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

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ABSTRACT

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

1. Introduction

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

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

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

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

2. Methodology

2.1. Study site

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