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Seven-year responses of trees to experimental hurricane effects in a tropical rainforest, Puerto Rico

Jess K. Zimmerman *, James Aaron Hogan, Aaron B. Shiels [1], John E. Bithorn, Samuel Matta Carmona, Nicholas Brokaw

Department of Environmental Science, University of Puerto Rico, Rio Piedras Campus, P.O. Box 70337, Rio Piedras, PR 00936-8377, USA

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ABSTRACT

We experimentally manipulated key components of severe hurricane disturbance, canopy openness and detritus deposition, to determine the independent and interactive effects of these components on tree recruitment, forest structure, and diversity in a wet tropical forest in the Luquillo Experimental Forest, Puerto Rico. Canopy openness was increased by trimming branches, and we manipulated debris by adding or subtracting the trimmed materials to the trimming treatments, in a 2×2 factorial design replicated in three blocks. Tree (stems $\geqslant 1$ cm diameter at breast height) responses were measured during the 9-year study, which included at least 1 year of pre-manipulation monitoring. When the canopy was trimmed, stem densities increased >2-fold and rates of recruitment increased >25-fold. Deposition of canopy debris did not markedly affect stem densities but did have small yet significant effects on tree basal area. Basal area increased about 10% when debris was added to plots with intact canopies; the other treatments exhibited smaller or no increases in basal area over time. Much of the dynamics of stem densities were due to changes in the smallest size class (1–2.5 cm diameter), which responded with a pulse of recruitment in the canopy trimmed treatments, and a steady loss in plots with intact canopies. The decreases in stem densities in the plots with intact canopies is attributed to observed on-going forest thinning from the last natural severe hurricane disturbance in 1998. Given these repeated hurricane effects, our study enabled an experimental test of the Intermediate Disturbance Hypothesis (IDH), for which we predicted an increase in species diversity in canopy trimmed treatments and a loss of species in the treatments with intact canopies. Measured patterns of diversity gave partial support to the predictions of IDH, although raw species richness of sampled plots fit the predictions better than richness adjusted for differences in stem densities among treatments. Ordination of species responses in the community identified a guild of pioneer species responding to the trimmed treatments, but not the debris additions, amongst substantial background variation in species composition unrelated to the experimental treatments. These results are consistent with a growing consensus that, while trade-offs of resilience and resistance govern many species responses to hurricane disturbance, other environmental and historical factors are equally or more important in governing community dynamics in hurricane-disturbed forests.

1. Introduction

Wind storms are a dominant component of the disturbance regime of forested ecosystems in many parts of the world (Everham and Brokaw, 1996; Whitmore and Burslem, 1998; Lugo, 2008). Many past studies describe the impacts of tropical cyclones on regional forests (Walker et al., 1991, 1996; Stone and Finkl, 1995; Burslem and Whitmore, 1999; Turton, 2008; Webb et al., 2014), and those in the Caribbean emphasize the resilience of forests to even the most severe hurricanes (Scatena et al., 1996; Vandermeer et al. 2000; Tanner and Bellingham, 2006; Imbert and Portecop, 2008; McGroddy et al., 2013). While such rapid tree recovery is largely a result of species adaptations to severe wind disturbance (Zimmerman et al., 1994; Bellingham et al., 1995; Brokaw et al., 2004), a mechanistic understanding of the tree responses during the first decade following hurricane disturbance is lacking. This can be determined by experimental manipulations similar to those conducted at Harvard Forest in the north-eastern

* Corresponding author. Tel.: +1 787 764-0000x2867.
E-mail address: jesskz@ites.upr.edu (J.K. Zimmerman).
[1] Present address: USDA, National Wildlife Research Center, Hawaii Field Station, P.O. Box 10880, Hilo, HI 96721, USA.

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USA (Carlton and Bazzaz, 1998; Cooper-Ellis et al., 1999; Barker Plotkin et al., 2013) and the Canopy Trimming Experiment (CTE) in the Luquillo Experimental Forest, Puerto Rico (Richardson et al., 2010; Shiels et al., 2010; Shiels and González, 2014).

The CTE was designed to separate two critical effects normally confounded in a hurricane – increased canopy openness and the deposition of debris on the forest floor (Shiels and González, 2014). Earlier, Shiels et al. (2010) reported on the initial responses of woody vegetation in the CTE, focusing on the dynamics of the seedling layer. The deposition of debris killed many existing woody seedlings and provided a mechanical barrier that suppressed seedling recruitment, but these effects were largely transient. The increase in understory light availability caused by canopy trimming appeared more important than the impacts of hurricane debris, stimulating increased seedling recruitment and density of pioneer species (e.g., *Cecropia schreberiana*) known to respond strongly to canopy opening caused by hurricanes (Zimmerman et al., 2010). This effect was apparent through the end of the study, four years after the implementation of treatments (Shiels et al., 2010).

While Shiels et al. (2010) were able to establish the impacts of canopy opening on tree sapling recruitment, their observations were not of sufficient length to clearly determine the full impacts of canopy openness on the existing trees. Patterns of mortality suggested little impact of canopy trimming, but these impacts may become more apparent as time proceeds (Walker, 1995). Also, while there was a small apparent increase in basal area caused by debris deposition (Shiels et al., 2010), suggesting a beneficial effect of debris on tree growth, this only became apparent at the end of the study. In addition, even though Shiels et al. (2010) showed that the trimming treatments influenced the tree community by causing recruitment of key pioneer species, they did not determine the impact of the treatments in the CTE on patterns of species diversity. Furthermore, a longer post-treatment observation period offers the opportunity to investigate species responses to the experimental treatments in more detail in view of the decadal impacts that a single hurricane can have on community dynamics (Crow, 1980; Lugo et al., 2000).

One relevant theory describing the diversity response of tree communities to wind disturbance is the Intermediate Disturbance Hypothesis (Connell, 1978; Doyle, 1981; Sheil and Burslem, 2004). The theory assumes trade-offs either in species competitive abilities or niche partitioning whereby more recently disturbed forest patches serve as opportunities for the establishment of rapidly growing, shade intolerant guild of pioneer species that persist in a community dominated by slower-growing species tolerant of low resource conditions (Pacala and Rees, 1998; Uriarte et al., 2012). To the degree that the presence of two (or more) generalized species groups with different light requirements overlap in space and time (Miller et al., 2011), species diversity of local, recently disturbed forest patches will reach a maximum before declining, as shade tolerant species come to dominate the patch. While the validity of the theory is still debated on both empirical and theoretical grounds (Bongers et al. 2009; Fox, 2013; Sheil and Burslem, 2004; 2013), Miller and his colleagues have given new life to IDH by strengthening its theoretical underpinnings (Miller and Chesson, 2009; Miller et al., 2011). We take advantage of previous severe hurricane disturbance at our site to frame our test of IDH (Zimmerman et al., 1994; 2010). Since no severe hurricanes affected our study once it started, we can effectively compare the more recent experimental canopy opening to that caused by a hurricane 14 years in advance of the start of our observations.

Shiels et al. (2010) showed that an initial response by species to canopy trimming was increased recruitment of two common pioneer species, *Cecropia schreberiana* and *Psychotria berteroana* with no species responding to debris deposition detected at the time of the study. Again, with a greater time span of observations, it is possible to further detail species responses to the experimental manipulations. In particular, we wish to investigate the generality of our previous observations by utilizing ordination methods to illuminate the responses of all species in the forest community, not just the most common species as was analyzed by Shiels et al. (2010). This approach would support the goal of understanding diversity responses to the manipulations in the context of trade-offs in species resistance and resilience to hurricane disturbance (Boucher et al., 1994; Zimmerman et al., 1994; Burslem and Whitmore, 1999; Tanner and Bellingham, 2006; Uriarte et al., 2012).

Therefore, we revisit the response of woody vegetation to treatments in the CTE (Shiels et al., 2010), addressing the following questions:

(1) What are the long-term mortality and growth rates of saplings (woody plants $\geqslant$1 cm DBH) recruited into the CTE treatments where the canopy was trimmed and how does this relate to forest dynamics in forest naturally disturbed by hurricanes?
(2) How does the deposition of debris generated by trimming the forest canopy influence forest dynamics, particularly long-term patterns of tree growth and mortality? Moreover, is there a positive effect of debris deposition and does this effect interact with the trimming treatments?
(3) To what degree do patterns of changes in species diversity in the CTE support or refute patterns predicted by IDH?
(4) How does species composition respond to the experimental treatments and how does this enhance our understanding of community dynamics in hurricane-disturbed forests.

2. Materials and methods

2.1. Study site

This study took place in the Luquillo Experimental Forest (LEF) in north-eastern Puerto Rico, near the El Verde Field Station (EVFS; 18°20′N, 65°49′W), where annual rainfall averages 3500 mm (Zimmerman et al., 2007), elevation is 340–485 m a.s.l., and the terrain is steep (24% average slope) and rocky (25% of the soil surface covered by boulders; Soil Survey Staff, 1995; Shiels et al., 2010). The study site is in tabonuco forest (subtropical wet forest in the Holdridge System; Ewel and Whitmore, 1973), which is the lowermost and dominant of four general vegetation zones along an altitudinal gradient across the LEF. The prominent tree species at the site include *Sloanea berteroana* (Elaeocarpaceae), *Dacryodes excelsa* (Burseraceae), *Prestoea acuminata* var. *montana* (Arecaceae), and *Manilkara bidentata* (Sapotaceae). Before our study, the two most recent severe hurricanes passing over our site 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. No storms of hurricane strength impacted the site during our study and there were not significant droughts (Shiels and González, 2014).

2.2. Experimental design

Three blocks were established in tabonuco forest of similar age and land-use history (>80% cover in 1936; Foster et al., 1999; Thompson et al., 2002) and topography. The three blocks were located in an area of approximately 50 ha near EVFS at similar elevations (340–485 m a.s.l.). Individual plot size was 30 × 30 m, selected to reflect the average size of damaged patches of canopy that were observed following Hurricanes Hugo and Georges (Brokaw and Grear, 1991; Zimmerman et al., 2010). Plots were