Cascading Effects of Canopy Opening and Debris Deposition from a Large-Scale Hurricane Experiment in a Tropical Rain Forest

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Intense hurricanes disturb many tropical forests, but the key mechanisms driving post-hurricane forest changes are not fully understood. In Puerto Rico, we used a replicated factorial experiment to determine the mechanisms of forest change associated with canopy openness and organic matter (debris) addition. Cascading effects from canopy openness accounted for most of the shifts in the forest biota and biotic processes, which included increased plant recruitment and richness, as well as the decreased abundance and diversity of several animal groups. Canopy opening decreased litterfall and litter moisture, thereby inhibiting lignin-degrading fungi, which slowed decomposition. Debris addition temporarily increased tree basal area. Elevated soil solution nitrate was a dominant response after past hurricanes; this effect only occurred in our experiment with simultaneous canopy-opening and debris treatments. Although debris is an important carbon and nutrient source, short-term responses to cyclonic storms appear to be largely driven by canopy opening.

Keywords: Large-scale disturbance, Luquillo Experimental Forest biodiversity, plant–animal–microbial interactions, resistance–resilience, soil solution chemistry

The twentieth-century paradigm of tropical forests as equilibrial systems characterized by relative constancy has given way to a twenty first–century view of tropical forests as dynamic systems that vary in time and space, partly in response to local and regional disturbance regimes (Pickett and Parker 1994, Lugo et al. 2012). Disturbances affecting tropical forests can range in scale from large, landscape, or regional occurrences, such as volcanic eruptions and hurricanes (Walker 2012), to smaller canopy gap-sized disturbances, such as treefalls (Denslow 1987) and landslides (Walker and Shiels 2013). Disturbance affects most aspects of forest ecosystems, including biodiversity, species interactions, the spatiotemporal dynamics of populations and communities, and biogeochemical cycling (Chazdon 2003, Brokaw et al. 2012, Walker 2012). Repeated disturbances over ecological and evolutionary time scales (i.e., disturbance regimes) shape an ecosystem's structure and functioning by filtering particular species, consequently imbuing the system with characteristic resistance and resilience.

Wind storms, including gales and squall lines (derechos), can damage trees and affect forest ecosystem processes over large areas (Lundquist et al. 2011). Among these disturbances, hurricanes (also called *cyclones* and *typhoons*), which impact all continents except Antarctica (Lugo 2008), stand out because they induce the landscape-level effects of canopy loss and the deposition of organic matter (debris) onto the forest floor. Hurricanes affect hundreds of square kilometers (km) and have sustained wind speeds of at least 119 km per hour that strip leaves and branches from canopy trees and, at greater speeds, snap stems and uproot trunks (Walker et al. 1991, Everham and Brokaw 1996). The removal of an intact canopy alters understory light, temperature, and moisture; the deposited debris provides resources for some organisms but may deter or delay colonization by others (Richardson et al. 2010, Shiels et al. 2010). The direct physical effects of hurricanes influence a large suite of biotic and abiotic factors, as well as initiate changes in ecosystem processes (e.g., decomposition, nutrient cycling, and productivity). Recent models that predict a shift toward an increased frequency of severe cyclonic storms as a consequence of global climate change (Bender et al. 2010) have renewed interest in the effects of hurricanes on tropical forests.

Despite decades of studies that have assessed hurricane-induced forest dynamics, the key mechanisms that mediate forest responses to hurricane disturbance remain ambiguous (Lugo 2008). Whereas much knowledge has been gained about patterns of responses to hurricanes from observational studies

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(e.g., Zimmerman et al. 1996, Burslem et al. 2000, Turton 2008, Ruiz et al. 2010), the mechanistic understanding of forest responses requires experimental manipulations to identify key factors responsible for the empirical responses following a disturbance. For example, a whole-tree pull-down treatment simulating a hurricane blowdown was conducted in a temperate forest in the US (Harvard Forest); the primary response to increased understory light was an increase in plant recruitment (Cooper-Ellis et al. 1999). In the Luquillo Experimental Forest (LEF) of Puerto Rico, a multidisciplinary team of scientists used a large-scale experimental manipulation, implemented as a replicated factorial design, to determine the independent and synergistic consequences of two simultaneously occurring direct effects of hurricanes—canopy openness and debris deposition—on forest structural and functional characteristics (Shiels and González 2014). The inclusion of simultaneous measurements of many forest attributes, both prior to and following experimental treatments, facilitated a deeper understanding of the synergistic and cascading effects that result from hurricane disturbance. Here, we describe the motivation and justification for this experiment (i.e., the Canopy Trimming Experiment, or CTE) in the context of many well-documented observational studies of tropical hurricanes. We then integrate and synthesize research findings from the CTE and describe how our emergent understanding of tropical forest responses to hurricanes will influence future research.

Past hurricane studies and the motivation for the CTE

Hurricane effects have long been studied in tropical forests (e.g., Webb 1958), and the number of studies that describe them has increased in the past three decades, as has been evidenced by many publications, including several special issues of ecological journals (e.g., Walker et al. 1991, Turton 2008, Shiels and González 2014). Most of these studies reflect "major" hurricanes, which are those with sustained wind speeds of at least 178 km per hour (category 3 or above on the Saffir-Simpson Hurricane Wind Scale). Such storms cause long-term changes to forest structure and composition (Burslem et al. 2000, Chazdon 2003, Brokaw et al. 2012); responses include 2–3 fold increases in understory light (Turton 1992) and surface organic matter (Lodge et al. 1991), increased pioneer plant abundance (box 1) and rates of tree resprouting (Bellingham et al. 1994, Zimmerman et al. 1994), shifts in microhabitat use by vertebrates (Wunderle et al. 1992), and nutrient pulses in soil solution and streams (McDowell et al. 1996).

The biotic and abiotic responses to hurricanes can differ by region, and forests typically exhibit more resistance (withstanding disturbance and not changing in structure or function) or resilience (recovering to predisturbance conditions at a rapid rate) to hurricane disturbances in regions where these storms have occurred more frequently over millennial timescales, as in the Caribbean and parts of southeast Asia. In contrast, in South America, continental Africa, and northern Malaysia, hurricanes are rare, and therefore forests are less resistant and resilient to cyclonic storms (Scatena et al. 2012). In areas where hurricanes are a dominant component of the disturbance regime, tropical tree resistance to hurricane winds is generally high, and average mortality is only 10% (median, 7%; range, 1%–33%; reviewed in Shiels et al. 2010). Many factors may concomitantly affect the levels of tree mortality and resilience, including the intensity of the hurricane, the local disturbance regime (including hurricane frequency), and the biotic and abiotic characteristics of the forest (Everham and Brokaw 1996). Because both light (Denslow 1987) and nutrients (Vitousek and Sanford 1986) are well known factors that limit tropical tree growth, canopy openness and debris deposition are two of the most likely factors that affect forest succession following hurricanes (Lodge et al. 1991, Brokaw et al. 2012).

As a result of a focus on plants and plant recovery, few studies have linked the effects of hurricanes on vegetation and habitat alteration to the subsequent effects on animals, microbes, or ecosystem processes. In those studies, vertebrate groups strongly responded to hurricane alterations of forest structure via altered habitat use, diet, reproduction, or immigration (e.g., Wunderle et al. 1992, Grant et al. 1997, Willig and McGinley 1999). Although responses by invertebrates and microbes to hurricanes are the least well understood, their posthurricane roles in affecting ecosystem processes has received some study, especially with regard to decomposition (Herbert et al. 1999), nutrient cycling (Lodge et al. 1991, Steudler et al. 1991, McDowell et al. 1996, Xu et al. 2004), and herbivory (Angulo-Sandoval et al. 2004).

Although studies of particular aspects of hurricane-affected forest ecosystems are plentiful, what is rare or missing from our understanding of forest responses are (a) integrated responses across an ecosystem, including interactions among species and trophic levels, biotic processes, and microclimate; and (b) the key drivers and processes of forest change following a hurricane. The primary studies that motivated our large-scale hurricane experiment (i.e., the CTE) included those associated with Hurricane Hugo (September 1989) in Puerto Rico (e.g., Walker et al. 1991, Zimmerman et al. 1996) and the large-scale experimental blowdown in the northeastern US (Cooper-Ellis et al. 1999). In the LEF, pre- and post-Hurricane Hugo measurements of a wide range of forest attributes were facilitated by the establishment of long-term plots (Walker et al. 1991); no previous studies had resulted in a more extensive understanding of how a multitude of components of a tropical ecosystem—biotic, abiotic, and key processes—respond to hurricanes. From the diverse studies related to Hurricane Hugo in Puerto Rico (more than 80 peer reviewed journal articles published; 11 April 2015; *http://luq.lternet.edu/publications*), two key hypotheses were developed to explain the mechanistic drivers of tropical forest change following hurricanes (Willig et al. 2012): Short-term changes in forest properties result from canopy openness and associated abiotic or microclimatic changes; long-term changes (more than 7 years) result from organic matter (carbon [C] and nutrients) deposited onto the forest floor. Part of the short

Box 1. The importance of pioneer species following hurricanes.

Pioneer species are particularly abundant in disturbed forests following hurricanes; these species possess key functional traits that favor rapid recruitment, individual growth, and population expansion. Such traits typically include high fecundity, small body (or seed) size, reduced time to reproduction, the ability to disperse offspring widely, and high tolerance to light, temperature extremes, and moisture stress (Walker and Shiels 2013). Increased canopy openness increases light, temperature, and moisture stress; both insects and many pioneer plants have evolved waxy cuticles to limit water loss and therefore tolerate drought-prone environments. In open canopy plots in the Canopy Trimming Experiment (CTE), Richardson and colleagues (2010) discovered that more than 80% of the arthropods in the litter community are mites and Collembola; part of the success of these animals following disturbance (particularly mites) is reproduction via *parthenogenesis*, or when unfertilized eggs develop into new individuals. Nutrient cycling, forest productivity, and animal abundances and behaviors are closely influenced by the structure and composition of the local plant community following disturbance. Pioneer trees in the genus *Cecropia* often dominate Neotropical forest understories and midstories immediately after hurricanes (Guzmán-Grajales and Walker 1991, Behie et al. 2014) and canopy-opening manipulations in the CTE (figure 1; Shiels et al. 2010, Zimmerman et al. 2014). The white underside of *Cecropia*'s large leaves can be easily observed across the canopy of the Luquillo Experimental Forest, and its density and presence can indicate the patchiness of disturbance from previous hurricanes (figure 2), as well as a rough estimate of the period since the previous hurricane. Forests may only be converted to pioneer dominance for a few years after a hurricane, and the longer-term structure of the hurricane-altered forest is a result of a combination of the pioneer species that recruited after the storm, the resilient species (Ostertag et al. 2005, Metcalfe et al. 2008), and the taxa that were resistant to hurricane damage. Following a hurricane, the vegetation shift from nonpioneer dominance to pioneer dominance has significant bottom-up and cascading effects on the ecosystem. For example, Behie and colleagues (2014) found that the diets of the black howler monkey (*Alouatta pigra*) and disease exposure were altered after Hurricane Iris in forests in Belize because of the dominance of *Cecropia peltata* after the storm. *Cecropia peltata* has a mutualistic relationship with ants. Increases in the abundance of *C. peltata* after the disturbance results in the increased feeding by monkeys on fruits of *C. peltata.* As a consequence, the monkeys were more exposed to a disease-causing parasite (*Controrchis* spp.), which is associated with the ants (intermediate hosts).

Figure 1. **Cecropia schreberiana** *(large-leaved species pictured) recruited from seed in high abundance in the Canopy Trimming Experiment canopy-opening plots, in Puerto Rico. This photograph was taken approximately 1 year posttreatment. Photograph: Paul D. Klawinski.*

Figure 2. The Luquillo Experimental Forest in Puerto Rico, where **Cecropia schreberiana** *is identifiable by the whitish upturned leaves (from upslope wind movement) in the canopy. This photograph was taken approximately 5 years after Hurricane Georges. Photograph: Aaron B. Shiels.*

term–change hypothesis was based on the temperate forest experimental blowdown (simulating a hurricane in the region), in which increased plant recruitment followed an increase in understory light. Part of the long term–change hypothesis was based on adaptation of the Century model to the LEF after Hurricane Hugo (Sanford et al. 1991), in which increases in nutrient availability in soils—primarily phosphorus (P), from repeated hurricanes and associated debris deposited on the forest floor—led to forestwide increases in primary productivity. Insufficient data were available to validate predictions from the Century model for the LEF, highlighting the crucial need for long-term empirical studies of the effects of debris deposition following hurricanes. To test these hypotheses about the mechanistic drivers of short- and long-term change associated with hurricanes, we devised the CTE.

The large-scale experiment (CTE)

The CTE was established in the LEF of Puerto Rico (18 degrees [°] 20 minutes [′] north, 65°49′ west), an

11,000-hectare (ha) tropical evergreen wet forest that spans elevations from approximately 100 meters (m) to 1075 m. The LEF is the primary study site of the Luquillo Mountains Long-Term Ecological Research (LTER) Program, and major hurricanes pass over the LEF once every 50–60 years on average (Scatena et al. 2012), although just 9 years separated the last two major hurricanes (Hugo in 1989, Georges in 1998). The CTE is located in the northwestern portion of the LEF in tabonuco forest, where the mean annual rainfall is 3600 millimeters (mm) and the mean annual air temperature is 21 degrees Celsius (°C)–25°C (LTER climate data: 11 April 2015; *http://luq.lternet.edu/data/datacatalog*). The site is a mid- rather than low-elevation forest because of the downward compression of climatic zones that occurs on isolated mountains on tropical islands (Grubb 1971). The most common trees at the site (subtropical wet forest in the Holdridge System; Ewel and Whitmore 1973) are *Dacryodes excelsa* (Burseraceae), *Prestoea acuminata* var. *montana* (syn. *Prestoea montana*; Arecaceae), *Sloanea berteroana* (Elaeocarpaceaea), and *Manilkara bidentata* (Sapotaceae; Shiels et al. 2010). The maximum tree height just prior to the experiment averaged 18.1 m (standard error [SE] = 0.3 m, range = 13–30 m; Shiels and González 2014).

The CTE represented a two-factor, randomized block design with canopy trimming and debris addition as main factors. At approximately 400 m elevation in a 50-ha area, we established 12 plots (30 × 30 m each) distributed among three blocks in a completely replicated block design (n = 3 replicates for each of four treatments). The four treatments were the following: (1) no trim + no debris, in which neither the canopy nor the forest floor were altered (i.e., unmanipulated reference plots); (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 a trim + no debris plot was deposited on the forest floor; and (4) trim + debris, which most closely simulated conditions after a hurricane, in which the canopy was trimmed and the resulting debris was distributed on the forest floor (figure 3). This methodology focused on branch loss because it is the dominant empirical effect from past hurricanes at our site (figure 4; Zimmerman et al. 1994), in contrast to the situation in New England, where tree falls predominated in the severe hurricane of 1938 (Cooper-Ellis et al. 1999). In our trim plots, all nonpalm trees more than or equal to 15 centimeters (cm) in diameter at a height of 1.3 m (diameter at breast height, dbh) had branches removed that were less than 10 cm in diameter. Trees other than palms with dbh between 10 cm and 15 cm were trimmed at a height of 3 m. For palms, fronds extending more than or equal to 3 m above ground were trimmed at the connection with the main stem, but the apical meristem was not removed. The sizes of forest patches of near complete canopy loss following Hurricane Hugo were 0.01 ha–0.10 ha (Shiels and González 2014), which guided our choice of plot size (0.09 ha). Debris was added to plots (only trim + debris, and no trim + debris) by distributing it evenly across each 30 × 30 m area (figure 3b), and all six plots subject to debris addition had similar amounts of debris added (mean = 5408, SE = 143 kilograms [kg] dry-mass basis, or 6 kg per square meter [m^2], representing 67% wood, 29% leaves and twigs, and 4% palm fronds; Shiels et al. 2010). All treatments within a block were completed within 75 days.

All response variables in the CTE were measured in the central 20 × 20 m of each plot and included the population and community characteristics of diverse taxa ranging from microbes to plants and vertebrates, biogeochemical attributes, microclimate, and various ecosystem processes (for detailed methodology see Shiels and González 2014). This was one of most comprehensive, large-scale tropical experiments ever conducted, particularly considering the diverse suite of biotic and abiotic characteristics that were documented before and after experimental manipulation.

Responses to experimental manipulations

The synthesis figures (figures 5–7) depict most of the significant responses of the forest biota and ecological processes to the independent effects of canopy opening (trim + no debris; figure 5) or debris addition (no trim + debris; figure 6), as well as the cumulative effects (both additive and synergistic) of canopy opening plus debris addition (trim + debris; figure 7) relative to the unmanipulated reference plots. The experimental hurricane treatments triggered cascading effects involving the microclimate, the biota, and the ecosystem processes; the most influential response variables and interactions differed by treatment during the first 5–7 years after experimental manipulation (figures 3–5).

Canopy opening. The percentage of canopy openness (trim + no debris; figures 3d and 5) doubled relative to the unmanipulated control plots and therefore increased solar radiation to the understory and forest floor (Richardson et al. 2010, Shiels et al. 2010, Prather 2014), which decreased litter moisture via evaporation but increased soil moisture during the first year in response to reduced foliage surface for evapotranspiration and increased throughfall (figure 5; Richardson et al. 2010, Shiels and González 2014). These changes in microclimate induced changes in the biota and the biotic processes that cascaded through the ecosystem. For example, increased solar radiation and decreased demand for nutrients and water from canopy trees led to increased seedling recruitment and tree densities, particularly of pioneer trees and shrubs (box 1; Shiels et al. 2010, Zimmerman et al. 2014). Such shifts in the plant community resulted in higher nitrogen (N) and P concentrations in foliage and therefore leaf litterfall N and P (Silver et al. 2014), and these changes were associated with increased herbivory on pioneer plants (figure 5; Prather 2014). In addition, increased solar radiation led to the increased species richness of trees and ferns and doubled the leaf and spore production by ferns when compared with those in plots with intact canopies (Shiels et al. 2010, Sharpe and Shiels 2014, Zimmerman et al.

Figure 3. Photographs of the four treatments in the Canopy Trimming Experiment, Luquillo Experimental Forest, Puerto Rico: (a) no trim + no debris (understory view); (b) trim + debris (understory view); (c) no trim + debris (canopy view); (d) trim + no debris (canopy view). Photographs: Sarah A. Stankavich (a–c), and Aaron B. Shiels (d).

2014). Reductions in litter moisture and litter invertebrate richness (particularly macroinvertebrate prey) likely contributed to significantly decreased frog (*Eleutherodactylus coqui*) density (figure 5; Klawinski et al. 2014). In the detrital food web, high solar radiation in the trim + no debris plots (figure 5) led directly—and indirectly through decreased litter moisture and adverse light responses—to decreased litter invertebrate richness, diversity, and biomass (Richardson et al. 2010). Such changes were associated with losses in macroinvertebrates that consume and fragment litter (comminutors) and the increased abundance of microbiovores (mites, Collembola, Psocoptera) that primarily feed on microfungi (Richardson et al. 2010). This shift in invertebrate composition was associated with an inferred shift in the fungal community from macro- to microfungal dominance. Inferred changes were supported by observed reductions in macrofungal connections between litter layers (Richardson et al. 2010, Lodge et al. 2014) and reduced P translocation into decaying senesced leaves (Lodge et al. 2014). Furthermore, reductions in the abundance of macrofungi that degrade lignin, litter moisture, and litter comminution by macroinvertebrates were most likely responsible for the reductions in leaf decomposition rates (González et al. 2014, Lodge et al. 2014). Therefore, several key biotic responses and processes following hurricanes are driven by the microclimate attributes of the increased solar radiation and decreased litter moisture associated with canopy disturbance.

Debris addition without canopy opening. Leaf litterfall mass, nutrient concentrations, and nutrient inputs to the forest floor remained unchanged for 2.5 years after debris addition under closed canopy (no trim + debris; Silver et al. 2014). However, the addition of debris induced a modest and temporary increase in the tree basal area (figure 6; Shiels et al. 2010, Zimmerman et al. 2014), which was probably a result of the ephemeral reduction in competition from understory plants (seedlings and ferns), and possibly added nutrients and enhanced microbial activity (Shiels et al.

Figure 4. Photograph of the Luquillo Experimental Forest, Puerto Rico, after the passage of Hurricane Hugo on 18 September 1989. The photograph was taken from El Verde Field Station (fence and powerline in view), less than 1 kilometer from the Canopy Trimming Experiment plots. Photograph: Paul A. Steudler.

2010). Debris addition initially induced higher fern mortality (Sharpe and Shiels 2014) and decreased seedling density (Shiels et al. 2010) by burying these low-stature plants and impeding their access to light; this same pattern of initial reductions in seedling densities from debris addition was reported following Hurricane Hugo (Guzmán-Grajales and Walker 1991). Organic matter substrate and associated habitat resulting from debris addition most likely contributed to the observed increases in the diversity of soil and litter microbes (Cantrell et al. 2014), gastropods (Willig et al. 2014), and some canopy arthropods collected from three tree species (figure 6; Schowalter et al. 2014). The cascading effects from debris addition appear to further stimulate key biotic processes: herbivory on some nonpioneer plants in the understory (Prather 2014) and leaf litter decomposition (figure 6; González et al. 2014). In addition, decomposition rates were most likely influenced by interactions with microbial groups and their concomitant influences on nutrient availability; specifically, macrofungal connections were more abundant with debris additions and were positively related to P translocation into senesced leaves (Lodge et al. 2014), N and P immobilization in decomposing leaves, and increased rates of decomposition (figure 6; González et al. 2014, Lodge et al. 2014). Faster decomposition could have also led to the observed increase in bacterial diversity through the duration of substrate decay (Cantrell et al. 2014).

Hurricane debris in the LEF causes short-term changes in the diversity of microbes and some animal groups, N and P in decomposing leaves, leaf decomposition rates, basal area, seedling and fern densities, and understory herbivory. These responses were mediated by the increase in surface organic matter. Unlike canopy-opening effects, the independent addition of hurricane debris results in fewer changes in species abundances.

Canopy opening with addition of debris. Responses to the combined treatment (i.e., trim + debris) represent the cumulative effects of a hurricane, including simple additive (reinforcing or opposing) effects and interactive or synergistic effects. As in the canopy opening treatment (trim + no debris), the

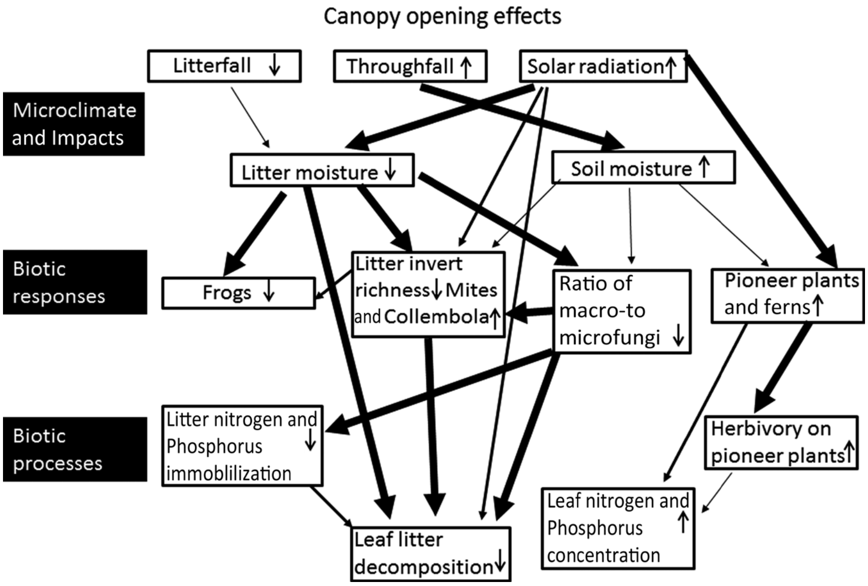

Figure 5. The effects of canopy opening (trim + no debris) during the first 1–7 years postmanipulation relative to unmanipulated reference plots (no trim + no debris) in tropical wet forest in the Luquillo Mountains of Puerto Rico. The changes in microclimate (first 1 year) and litterfall inputs (first 2.5 years), and responses in the biota and biotic processes are shown, including the effects that cascaded through the food web. In the boxes, the arrows depict increases (the upward arrow) or decreases (the downward arrow); the arrows connecting the boxes represent the influential flows of three levels of strength: strong (the thickest arrows), medium (the medium arrows), and small (the thinnest arrows).

trim + debris treatment increased solar radiation, throughfall, and soil moisture (figure 7). Similar to the independent effects of debris (figure 5), an enhanced layer of surface organic matter (6 kg per m^2) that covered the understory in trim + debris initially inhibited seedlings and small-stature ferns (figures 3b; Shiels et al. 2010, Sharpe and Shiels 2014). However, the debris only slightly delayed the benefits of increased canopy openness on seedling recruitment of pioneer species, fern growth and spore production, and species richness of woody seedlings, saplings, and ferns—ultimately, a dense forest understory developed in the simulated hurricane treatment (figure 7, box 1). The reduced nutrient demand by canopy trees and increased leaf litterfall N (Silver et al. 2014) resulted in greater nutrient availability for pioneer seedlings and ferns; in addition, with increased throughfall and fresh surface organic matter, excess N was converted by soil bacteria to nitrate, which leached into groundwater (figure 7). The elevated nitrate that leached through the soil and appeared 9–12 months after trim + debris treatment was an emergent property—one that was not predictable when its individual components (i.e., the independent effects of canopy openness or debris addition) were examined (McDowell and Liptzin 2014).

In contrast to the single treatment effects in which canopy trimming increased herbivory on pioneer plants and debris addition increased herbivory on nonpioneer species, the combined treatment had no effect on herbivory in either plant group in the understory (figure 7; Prather 2014). Regardless of whether hurricane debris is present in the understory, decomposition rates were lower in the trim plots relative to those in intact-canopy plots for both green (fresh) and senesced leaves (González et al. 2014, Lodge et al. 2014), and these lower rates were associated with decreased litter moisture (figure 7; Lodge et al. 2014). The reduced decomposition rates resulted from cascading effects in which increased solar radiation dried litter and most likely caused shifts in community structure, from macroinvertebrate comminutors to mites and Collembola (box 1; Richardson et al. 2010) and from macro- to microfungi (Lodge et al. 2014). Population declines within trim treatments were quantified for frogs that are sensitive to moisture loss (Klawinski et al. 2014), but the reduced abundance of prey (macroinvertebrates that avoid sunlight; Richardson et al. 2010) may have contributed to their decline (figure 7). However, gastropod richness and diversity increased, as did the abundance of all gastropods, especially *Caracollus caracolla*, in the trim + debris treatment (Willig et al. 2014).

Aside from possible habitat enhancements for gastropods and a temporary increase in tree basal area, fresh surface organic matter only facilitated forest change (enhanced nitrate in soil solution) when combined with conditions of open canopy (figure 7). Otherwise, forest responses and cascading effects in the hurricane treatment plots (trim + debris) primarily resulted from open-canopy conditions.

Lessons and future research directions

Hurricanes trigger a multitude of complex dynamics and cascading effects in the LEF (figures 5–7). Our understanding of these effects was enhanced by using a factorial experimental design to distinguish the separate and interactive effects of canopy openness and debris deposition, documenting forest properties before and after experimental manipulations, using a multidisciplinary approach, and integrating a diverse array of biotic and abiotic features of the ecosystem. Perhaps our foremost finding is that short-term tropical forest responses to cyclonic storms appear to be largely driven by canopy openness rather than by debris addition, even though the latter represents an important carbon and nutrient source for the biota (Vitousek and Sanford 1986).

Hurricanes create a patchwork of resource states and conditions at multiple spatial scales, from microsites to landscapes. The CTE enabled us to better understand such a

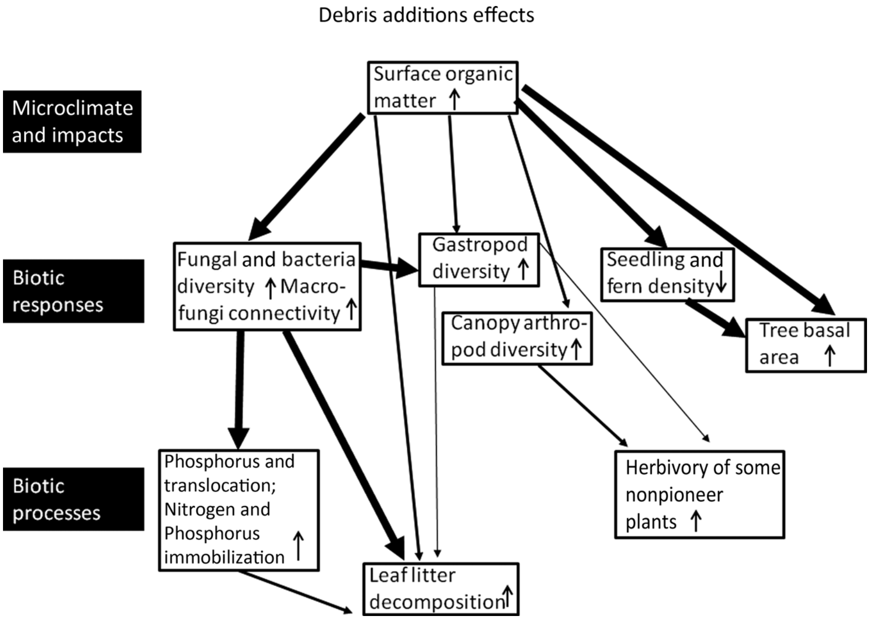

Figure 6. The effects of debris addition (6 kilograms per square meter) under intact canopy conditions (no trim + debris) during the first 1–7 years postmanipulation relative to unmanipulated reference plots (no trim + no debris) in tropical wet forest in the Luquillo Mountains of Puerto Rico. The changes in microclimate (first 1 year) and surface organic matter (first 2.5 years), and responses of the biota and biotic processes are shown, including the effects that cascaded through the food web. In the boxes, the arrows depict increases (the upward arrow) or decreases (the downward arrow); the arrows connecting boxes represent the influential flows of three levels of strength: strong (the thickest arrows), medium (the medium arrows), and small (the thinnest arrows).

patchwork on the scale of 30 × 30 m plots. Simulating hurricane effects on a mesoscale stressed our logistical capabilities, and therefore the sizes of the experimental plots can be viewed as a limitation of such a large manipulative experiment. A lack of correspondence between our results with those from observational studies after hurricanes (see Shiels et al. 2014) may arise for a number of reasons. The execution of a large manipulation over a short enough period to capture ephemeral responses (e.g., transporting and storing fresh leaves between plots to unify blockwide debris-addition treatments) is a significant logistical challenge. Contrasting results may also arise because of differences in site attributes such as disturbance history. For example, our analyses do not show increased rates of trunk growth in canopy trees as was expected from observational studies after Hurricane San Ciprian in Puerto Rico (Weaver 1986), Hurricane Joan in Nicaragua (Ruiz et al. 2010) or after Hurricane Gilbert in Jamaica (Bellingham et al. 1995) and Mexico (Whigham et al. 1991), in part because the CTE (2004–2005) occurred only 6–7 years after direct passage of Hurricane Georges (category 3 storm in 1998) over the plots. Increases in trunk growth rates after hurricanes occur during the thinning stage due to release from competition (Whigham et al. 1991, Ruiz et al. 2010). The interval between Hurricane Georges and the CTE manipulation may have been too short for trees to benefit from thinning. Other responses to the CTE treatments, such as those involving structure and composition of the plant community, tree mortality (5.3%), and duration of increased canopy openness (18 months) were almost identical to those after past major hurricanes in the LEF (see Shiels et al. 2010). Furthermore, the characteristic canopy openness and debris deposition produced as part of the CTE were similar to those following a category 3–4 hurricane, such as Hurricane Hugo, in this same part of the LEF (reviewed by Shiels et al. 2010, Shiels and González 2014).

The appearance of high concentrations of nitrate-N in groundwater was an emergent property in the hurricane simulation treatment that was not observed in either single treatment (figures 5 and 6), and both the timing and magnitude closely mimicked the appearance of N in groundwater and streams that was observed after Hurricanes Hugo and Georges at the same site (McDowell et al. 2013, McDowell and Liptzin 2014). Until our study, it was unknown if the pulse in stream water nitrate following major hurricanes originated from the terrestrial or aquatic ecosystem. Furthermore, comparing our results from the trim + no debris and the trim + debris conditions provide clarity that the increased soil solution nitrate after a hurricane is largely related to the decomposition of the hurricane debris rather than root mortality associated with tree damage. Responses (or lack of responses) in the combined treatment (i.e., trim + debris, figure 7) would therefore not have been interpretable on a mechanistic level if this experiment had not been conducted as a factorial design.

Hurricanes alter the detrital food web and cause shifts in microbial and detritivore communities, and consequently reduce decomposition rates and alter nutrient cycling. Knowledge of these interactions and processes has been minimal in most nonmanipulative studies of hurricane effects. Reduced moisture and increased light at the forest floor drives larger-bodied litter arthropods from the open canopy, thereby reducing leaf fragmentation. At the same time, macrofungi (Basidiomycota), which are largely responsible for breaking down lignin and translocating limiting nutrients such as P, are reduced in open canopy plots. This microbial shift favors small microbiovores, and is associated with increased leaching of P from the surface litter. Therefore, canopy disturbance following a hurricane initiates a complex series of events that cascade through the detrital food web and ultimately accounts for reduced rates of leaf litter decomposition.

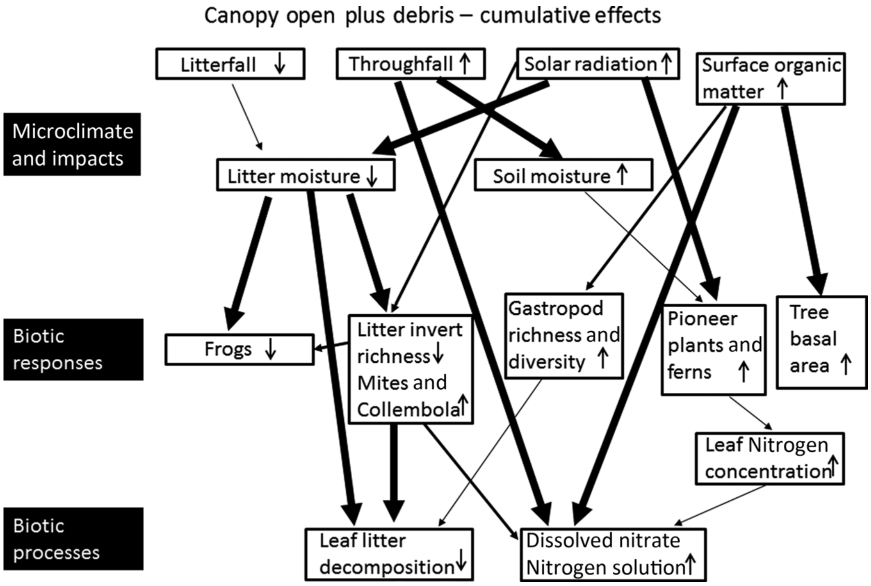

Figure 7. The effects of canopy opening and debris addition (trim + debris) during the first 1–7 years postmanipulation relative to unmanipulated reference plots (no trim + no debris) in tropical wet forest in the Luquillo Mountains of Puerto Rico. The changes in microclimate (first 1 year), litterfall inputs (first 2.5 years), soil organic matter inputs (first 2.5 years), and the responses of the biota and biotic processes are shown, including the effects that cascaded through the food web. In the boxes, the arrows depict increases (the upward arrow) or decreases (the downward arrow); the arrows connecting the boxes represent the influential flows of three levels of strength: strong (the thickest arrows), medium (the medium arrows), and small (the thinnest arrows).

Although the short-term hypothesis of canopy openness driving most forest changes following hurricane effects was supported by the CTE, measurements from the manipulation plots are ongoing to test the long-term hypothesis of the importance of woody debris in driving forest change. The next stage of the CTE has been initiated, allowing for future evaluation of the effects of repeated hurricanes on abiotic, biotic, and ecosystem characteristics. Quantification of repeated effects of intense disturbances will better inform predictions of how this forest and others with similar disturbance regimes will respond to predicted increases in the frequency of major hurricanes (Bender et al. 2010), and otherwise how recurrent disturbances influence forest attributes and interactions (e.g., Burslem et al. 2000, Ostertag et al. 2005). Based on findings from the CTE, we expect that increased frequency of severe storms will increase the dominance of shade intolerant, pioneer plant species, which will increase soil C storage relative to aboveground C storage over the long term. Aboveground biomass and C reductions will occur directly by increased frequency of canopy damage, and indirectly as a consequence of the shift toward less densely wooded pioneer species (Shiels et al. 2010, Zimmerman et al. 2014). Rates of C accumulation may be higher between storms because of the greater productivity of pioneers and the increased canopy openness. According to predictions derived from the Century model for the LEF, we also expect higher soil organic matter with more frequent severe hurricanes and greater soil organic P will increase forest productivity between storms (Sanford et al. 1991), but higher soil carbon dioxide flux rates for two years following simulated hurricane disturbance may counter this predicted effect (Whendee Silver, University of California Berkeley, personal communication, June 4, 2014). Dominance of pioneer species, more frequent canopy opening, and higher soil organic matter will favor heterotrophs, including microbes, associated with pioneer plant species and the more frequent hot and dry conditions (box 1). These, in turn, will have cascading effects on C and nutrient fluxes.

Future research aimed at enhanced understanding of hurricane effects to tropical forests will benefit from experimental manipulations of key factors hypothesized to shift abiotic and biotic characteristics. Although the Harvard Forest blowdown was not a replicated or factorial experiment, the findings from both the CTE and blowdown indicate that the key driver of forest response to hurricanes is the increase in understory light associated with canopy openness (Cooper-Ellis et al. 1999, Shiels et al. 2014). Additional experiments are needed to fully demonstrate the mechanisms that cause cascading effects such as those that we have documented through correlative analyses (figures 5–7). We highlight the importance of understanding the dynamics of posthurricane shifts in microbial communities and extent to which such shifts affect decomposition and nutrient cycling. Moreover, elucidating key predator–prey dynamics following hurricanes in tropical forests will help to identify the drivers of change, and their cascading effects on above- and belowground ecosystems.

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