significantly higher than in TD plots (time $\times$ detritus $\times$ trim: $P > 0.05$ for each). The taller graminoids in TR and TD, relative to UD and CN, persisted through 2008

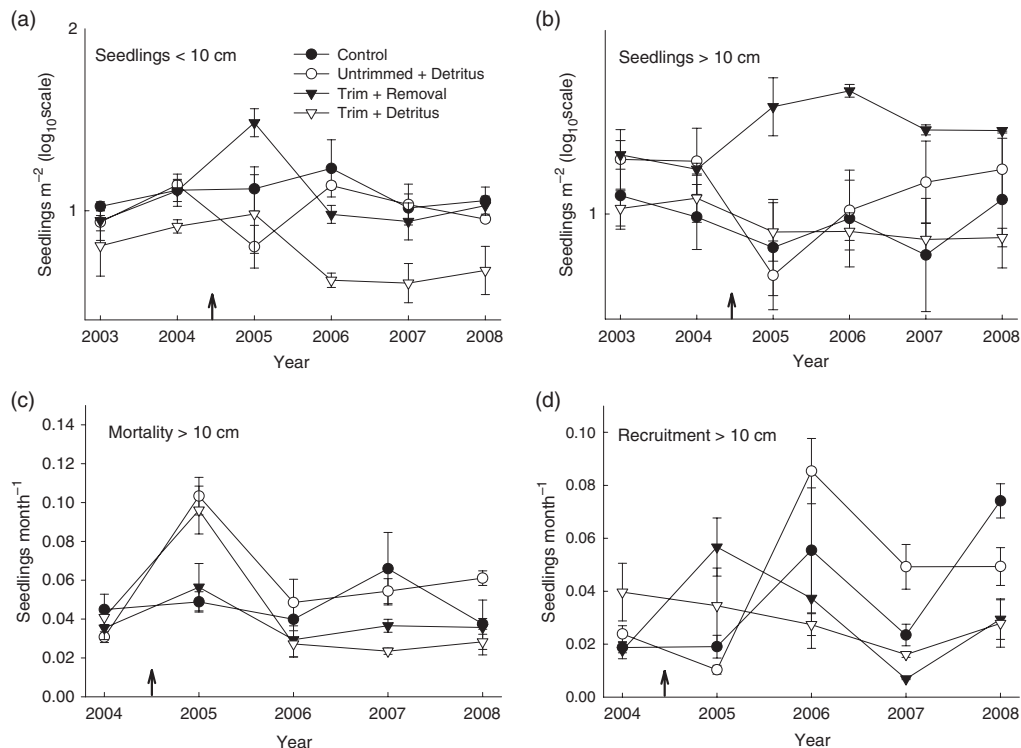


Fig. 3. Seedling responses (mean $\pm$ SE) to simulated hurricane conditions in the Luquillo Experimental Forest, Puerto Rico. Annual measurements (2003–2008) from $n = 15$ plots per treatment for (a) densities of seedlings < 10 cm tall, (b) densities of seedlings ≥ 10 cm tall, (c) mortality rates of seedlings ≥ 10 cm tall, and (d) recruitment rates of seedlings ≥ 10 cm tall. Canopy trimming and detritus treatments were completed in the months prior to the 2005 census (marked by an arrow).

(time $\times$ trim: $P = 0.0004$; Fig. 2f). Although graminoid cover in TR and TD declined after 2006, it had not returned to pre-treatment conditions by 2008 (time $\times$ trim: $P < 0.0001$; Fig. 2e).

SEEDLING RESPONSES

Densities of seedling < 10 cm tall in all treatment types were similar prior to canopy and detritus manipulations (i.e. in 2003 and 2004), but following treatments in 2005 the density of seedlings increased in TR and decreased in UD (Fig. 3a). Treatments tended to be different during the remainder of the study (2006–2008) such that the TD plots consistently exhibited the lowest density of seedlings relative to all other treatments. Also, unlike the remaining treatments, seedlings in TD did not return to pre-treatment densities (no significant time $\times$ trim $\times$ treatment interaction; Fig. 3a).

The density of seedlings ≥ 10 cm tall changed significantly over time ($P = 0.0005$). Prior to treatment application (i.e. in 2003 and 2004), CN and TD plots tended to have lower densities of seedlings compared with UD and TR plots (Fig. 3b). Immediately after the manipulations were completed (2005) seedling density increased in the TR, while in all other treatments (especially UD) seedling density declined (time $\times$ trim $\times$ detritus interaction: $P = 0.0269$; Fig. 3b). Detritus addition reduced seedling densities initially, but the effects of detritus addition had a progressively smaller effect during the

remainder of the sampling period (time $\times$ detritus: $P < 0.0001$). Mean density of seedlings ≥ 10 cm in UD was lowest in 2005, but it increased each following year such that by 2008 it had returned to pre-treatment levels (Fig. 3b).

Immediately following canopy and detritus manipulations in 2005, the plots that received supplemental detritus (TD and UD) had much higher seedling mortality rates than those in TR and CN (time $\times$ detritus: $P < 0.0001$; Fig. 3c). Mortality tended to be lowest in the trim plots (TD and TR) from 2006 to 2008, particularly in 2007 (time $\times$ trim: $P = 0.0017$; Fig. 3c).

Rates of recruitment for seedlings ≥ 10 cm changed significantly over time ($P < 0.0001$; Fig. 3d). In 2004, prior to treatment initiation, rates of recruitment appeared to be highest in the TD treatment compared with other treatments. Immediately following treatments (i.e. during the 2005 census only), detritus addition (in UD and TD plots) reduced recruitment (time $\times$ detritus: $P = 0.0012$; Fig. 3d), while the rate of seedling recruitment increased in TR (time $\times$ trim $\times$ detritus: $P = 0.0116$). However, through 2006–2008, the untrimmed plots tended to have higher recruitment rates (particularly UD in 2006–2007 and CN in 2008) than the trim plots (Fig. 3d).

When individual species were assessed for changes in the densities of seedlings ≥ 10 cm, several early successional (pioneer) species increased substantially in plots where the canopy was trimmed (TD and TR) and particularly so in the TR plots (Fig. 4a–d). The two species that experienced the largest

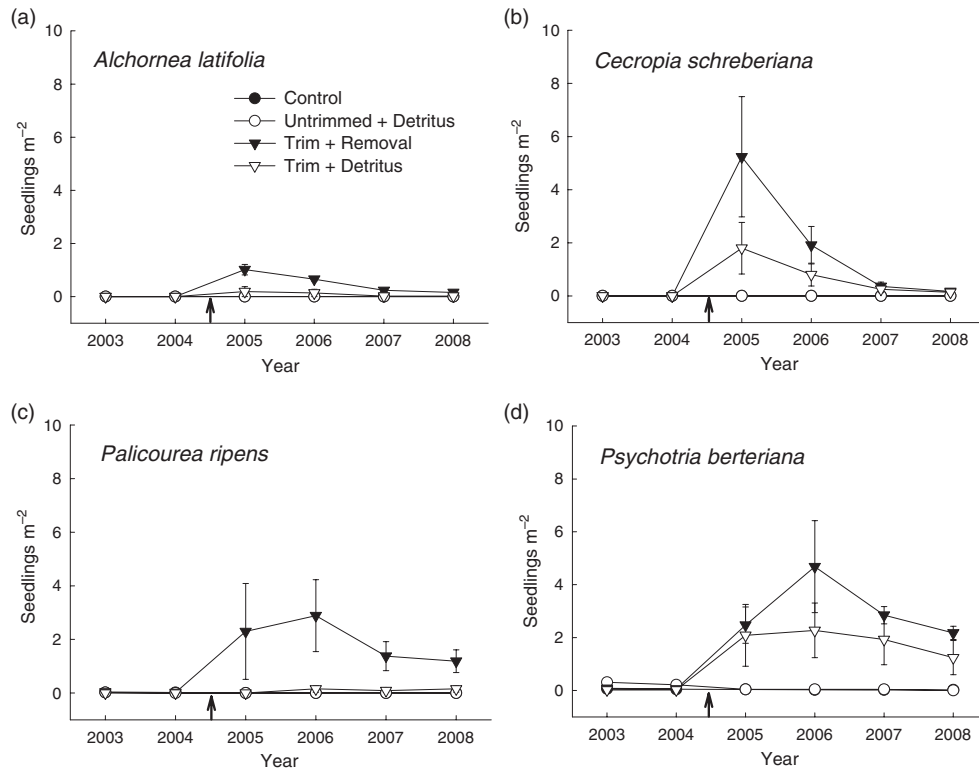


Fig. 4. Mean ($\pm$ SE) seedling (≥ 10 cm tall) density of some common pioneer species (a–d) during the 6-year study in the Luquillo Experimental Forest, north-eastern Puerto Rico. Canopy trimming and detritus treatments were completed in the months prior to the 2005 census (marked by an arrow).

increases in seedling density were *Cecropia schreberiana* and *Psychotria berteriana* (Fig. 4b,d). Prior to canopy trimming, few, if any, of these pioneer species had been recorded in the study plots (Fig. 4a–d). In contrast to the pioneer species, non-pioneer seedling densities declined in all trimmed plots and in many detritus addition plots following treatments in 2005 (Fig. 5). Seedling densities (relative to 2005) recovered in most species over subsequent time periods. *Dacryodes excelsa* and *M. bidentata* seedling recovery occurred only in plots without canopy trimming (Fig. 5a,b). Seedling density for the palm *P. acuminata* increased rapidly in UD between 2006 and 2008 and in CN between 2007 and 2008 (Fig. 5c), and density recovered towards pre-treatment levels more slowly in trimmed plots (TD and TR). *Prestoea acuminata* was the only non-pioneer species that had higher seedling densities in untrimmed plots (UD and CN) at the end of the study than during pre-treatment sampling. Seedling densities for *Rourea surinamensis*, which is the most common vine in the understorey of the forest near EVFS, declined the most in the detritus addition plots following treatments in 2005 and did not appear to recover to pre-treatment densities in detritus addition plots (Fig. 5d).

STEM RESPONSES

In 2007, which was *c.* 2.3 years after treatments were completed, there were large (2000–4000 individual ha^{-1}) increases

in stem densities in the plots that had been trimmed ($P < 0.0001$; Fig. 6a). Detritus addition did not significantly influence stem density ($P = 0.2116$) and did not result in significant differences over time (time $\times$ detritus: $P = 0.0903$). Stem densities continued to be higher in trimmed plots (TD and TR) than untrimmed plots (UD and CN) through 2008 (time $\times$ trim: $P < 0.0001$; Fig. 6a); this significant interaction also reflected a decrease in stem density in the UD and CN plots throughout the study. For stem density, there were no significant interactions between trimming and detritus additions (trim $\times$ detritus: $P = 0.4049$; time $\times$ trim $\times$ detritus: $P = 0.1455$).

Stem basal area showed a less dramatic response than did stem density to the treatment applications, and there were no significant differences between trimmed plots and untrimmed plots (trim: $P = 0.4864$; time $\times$ trim: $P = 0.2659$; time $\times$ trim $\times$ detritus: $P = 0.9059$). Following treatment applications, stems in the detritus addition plots (UD and TD) had slightly, although significantly, greater basal area than plots without detritus added (time $\times$ detritus: $P = 0.0428$; Fig. 6b).

There were no apparent effects of the treatments on stem mortality from 2004 to 2007 ($P > 0.05$; Fig. 6c). In fact, mortality appeared to be slightly higher in the untrimmed plots in the period that included the manipulations. At the onset of treatment applications, a total of 93 palms (*P. acuminata*) and 143 non-palm stems (23 species) were established within the

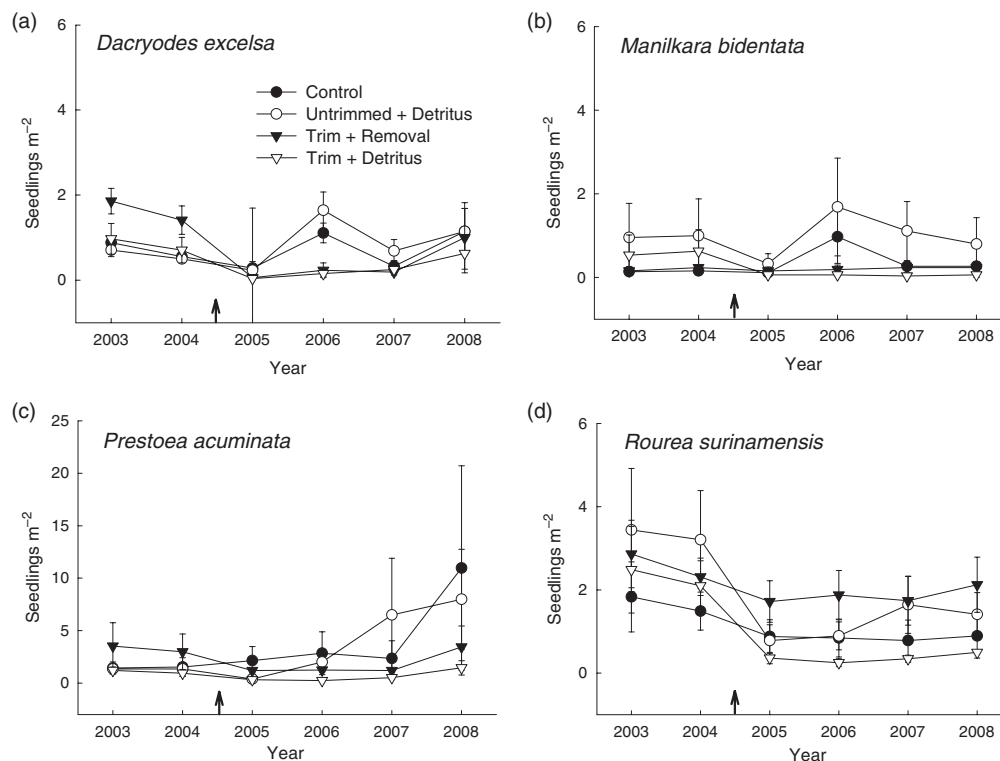


Fig. 5. Mean ($\pm$ SE) seedling (≥ 10 cm tall) density of some non-pioneer species (a–d) during the 6-year study in the Luquillo Experimental Forest, north-eastern Puerto Rico. Note the different scaling on the vertical axis. Canopy trimming and detritus treatments were completed in the months prior to the 2005 census (marked by an arrow).

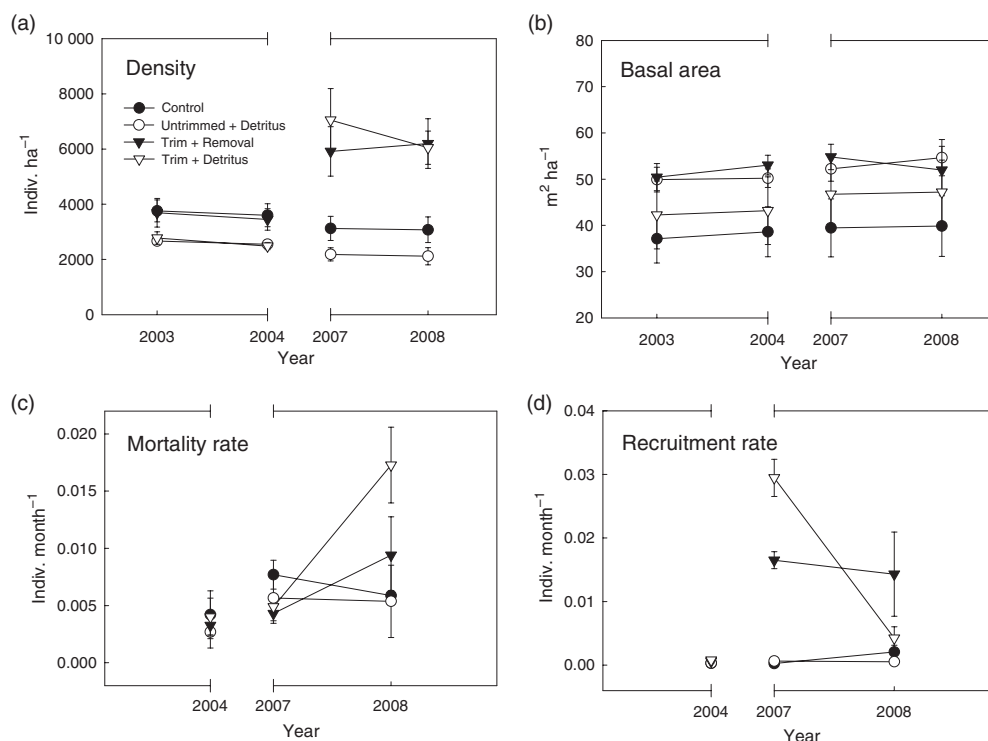


Fig. 6. Responses of stems (individuals ≥ 1 cm d.b.h.) to simulated hurricane conditions in the Luquillo Experimental Forest, Puerto Rico, including mean ($\pm$ SE) for: (a) density, (b) basal area, (c) mortality rate and (d) recruitment rate. Canopy trimming and detritus treatments occurred immediately after the 2004 census. There were no measurements during 2005 or 2006. $n = 3$ for each treatment.

measurement area of the six trim plots (TD and TR). In 2007, which was when the first census of stems occurred after the treatments were applied, the average mortality of the treated stems (i.e. those cut by arborists) was 5.3% (range: 0–13% among the six trimmed plots), or 4.2% if palms were not included. Among trimmed plots in the study, there were just four species with individuals that died from treated stems, including *P. acuminata* (seven of 93 individuals), *Matayba domingensis* (three of seven), *Tabebuia heterophylla* (one of two) and *Calycogonium squamulosum* (two of two). Mortality in 2007 among stems in the trimmed plots averaged 8.2% (range: 5–11%), thus even with the treated stems there appeared to be no significant impact of trimming on stem mortality. Rates of stem mortality increased significantly from 2007 to 2008 in the trimmed plots due to self-thinning among the new recruits (time $\times$ trim: $P = 0.0085$; Fig. 6c), which were individuals that grew into the stem size class during 2005–2008. Although TD plots tended to have the highest mortality rate in 2008, there were no significant effects of detritus on mortality rates ($P = 0.5994$) or interactions between trimming and detritus and time ($P = 0.4753$; Fig. 6c).

Similar to the responses of seedlings by 2005 (Fig. 3d), stems dramatically increased in recruitment rates by 2007 in the trimmed plots (TD and TR) and were significantly greater than recruitment rates in untrimmed plots following treatment application (time $\times$ trim: $P < 0.0001$; Fig. 6d). During the 2007 census, the stem recruitment rate in TD plots was double that of the TR plots, yet in 2008 the rate of recruitment in the TD plots was reduced to less than half that in the TR plots, which remained unchanged from the year before (time $\times$ trim $\times$ detritus: $P = 0.0170$; Fig. 6d). Stem recruitment rates were extremely low for UD and CN plots throughout the study.

Individual species (≥ 1 cm d.b.h.) responded differently to canopy trimming and detritus manipulation. Prior to treatment application, *P. acuminata* and *S. berteriana* were the two most abundant species (Table 1; Fig. 7). Following the treatment application in late 2004–2005, the two pioneer species, *C. schreberiana* and *P. berteriana*, dramatically increased in abundance in the trimmed (TD and TR) plots where they persisted as the two most abundant species through the 2008 census (Fig. 7). Non-pioneer species, such as *P. acuminata*, *S. berteriana*, *D. excelsa* and *M. bidentata*, tended to be less abundant in TR and TD plots following treatment applications (Fig. 7). In the untrimmed plots (UD and CN), several pioneer species, such as *P. berteriana*, *Psychotria brachiata*, *Palicourea riparia* and *Miconia prasina*, tended to decrease in abundance through time, presumably because of mortality associated with canopy closure from Hurricane Georges in 1998 (Fig. 7).

Discussion

Our evaluation of two key components of simulated hurricane impacts demonstrates that both canopy openness and detritus deposition are important determinants of woody plant responses, and that variations of these key aspects affect plant responses and trajectories differently depending

Table 1. Pioneer (early successional) and non-pioneer (mid- and late-successional) woody plant species that were most common in our simulated hurricane study in the Luquillo Experimental Forest, Puerto Rico. Species codes are used in Fig. 7

Species	Family	Species code
Pioneer		
<i>Alchornea latifolia</i> Sw.	Euphorbiaceae	ALCLAT
<i>Cecropia schreberiana</i> Miq.	Moraceae	CECSCH
<i>Miconia prasina</i> (Sw.) DC.	Melastomaceae	MICPRA
<i>Palicourea riparia</i> Benth.	Rubiaceae	PALRIP
<i>Psychotria berteriana</i> DC.	Rubiaceae	PSYBER
<i>Psychotria brachiata</i> Sw.	Rubiaceae	PSYBRA
<i>Schefflera morototoni</i> (Aubl.) Decne. & Planch.	Araliaceae	SCHMOR
Non-pioneer		
<i>Casearia arborea</i> (L.C. Rich.) Urban	Flacourtiaceae	CASARB
<i>Cordia borinquensis</i> Urban	Boraginaceae	CORBOR
<i>Dacryodes excelsa</i> Vahl	Burseraceae	DACEXC
<i>Eugenia stahlia</i> (Kiaersk.) Krug & Urb.	Myrtaceae	EUGSTA
<i>Rheedia portoricensis</i> Urban	Guttiferae	RHEPOR
<i>Guatteria caribaea</i> Urban	Annonaceae	GUTCAR
<i>Hirtella rugosa</i> Pers.	Chrysobalanaceae	HIRRUG
<i>Homalium racemosum</i> Jacq.	Flacourtiaceae	HOMRAC
<i>Manilkara bidentata</i> (A. DC.) A. Chev.	Sapotaceae	MANBID
<i>Matayba domingensis</i> (DC.) Radlk.	Sapindaceae	MATDOM
<i>Myrcia leptoclada</i> DC	Myrtaceae	MYRLEP
<i>Prestoea acuminata</i> (Willd.) H.E. Moore var. <i>montana</i> (Graham) Henderson and Galeano	Arecaceae	PREMON
<i>Rourea surinamensis</i> Miq.	Connaraceae	ROUSUR
<i>Sloanea berteriana</i> Choisy	Elaeocarpaceae	SLOBER
<i>Tetragastris balsamifera</i> (Sw.) Kuntze	Burseraceae	TETBAL

on the life stage and successional status of the plant. By experimentally separating the confounding effects of canopy openness and detritus deposition, we found that increased canopy openness (light availability) is the dominant factor affecting forest regeneration after hurricane impacts, as seedlings (in TR plots only) and stems both responded to increased canopy openness by increased rates of recruitment (into ≥ 1 cm size class for stems) and increased densities. Canopy detritus deposition on the forest floor generally had a negative effect on seedlings, but this negative effect was less pronounced in TD plots immediately after treatment applications. For stems, detritus addition did not affect density, recruitment or mortality but increased basal area. Many pioneer species (both seedlings and stems), especially *C. schreberiana* and *P. berteriana*, increased in density with canopy trimming, whereas many non-pioneer species experienced decreased densities or did not change with canopy trimming. The most pronounced changes to plants for all treatments occurred within 1–2 years following the completion of the

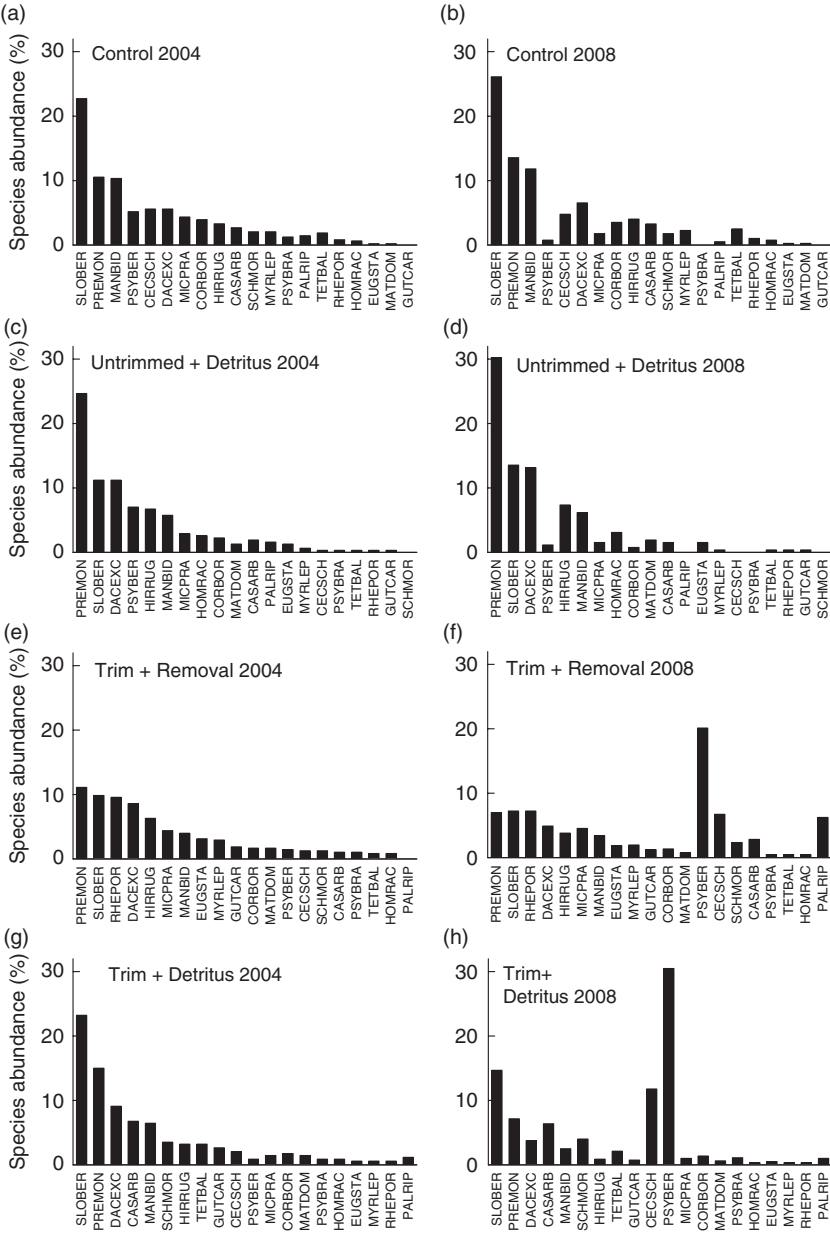


Fig. 7. Species abundances for 20 of the most common species (individuals ≥ 1 cm d.b.h.) in the study plots. The 10 most common species in 2003–2004 (pre-treatment) were combined with the 10 most common species post-treatment (2007–2008). Canopy trimming and detritus treatments occurred immediately after the 2004 census. See Table 1 for definitions of species codes on the horizontal axis.

manipulations, which highlights the short time span of opportunity for understorey plants to colonize, and subsequently alter, forest structure following hurricane disturbance. While some patterns of past hurricane effects on plants were confirmed by our study (e.g. increased light increased seedling density, and canopy detritus deposition reduced seedling density; Guzmán-Grajales & Walker 1991; Walker *et al.* 2003), a mechanistic explanation of the relative importance and interaction of the key components of hurricane impacts could not have been determined without the experimental manipulations we completed.

LIGHT AND DETRITUS RESPONSES: COMPARISONS TO NATURAL HURRICANES

The increase in light availability into the understorey following canopy disturbance is one of the most dramatic effects of a

hurricane. Immediately following our simulated hurricane, understorey light availability was approximately twice as high as the light conditions when the canopy was intact. In the LEF following Hurricane Georges in 1998, understorey light availability increased nearly 4-fold over estimated pre-hurricane levels (Comita *et al.* 2009). Turton (1992) measured a 2- to 3-fold increase in understorey light after Cyclone Winifred struck an Australian rainforest. Comparisons with other studies following hurricanes are challenging because of the various ways in which light can be measured (e.g. photosynthetic photon flux density, Fernández & Fetcher 1991; versus percentage transmittance, Bellingham *et al.* 1996) and because most studies did not conduct pre-hurricane light measurements (but see Turton 1992). Our study disturbed portions of the forest (i.e. 30×30 m plots) that are similar to the patch structure observed after Hurricane Hugo (c. 0.1 ha; Brokaw & Gear 1991; Fernández & Fetcher 1991). This study, however, proba-

bly created less diffuse light than a natural hurricane, because the tree crowns surrounding the plots remained intact. Understorey light levels recovered to pre-disturbance levels within 18 months in this study, similar to the 14 months that it took for light levels to return to near pre-disturbance levels in the understorey of the LEF following Hurricane Hugo in 1989 (Fernández & Fetcher 1991). It took *c.* 24–28 months for understorey light to recover to pre-disturbance levels in higher-elevation (1600 m a.s.l.) montane forests in Jamaica after Hurricane Gilbert (Bellingham *et al.* 1996). Similar to observations during our study, the shorter recovery of understorey light documented after Hurricane Hugo may have been partially influenced by newly established pioneers, such as *C. schreberiana*, growing above the 1-m height where light was measured (Fernández & Fetcher 1991). The decrease in understorey light in the untrimmed plots (*c.* 2.5% decrease in light availability from 2003 to 2006; Fig. 1) was probably because of the continued forest recovery from Hurricane Georges in 1998 (Comita *et al.* 2009).

Hurricane effects on forests, including detritus deposition and canopy damage, differ widely within and among storms and locations (Brokaw & Walker 1991; Lugo 2008). While it would have been preferable to mimic fully the impact of hurricanes by placing fresh detritus on the experimental plots (canopy detritus naturally decomposed several weeks outside the plots prior to detritus addition), our methods closely mimic the key impacts of hurricane detritus on key ecosystem functions. Effects of hurricane detritus on plant establishment are largely physical (Guzmán-Grajales & Walker 1991; Walker *et al.* 2003). No significant impact of green litter on total soil carbon and total soil nitrogen was detected by Ostertag, Scatena & Silver (2003) following Hurricane Georges in Puerto Rico, and Zimmerman *et al.* (1995) identified wood deposition, and not green litter, as a key component of below-ground effects influencing above-ground productivity. Thus, green litter, while predominant on the landscape following a severe hurricane, is a minor component of the total hurricane detritus (Lodge *et al.* 1991; Zimmerman *et al.* 1995), which apparently has little or no long-term impact on the recovering forest.

Fine litter, or the amount of litter categorized as leaves, twigs and palm fronds that was added to each plot in this study ($1989 \pm 26 \text{ g m}^{-2}$), was nearly identical to the fine litter generated by Hurricane Hugo in the same section of the LEF (1934 g m^{-2} of suspended litter fall combined with litter deposited onto the ground; Lodge *et al.* 1991). Litter depth in the detritus addition plots in this study ($5.6 \pm 0.5 \text{ cm}$) was also similar to that measured after Hurricane Hugo near EVFS ($4.1 \pm 0.9 \text{ cm}$; Guzmán-Grajales & Walker 1991). Wood deposited on the forest floor from Hurricane Hugo was estimated at nearly 3000 g m^{-2} in the El Verde section of the LEF (Zimmerman *et al.* 1995), which was less wood than that deposited on the forest floor during our simulated hurricane ($4020 \pm 139 \text{ g m}^{-2}$). In a different section of forest near EVFS, Vogt *et al.* (1996) reported levels of fine litter at 1234 g m^{-2} and coarse woody debris at 763 g m^{-2} after Hurricane Hugo. The patchiness of hurricane damage and hurricane detritus deposition for a given storm is common in the LEF (Lodge *et*

al. 1991; Ostertag, Silver & Lugo 2005) and elsewhere (Imbert, Labbé & Rousteau 1996; Turton 2008b) and may explain the discrepancies across studies. In 1998, 9 years after Hurricane Hugo, a category 3 hurricane struck the LEF (Hurricane Georges) and produced less structural damage and deposited much less detritus (*c.* 500 g m^{-2} fine litter fall and *c.* 250 g m^{-2} wood in the Bisley section of the LEF; Ostertag, Scatena & Silver 2003) than Hurricane Hugo or our simulated hurricane.

One critical impact of a severe hurricane, the presence of downed wood $> 10 \text{ cm}$ in diameter, is lacking in this study. Our strategy was to simulate branch loss during severe hurricane disturbance and ameliorate the spatial heterogeneity in coarse woody inputs by placing this material as uniformly as possible over the treatment plots. Recognizing that inputs of very large woody debris (tree trunks) would be difficult to simulate in a uniform manner at the scale of our plots, we decided not to attempt to duplicate its effects. The only other attempt to experimentally simulate a hurricane was a study at Harvard Forest in north-eastern USA, which began in 1990 (Bowden *et al.* 1993; Carlton & Bazzaz 1998; Cooper-Ellis *et al.* 1999). This study focused on the damage to whole trees caused by hurricanes (the predominant effect of the 1938 hurricane there; Rowlands 1941; Foster 1988) and employed winches to pull down a number of trees in a single $50 \times 160 \text{ m}$ plot. Comparison to a reference plot indicated that the primary effects were increased light levels and soil disruption from tree uprooting which increased establishment of pioneer species, predominantly *Betula* spp. (Carlton & Bazzaz 1998; Cooper-Ellis *et al.* 1999). They noted few, if any, additional impacts on vegetation beyond the reduction in basal area associated with the physical application of the manipulation (Bowden *et al.* 1993; Cooper-Ellis *et al.* 1999). In this study, we were able to provide amounts of coarse woody debris inputs similar to those seen in an actual hurricane, but the size distribution and spatial heterogeneity of these inputs were not duplicated.

SEEDLING RESPONSES

Increased canopy openness, as demonstrated in TR plots, is a critical factor for rapid colonization of the understorey (tripling seedling recruitment rates and doubling seedling densities) following hurricane impacts. These findings were similar to seedling responses in studies following natural hurricanes in the tropics where the influence of canopy detritus was removed (as we did using TR plots; Guzmán-Grajales & Walker 1991; Walker *et al.* 2003; Murphy *et al.* 2008). Following Hurricane Hugo, the majority of the seedlings responsible for the increased densities in plots where detritus was removed were species adapted to high light (e.g. *C. schreberiana*; Guzmán-Grajales & Walker 1991). Similarly, we found that seedlings of pioneer species, particularly *C. schreberiana* and *P. berteriana*, increased in density (by recruitment from seed) in canopy-trimmed plots (TD and TR), and the most pronounced increases in seedling densities for these two pioneer species and several others (e.g. *Alchornea latifolia*, *P. riparia*) were in TR plots. The necessity of a light gap for germination has been reported for multiple species of *Cecropia* (Holthuijzen &

Boerboom 1982; Brokaw 1998), and although germination of *P. berteriana* is unstudied, this species appears to require a light gap for seedling establishment (Walker *et al.* 2003). Following impacts of Cyclone Larry in an Australian rainforest, Murphy *et al.* (2008) documented large increases in seedling abundances for non-native species in debris removal plots. Although graminoids commonly establish following hurricanes in the LEF (Walker *et al.* 1996b) and increased 10- to 20-fold in the trimmed plots in this study (but rarely exceeded 20% cover), these graminoids were native to Puerto Rico. Non-native plants are relatively uncommon in most of the LEF and were not observed in any of our plots.

Many tropical tree species of both pioneer and non-pioneer status germinate more frequently in high-light conditions of forest gaps, particularly in the absence of surface litter (Vázquez-Yanes *et al.* 1990; Everham, Myster & VanDeGenachte 1996; Walker *et al.* 2003). Despite possible benefits of light gaps for germination of non-pioneer species (Everham, Myster & VanDeGenachte 1996), there were very few non-pioneer seedlings that established in the ≥ 10 cm seedling size class in our hurricane simulation plots. Reduced seedling densities of non-pioneer species, such as *D. excelsa*, *M. bidentata* and the liana *R. surinamensis*, following canopy trimming in the TR plots may have resulted from mortality directly associated with sunscald and photoinhibition (Comita *et al.* 2009), or possibly indirectly through reduced water availability or from competition with nearby pioneer species. Sunscald and photoinhibition are probably at least partially responsible for seedling mortality of *D. excelsa* in trimmed plots, as a previous study in the LEF comparing multiple microhabitat factors demonstrated that seedlings of *D. excelsa* do not survive in gaps and only survive in the (non-gap) forest understorey (Everham, Myster & VanDeGenachte 1996). Thus, the increase in understorey light following hurricanes stimulates seed germination and establishment of pioneer species, but not non-pioneer species.

Canopy detritus deposition initially doubled seedling (≥ 10 cm height) mortality in both TD and UD plots. The independent effect of canopy detritus (UD) on reducing seedling density was pronounced, whereas the interactive effects of increased detritus deposition and light availability (TD) reduced seedling density much less immediately after treatment applications due to establishment of pioneer species, particularly *C. schreberiana* and *P. berteriana*. Detritus may act as a mechanical barrier for seed germination and seedling emergence, as previously demonstrated in the LEF (Guzmán-Grajales & Walker 1991; You & Petty 1991) and described in other tropical and temperate environments (Sydes & Grime 1981; Vázquez-Yanes *et al.* 1990; Xiong & Nillson 1998; Sayer 2006). Therefore, under open canopy conditions following a hurricane, pioneer species will establish and their densities will reflect the deposition patterns of detritus such that areas without detritus will experience the greatest increase in seedlings and there will be relatively fewer seedlings in areas where detritus is present. During a natural hurricane, non-pioneer species will most probably die from the physical deposition of canopy detritus and/or sunscald and photoinhibition by exposure to

higher-intensity light from the open canopy. The recovery in seedling densities in areas where detritus was added (UD and TD) is shortened if the canopy remains intact (i.e. UD plots), possibly because the seed production of adult trees would be less disrupted than in plots with damaged canopies (Walker & Neris 1993). Additionally, the high recruitment in UD plots beginning at the 2006 census (*c.* 1.5 years after treatments) may be a result of reduced competition because few seedlings were present after detritus deposition, or there may be some longer-term benefits of canopy detritus on seedling recovery that are only apparent in untrimmed plots.

Seedlings in this study responded differently to the treatments at different times, indicating the range of possible trajectories in the seedling layer that may occur following a hurricane. Furthermore, these treatment effects evidently outweighed the variability among blocks associated with the unequal periods from treatment establishment to first measurements. The high mortality in the detritus addition plots (in TD and UD), and the high recruitment rate of seedlings in TR plots, lasted only *c.* 1 year, whereas recruitment in TD and UD plots differed from pre-treatment conditions throughout the study. The initially deep litter and wood deposited on the forest floor killed seedlings and slowed recruitment. The 18-month window of increased canopy openness and light availability resulted in a conversion of much of the seedling layer from non-pioneer species to mostly pioneer species. These short-term changes to the seedlings eventually affect the larger size classes of plants (i.e. stems).

STEM RESPONSES

We recorded no significant impact of the trimming treatments used in this study on stem mortality. The average stem mortality in the trimmed plots was 8.2% in 2007 (2.3 years after treatments were completed). Stem mortality following a hurricane is surprisingly low, ranging from 1 to 13% among studies (Boucher *et al.* 1990; Brokaw & Walker 1991; Frangi & Lugo 1991; Bellingham *et al.* 1996; Everham & Brokaw 1996; Imbert, Labbé & Rousteau 1996; Herbert, Fownes & Vitousek 1999; Turton 2008b) and 7 to 9% near EVFS during Hurricane Hugo (Walker 1991; Zimmerman *et al.* 1994). Most of this mortality is related to trunk damage (Walker 1991; Zimmerman *et al.* 1994) and may be delayed for up to 3.3 years (Walker 1995). Stem mortality in the trimmed plots (TD and TR) was higher than in the untrimmed plots during the final census in our study, reflecting self-thinning of the pioneer species that had colonized immediately after treatment application. The observation that the trimming of branches alone does not significantly influence stem mortality makes clear the degree to which trees are resistant to mortality because of branch damage alone (Zimmerman *et al.* 1994).

Responses of stems to increased light from the canopy trimming were dramatic, as stem density doubled in TD and TR when compared to pre-manipulation densities and control plots, and recruitment rates into the stem size class increased several hundred-fold. The increase in stem density in trimmed

plots was almost exclusively due to individuals recruiting from seed and not sprouting from damaged stems. While sprouting is an important process following a hurricane (Bellingham, Tanner & Healey 1994, 1995; Zimmerman *et al.* 1994; Van Bloem, Lugo & Murphy 2006), it was largely confined to the areas on the tree where branches were cut during our trimming procedures, which was above 3 m height for all non-palm trees. The high recruitment into the stem size class in the TR plots, which continued until the end of the study, reflects the large seedling pool that was present. Similarly, the increase in stem density for pioneer species, particularly *C. schreberiana* and *P. berteriana*, in the trimmed plots mirror the changes in the seedling layer for trimmed plots. Our findings support the generalization that light is a major factor limiting plant recruitment and survival in wet tropical forests (Bazzaz & Pickett 1980; Augspurger 1984; Denslow 1987; Denslow, Ellison & Sanford 1998), and we have demonstrated this pattern for both seedlings and stems. Additionally, sprouting after hurricane damage is important for canopy recovery, but the recruitment of new plant colonists is largely a process originating from seeds of pioneer species.

Detritus addition to the forest floor had a slight positive effect on stem growth, as basal area increased in both the UD and TD plots relative to plots without detritus added. A similar result was found by Walker *et al.* (1996b) where basal area decreased in plots from which hurricane debris was removed. A number of factors could account for this pattern, but it is curious that there were no detectable differences in other tree measurements (i.e. density, recruitment, mortality) in this study from canopy detritus addition. Because seedlings were suppressed by detritus deposition, stems in the UD and TD plots may have experienced reduced (below-ground) competition. However, stems usually have a stronger negative effect on seedlings (Coomes & Grubb 2000; Barberis & Tanner 2005) than vice-versa (Schwinning & Weiner 1998). Additional factors that may also provide such beneficial effects from canopy detritus deposition include ameliorated microclimate (ground temperature and moisture; Facelli & Pickett 1991; Everham, Myster & VanDeGenachte 1996) and enhanced organic matter and nutrients (Denslow, Ellison & Sanford 1998; Sayer 2006). Soil moisture is typically less limiting to plant growth and survival in wet forests (but see Engelbrecht & Kursar 2003; Engelbrecht *et al.* 2007), and this has been demonstrated experimentally with seedlings in the LEF in both gap and non-gap environments (Everham, Myster & VanDeGenachte 1996). Additionally, trimmed plots in our study had higher soil moisture than untrimmed plots (L. Lebrón & D.J. Lodge, unpubl. data), presumably because of greater throughfall in trimmed plots (A. Ramírez, unpubl. data) and lowered transpiration from a reduced canopy, suggesting a greater importance of canopy openness rather than presence of detritus in influencing soil moisture. Hurricane debris clearly contains nutrients needed for plant growth, yet the addition of hurricane debris in the LEF did not produce any detectable changes in total soil nitrogen following Hurricane Hugo (Walker *et al.* 2003) or Hurricane Georges (Ostertag,

Silver & Lugo 2005). Additionally, woody debris negatively affected trees by decreasing available forms of soil nitrogen and transiently reducing primary production following Hurricane Hugo, probably because of nutrient immobilization (Zimmerman *et al.* 1995). This latter effect was thought to be primarily due to the impacts of very large coarse woody debris (Zimmerman *et al.* 1995), which was lacking in this study.

Conclusions

Treatment responses to simulated hurricane effects in this study changed through time for both seedlings and stems. In plots with trimmed canopy, light availability in the understorey returned to the lower levels of a pre-manipulation state after 18 months. The decline in seedling recruitment and densities (particularly for seedlings < 10 cm tall) in the TR plots after 18 months coincided with this canopy closure. Hence, there is a limited window of time following canopy opening in which rapid growth of understorey plants and recruitment from seed will occur (Angulo-Sandoval *et al.* 2004), and such recruitment following canopy disturbance is dominated by pioneer species (Walker *et al.* 2003) that quickly grow into larger size classes (i.e. stems). The successional trajectories following hurricane disturbance will continue to change after the canopy returns to pre-disturbance conditions because competition for light and other resources will probably increase, especially with the higher densities of both pioneer and non-pioneer seedlings and stems. The patchiness of detritus deposition (Lodge *et al.* 1991) following a hurricane has a large effect on seedling mortality but only a small effect on stems through increasing basal area. These separate and interactive effects of canopy openness and detritus deposition therefore result in variable short-term trajectories of forest recovery. However, it is the opening of the canopy and its influence on the recruitment of pioneer species that is the dominant effect that may ultimately alter the future structure and composition of the forest at least until a hurricane disturbs the canopy again.

With a better understanding of the key mechanisms affecting plant responses following hurricane impacts, we believe that additional, future manipulations of forest canopies and detritus are needed to test for effects of increased hurricane frequency on Caribbean forests, which is predicted for the future of this region (Emmanuel 2005; Nyberg *et al.* 2007; Bender *et al.* 2010).

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