



Divergent responses of leaf herbivory to simulated hurricane effects in a rainforest understory



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ABSTRACT

Hurricanes are major disturbances in many forests, but studies showing effects of natural hurricanes on herbivory rates have yielded mixed results. Forest managers could benefit from a better understanding of the effects of disturbances on herbivory to manage for particular recovery or restoration goals after anthropogenic or natural disturbances, such as logging and windstorms. I measured herbivory on eight understory plant species that are common pioneer and non-pioneer species in a rainforest in Puerto Rico, following experimental manipulation of forest plots to simulate the two major effects of a hurricane (canopy opening and a detrital pulse). I expected that greater leaf production and leaf quality would result from canopy trimming and detritus (debris) addition to the forest floor, respectively, and that both treatments would enhance herbivory rates independently and especially in combination. I found a significant interaction of trim and debris treatments that affected plant species within pioneer and non-pioneer plant groups differently: a debris pulse or canopy trimming alone stimulated understory herbivory over time on non-pioneer and pioneer plants, respectively, but the combination of these two treatments had no effect on herbivory rates. Specifically, herbivory was higher on pioneer plants in plots where the canopy was trimmed but debris had not been added, whereas herbivory was higher on non-pioneer plants in plots where debris was added to the forest floor under intact canopy conditions. Therefore, different mechanisms apparently controlled herbivory of pioneer and non-pioneer species. Pioneer plants likely experienced enhanced herbivory in trimmed plots in part because of the increased densities of pioneer plants responding to canopy trimming; pioneer plants were temporarily less abundant in debris addition plots. Non-pioneer species may have experienced greater herbivory in debris addition plots in part because of increased foliar quality resulting from enhanced nutrient availability associated with the debris pulse. Future, complementary greenhouse and field mesocosm experiments that manipulate the factors likely contributing to these results would help to reconcile results from previous studies that have documented both increases and decreases in herbivory or certain herbivore taxonomic groups resulting from natural hurricanes. Understanding the mechanisms that affect herbivory after hurricanes is important because herbivory can affect nutrient cycling, plant community structure, and ultimately forest recovery after disturbance.

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1. Introduction

Globally, herbivores influence how ecosystems function (Huntly, 1995; Weisser and Siemann, 2004; Prather et al., 2013), and it is therefore important to understand the factors that control herbivory. Many factors are known to influence herbivory rates, including: food availability (the higher the levels of primary production, the more food available for herbivores; Lawton, 1983; Lewinsohn et al., 2005); food quality (differences

in the concentration of leaf nitrogen and phosphorus or secondary compounds influence herbivory rates; White, 1984; Huberty and Denno, 2004); the strength of competition (competitors can alter feeding rates and behavior; Bonser and Reader, 1995); and strength of top-down pressures (the greater the pressure from predators and parasites, the lower the herbivory; Siemann et al., 1998). All of these factors may interact with one another, and each can be altered by disturbances, such as hurricanes.

Hurricanes are common disturbances in many forested ecosystems, especially in the Caribbean (Walsh, 1997). Hurricanes result in two major, and simultaneous, changes in forest structure: the opening of a usually closed canopy (Fernandez and Fetcher, 1991), and a pulse of non-senescent detritus to the forest floor

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(Lodge et al., 1991; Ostertag et al., 2003), which decomposes very rapidly and acts as a nutrient pulse. These two physical effects can both directly and indirectly influence all the major factors that affect herbivory described above. Previous studies looking at the effects of hurricanes on herbivory rates in forests have had mixed results, including both increases in herbivory and the abundance of certain herbivore taxonomic groups (Torres, 1992; Schowalter, 1994; Schowalter and Ganio, 1999; Hunter and Forkner, 1999), and reductions in herbivory and the abundance of certain herbivore groups (Willig and Camilo, 1991; Spiller and Agrawal, 2003; Angulo-Sandoval et al., 2004). Increases in herbivory after hurricanes, however, have mostly been observed in forest canopies (Schowalter, 1994; Schowalter and Ganio, 1999), while reductions in herbivory rates have mainly been observed in forest understoreys (Willig and Camilo, 1991; Spiller and Agrawal, 2003; Angulo-Sandoval et al., 2004). No studies, however, have determined the relative effects of debris addition and canopy trimming on levels of herbivory, either static or in terms of rates, for a community of plants in a rainforest understorey.

I utilized a large experiment (the Canopy Trimming Experiment, CTE) that simulated the main effects of natural hurricanes (canopy opening and debris pulse) in a Puerto Rican rainforest to test the following questions: (1) How do the independent and combined effects of canopy opening and debris addition to the forest floor affect understorey herbivory? (2) Are the effects of canopy opening and debris addition on herbivory different for pioneer non-pioneer species? I predicted that (H1a) both increases in light and debris would have positive effects on understorey herbivory through (H1b) increases in light to the understorey causing increasing food availability in the form of greater new leaf production, and (H1c) a nutrient pulse from decomposing debris increases food quantity and quality for understorey herbivores. I further expected that (H2) these two factors (canopy openness and debris deposition) combined would have even greater positive effects on herbivory than independently.

2. Material and methods

2.1. Site description

This study was conducted at the Luquillo Experimental Forest (LEF), located in the northeastern corner of Puerto Rico (18°19'N, 65°45'W). Animal diversity in this insular forest is generally lower than mainland tropical sites (Reagan and Waide, 1996). Invertebrates are the major folivores in this forest, and there are no extant folivorous mammals. Rates of herbivory in the understorey of this forest are generally lower than other tropical forests—about 16% of leaf material a month is eaten by folivores—and herbivory rates are relatively constant throughout the year (Angulo-Sandoval and Aide, 2000a). This site is frequently disturbed by hurricanes (every 6–60 years depending on intensity, Scatena and Larsen, 1991) during months with generally higher precipitation (May through December), and the effects of natural hurricanes on abiotic and biotic processes at this site have been extensively studied (Brokaw et al., 2012). This study took place in Tabonuco forest, the dominant and lowest vegetation type along an elevational gradient at LEF. The dominant, non-pioneer trees in the Tabonuco forest are *Dacryodes excelsa*, *Sloanea berteriana*, and the palm, *Prestoea acuminata* var. *montana* (syn. *Prestoea montana*). The study site is described more fully in Shiels and González (2014).

2.2. Experimental design

To test the effects of a simulated hurricane on understorey herbivory, I utilized the CTE, which was designed to differentiate the two main effects of hurricanes (the opening of the canopy, and

the influx of debris onto the forest floor). This experiment has been extensively described (Richardson et al., 2010; Shiels et al., 2010; Shiels and González, 2014). Briefly, this experiment used a completely randomized block, fully factorial design where three replicate blocks in Tabonuco forest with similar land use history had two main factors (canopy trimmed = trim, or debris added to forest floor = debris) that were combined factorially to result in a total of four treatments (trim + no debris, no trim + debris, trim + debris, and no trim + no debris [control]). There were a total of 12–30 × 30 m plots ($n = 3$ per treatment) with plots located no closer than 20 m from each other. Although each 30 m × 30 m plot was treated, only the core 20 × 20 m area within each plot was used for measurements, with 10 m of buffer zone along each side. The core measurement area was divided into 16 subplots (each ca. 4.7 × 4.7 m) designated for measuring different variables and to minimize the amount of disturbance to any one plot (see Shiels and González, 2014). Understorey herbivory measurements described in my study utilized four subplots dedicated to plant measurements for a total of 48 subplots.

Treatment application took place from October 2004 through June 2005. Light levels and canopy cover were reduced to levels that mimicked levels after Hurricane Hugo (Shiels et al., 2010). For the trim treatment plots, all branches ≤10 cm diameter that were above 3 m height were cut and removed from all non-palm trees that were >10 cm diameter at 1.3 m height. The fronds on all palm trees over 3 m in stem height were also removed. Material that was clipped from trimmed plots was used as the detritus added to debris-addition plots. This debris was separated into wood, leaves and twigs, and palm fronds. It was subsequently weighed, and a subsample was dried and reweighed to establish a wet to dry conversion rate. All material was piled along sides of the plots until trimming was complete, and subsequently the debris was added to respective plots. The process resulted in about 1 month of decomposition before treatment deposition. On average, 6500 kg (dry weight) was added to each debris-addition plot, an amount that mimicked debris that fell during Hurricane Hugo (Shiels et al., 2010).

2.3. Sampling methods

In all 12 plots, I measured herbivory in the summer before the experiment began in 2004, and annually for three summers after treatment application (2005–2007). I chose to measure herbivory on eight species of common understorey plants that represented the most common pioneer and non-pioneer species in the CTE plots (Shiels et al., 2010) and in the Tabonuco forest in general (McDowell et al., 2012). The pioneer species included four trees (*Cecropia schreberiana*, Cecropiaceae; *Miconia prasina*, Melastomataceae; *Miconia racemosa*, Melastomataceae; *Schefflera morototoni*, Araliaceae), and one perennial herb (*Piper glabrescens*, Piperaceae). The non-pioneer species included three trees (*Casearia arborea*, Flacourtiaceae; *S. berteriana*, Elaeocarpaceae; *Manilkara bidentata*, Sapotaceae). I used methods previously used at this and other field sites to measure leaf area missing and leaf production (Aide, 1993; Angulo-Sandoval and Aide, 2000a, 2000b; Angulo-Sandoval et al., 2004), but leaf area missing was quantified digitally using ImageJ shareware (Schneider et al., 2012) instead of a grid system for higher accuracy.

I flagged all individuals of my focal plant species between 0.5 and 2.5 m tall within the four plant measurement subplots in each plot of the experiment annually (2004–2007) during the peak time of leaf production (late May/early June; Angulo-Sandoval and Aide, 2000a). Using colored wire tied around leaf petioles, I randomly marked up to 10 emerging leaves spread throughout the plant (most understorey plants had fewer than 10 emerging leaves; median number of new leaves on pioneer species = 7.3; median

number of new leaves on non-pioneer species = 8.0). I returned when all leaves were fully flushed (August), and took pictures of each leaf against a white background. I used ImageJ to quantify the leaf area missing from each leaf. Percent leaf area missing was first averaged for all leaves on a plant, and all individuals from one species in one subplot were pooled to obtain a species-specific average of leaf area missing for each subplot. Likewise, at each plant, I used a spherical convex densitometer (Forestry Suppliers) to measure canopy openness in all 4 cardinal directions when held at 1 m height, and calculated the percentage of canopy openness based on instructions on the densitometer. To determine the amount of leaves available for herbivore consumption and if this was related to herbivory rates, I also counted both the total number of leaves and the number of new leaves (those not fully expanded) on each plant. Percent canopy openness and leaf production was also averaged at the subplot level. I also noted any herbivores that I observed on each plant.

2.4. Statistical analysis

Data was analyzed with SysStat 10 (SPSS, Chicago, Illinois, USA). The percentage of leaf area missing (i.e. the proportion of the area of the leaf that was missing due to herbivory) and canopy openness was arcsine-square root transformed to meet parametric assumptions, but the untransformed means are presented in the figures here for ease of viewing. The level of replication for these analyses was the subplot level. To determine the effects of experimental treatments on canopy openness, I used a mixed general linear model with three fixed factors (date, trim, detritus), controlling for the random block factor, where the level of replication for was the subplot level. The effects of treatments on leaf production (number of new and total leaves) and the percentage of leaf area missing (herbivory) on the different plant species sampled were analyzed with a mixed general linear model with four fixed factors (date, trim, detritus, and plant species nested within plant type), controlling for the random block factor. Because there were unequal numbers of plant individuals across years and treatments (Supplemental Table 1), plant species was nested within plant type (pioneer vs. non-pioneer species). The level of replication for these analyses was the specific-response at each subplot, and the total number of subplots used for each species in each treatment in each year is shown in Supplemental Table 2. This model was reduced by removing any interactions that had a P -value greater than 0.25. I used linear regression to determine if canopy openness predicted any variation in plant production (total number of leaves per plant or number of new leaves per plant where the unit of replication was individual plants), and consequently if canopy openness or measures of plant production predicted any variation in herbivory.

3. Results

Canopy openness increased significantly in trimmed plots, relative to intact canopy plots, after the treatment application

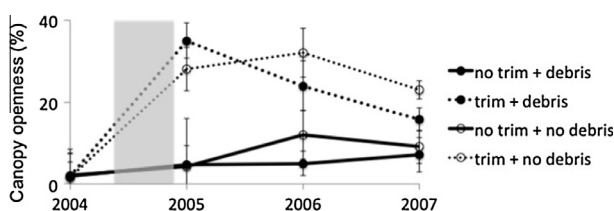


Fig. 1. Average percentage of canopy openness ($\pm$ SE) in understory plants in Luquillo Experimental Forest (Puerto Rico) across treatments. The treatment period for the canopy trimming experiment (October 2004–June 2005) is in gray.

(Fig. 1; date $\times$ trim: $F_{3,162} = 3.11$, $P = 0.008$), but this effect lessened over time, with canopy openness returning to near pre-treatment levels ca. 2 years after treatment application in 2007. Neither debris ($F_{1,162} = 0.132$, $P = 0.75$) or trim ($F_{3,162} = 0.49$, $P = 0.008$) treatments nor their interaction (debris $\times$ trim: $F_{1,162} = 0.462$, $P = 0.45$) affected leaf production (neither total number of leaves per plant nor number of new leaves). Canopy openness explained a very small amount of variation in the total number of leaves on a plant ($F_{1,457} = 2.67$, $R^2 = 0.026$, $P = 0.048$), but not the number of new leaves on a plant ($F_{1,457} = 0.31$, $P > 0.81$). Neither canopy openness nor measures of plant production predicted any of the variation in herbivory, even if regressions for pioneer and non-pioneer species were conducted separately ($P > 0.05$ for each regression).

Two plant species were not abundant enough across treatments and years to use in statistical analyses (*P. glabrescens* and *C. Schreberiana*; Supplemental Table 1). Individuals of all other plant species were found in unequal numbers across blocks, treatments, and years (Supplemental Table 1), but were in sufficient numbers of subplots for inclusion in statistical analyses (ranging from 10 to 25 subplots for each species per year out of a total of 48 possible subplots; Supplemental Table 2). The amount of herbivory varied across years ($F_{3,369} = 75.11$, $P < 0.001$): overall herbivory was higher treatments were applied (13.0% in 2005, 13.9% in 2006, and 16.9% in 2007) compared to before the experiment began (9.51% in 2004). Different amounts of herbivory occurred different plant species ($F_{5,369} = 26.99$, $P < 0.001$), with less herbivory occurring on *C. arborea* (6.74%) than the rest of the non-pioneer species, and less herbivory on *M. prasina* (10.26%) compared to the rest of the pioneer species. Debris and trim treatments alone did not significantly affect herbivory (see Table 1), but there was a significant interaction of these two treatments over time ($F_{10,369} = 23.89$, $P < 0.001$; Fig. 2). Herbivory steadily increased from 2005 to 2007 in plots that just received one type of treatment (trim + no debris and no trim + debris plots); however, herbivory on plants in trim + debris plots was not significantly different from control plots. Herbivory on pioneer and non-pioneer species responded differently to treatments over time (date $\times$ trim $\times$ debris $\times$ plant type (plant species): $F_{66,369} = 7.73$, $P < 0.001$): herbivory on non-pioneer species increased over time only in no trim + debris plots (Fig. 3), whereas herbivory on pioneer species increased over time only in trim + no debris plots (Fig. 4). The effects of treatments varied depending upon plant species (Figs. 3 and 4): treatments did not significantly affect herbivory on all species except *M. prasina* or *S. berteriana*.

I observed an outbreak of larvae from one lepidopteran species, the zebra mosaic butterfly (*Colobura dirce*, Nymphalidae), in 2005 and 2006 in trim + no debris plots (Supplementary Appendix, Fig. 1). This caterpillar largely feeds on the common pioneer species *C. schreberiana*, and most of the understory individuals of this plant in these plots were being fed on by at least one *C. dirce* individual. This species is large and showy, creating conspicuous “tents” in which to feed on *C. schreberiana* leaves.

Table 1

Results of fixed factor effects from a mixed generalized linear model analyzing differences in percent of leaf area missing (arcsine-square root transformed for analyses). The model was reduced by removing any interactions with P -values greater than 0.25. Information on replication for each species can be found in Supplementary Tables 1 and 2.

Source	df	F	P
Date	3	75.11	<0.001
Trim	1	0.38	0.85
Debris	1	0.51	0.47
Plant type (plant species)	5	26.99	<0.001
Date $\times$ trim $\times$ debris	10	23.89	<0.001
Date $\times$ debris $\times$ trim $\times$ plant type (plant species)	66	7.73	<0.001
Error	369		

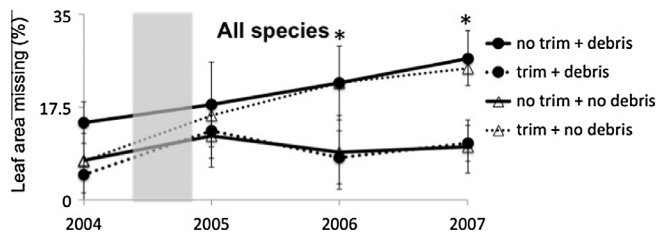


Fig. 2. Average percentage of leaf area missing ($\pm$ SE) across treatments for understory plant species in Luquillo Experimental Forest (Puerto Rico). The treatment period for the canopy trimming experiment (October 2004–June 2005) is in gray. Significant differences between treatments ($P < 0.05$) as determined by a general linear model are marked with *. Replication for each species can be found in [Supplementary Tables 1 and 2](#).

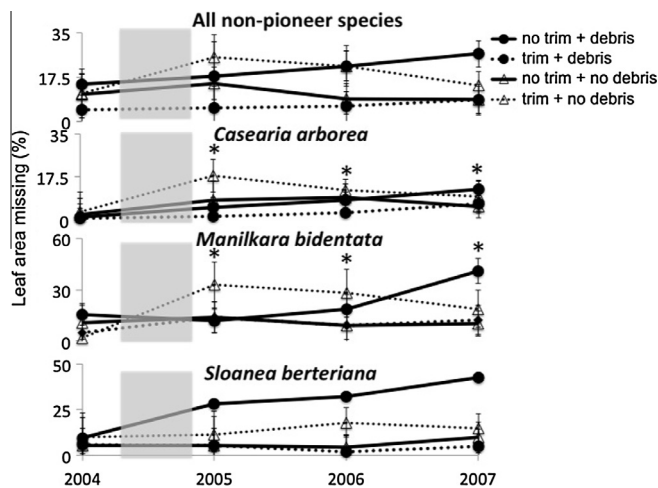


Fig. 3. Average percentage of leaf area missing ($\pm$ SE) of all non-pioneer understory species (top panel), and several non-pioneer understory species separately (bottom 3 panels) in Luquillo Experimental Forest (Puerto Rico). The treatment period for the canopy trimming experiment (October 2004–June 2005) is in gray. Significant differences between treatments ($P < 0.05$) as determined by a general linear model are marked with *. Replication for each species can be found in [Supplementary Tables 1 and 2](#).

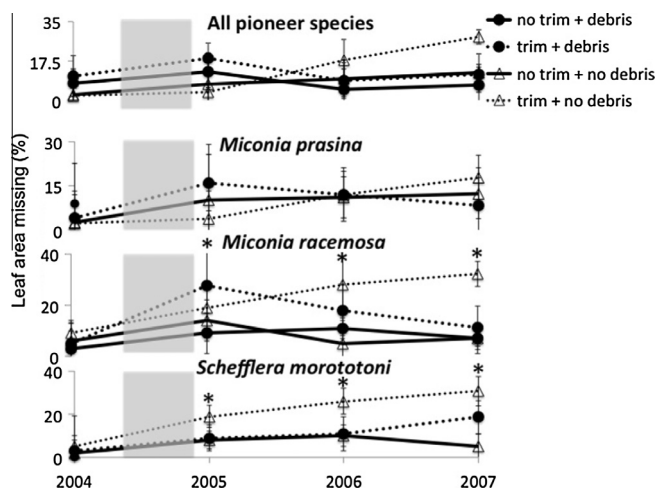


Fig. 4. Average percentage of leaf area missing ($\pm$ SE) of all pioneer understory species (top panel), and several pioneer understory species separately (bottom 3 panels) in Luquillo Experimental Forest (Puerto Rico). The treatment period for the canopy trimming experiment (October 2004–June 2005) is in gray. Significant differences between treatments ($P < 0.05$) as determined by a general linear model are marked with *. Replication for each species can be found in [Supplementary Tables 1 and 2](#).

4. Discussion

Studies examining the effects of hurricanes on herbivory remain relatively rare, and have yielded mixed results (Torres, 1992; Schowalter, 1994; Schowalter and Ganio, 1999; Hunter and Forkner, 1999; Koptur et al., 2002; Spiller and Agrawal, 2003; Angulo-Sandoval et al., 2004; ; Schowalter et al., 2014). I had expected that both canopy trimming and a debris pulse would lead to an increase herbivory rates (H1a) because of greater leaf production (H1b) and leaf quality (H1c), respectively, and that herbivory rates would be highest in plots with both treatments applied (H2). In contrast to my expectations, the independent effects of either a canopy trimming or detrital pulse increased understory herbivory. Surprisingly, the combination of these two treatments had no effect on herbivory rates. These findings may be explained by the finding that pioneer and non-pioneer species responded differently to debris and trimming treatments: herbivory generally was higher on pioneer plants in plots where the canopy had been trimmed but debris had not been added, whereas herbivory was generally higher on non-pioneer plants in plots where the canopy was intact and debris was added to the forest floor.

Although Angulo-Sandoval et al. (2004) documented reductions in understory herbivory after Hurricane Georges, which is opposite to the stimulated herbivory observed in some treatments in my study, they described four possible mechanisms for hurricane effects on understory herbivory that could also be operating in my study: (1) increased production of leaves due to release from light limitation in the understory; (2) changes in leaf chemistry resulting from increased light and nutrient availability due to canopy trimming and the detrital pulse, respectively; (3) altered herbivore community structure and (4) altered predator community structure. I will discuss the potential relevance of these mechanisms separately for pioneer and non-pioneer species.

4.1. Effects on herbivory of pioneer species

All five of the focal pioneer species experienced elevated levels of herbivory in plots where the canopy had been trimmed but debris had not been added (Fig. 4). Although patterns in leaf production did not explain the elevated levels of herbivory on pioneer species in trimmed plots (as determined by non-significant regressions), herbivores on pioneer species may have responded to increased density of pioneer plants in these plots. Trimming increased the density of pioneer plants, including some of the focal species in this study (*M. prasina* and *S. morototoni*), and this positive effect of trimming on plant recruitment was initially suppressed when debris was added (Shiels et al., 2010). This local increase in pioneer plant density could increase herbivory because understory herbivores in tropical forests often prefer the new leaves of woody species of plants (Coley, 1983; Coley and Barone, 1996), and herbivory rates are higher on plant species that are locally at higher densities (Schowalter and Ganio, 1999; Angulo-Sandoval and Aide, 2000b).

Increases in the abundances of certain herbivores that feed on early successional plant species may also help to explain why there were greater levels of herbivory in trim + no debris plots. Outbreaks of 15 herbivorous lepidopteran species occurred shortly after Hurricane Hugo (Torres, 1992), and these species fed almost exclusively on early successional plant species. Certain herbivore species in the canopy also increased in abundance after Hurricane Hugo (Schowalter, 1994; Schowalter and Ganio, 1999). Although I did not quantify the abundance of any herbivores in this study, there was an outbreak of at least one lepidopteran species (*Colobura dirce*) in 2005 and 2006 in trim + no debris plots (Supplemental Appendix, Fig. 1). Additional hypotheses for the observed changes in herbivore community structure require further testing.

Decreased populations of predators that feed upon invertebrate herbivores in trimmed plots may have also contributed to the enhanced herbivory. The density of coqui frogs that prey on all types of invertebrates was strongly reduced when the canopy was trimmed (Klawinski et al., 2014). Understory herbivory rates in this forest are relatively low (Angulo-Sandoval and Aide, 2000a) compared to other tropical forests (Aide, 1993), while predator densities are relatively high. Thus, predators have been hypothesized to have strong, negative effects on herbivory rates in this forest (Angulo-Sandoval and Aide, 2000a, Angulo-Sandoval et al., 2004). This phenomena has been shown in the canopy of this forest (Dial and Roughgarden, 1995), and so a decrease in predators would likely lead to an increase in herbivory.

Changes in leaf chemistry were unfortunately not measured in this study. One previous study, however, documented a decrease in leaf quality for herbivores due to increases leaf defenses (foliar astringency; Hunter and Forkner, 1999) after canopy opening resulting from a hurricane. This finding is not in line with greater quality leaf material as would be expected with increased herbivory as seen in this study. I hypothesize, then, that an increase in the density of pioneer plants and a reduction of predators resulted in an increase of the abundance of herbivore species that eat pioneer plants in trimmed only plots.

4.2. Effects of herbivory of non-pioneer species

Herbivory was generally higher on non-pioneer species in plots where the canopy was intact and debris was added to the forest floor. This finding is likely driven by changes in herbivore community structure resulting from increases in foliar quality. Consistent with my findings, Schowalter et al. (2014) observed that the debris pulse had greater effects on the community structure of canopy arthropods than did the canopy trimming, and that these effects were more prominent on later successional species than early successional species. It was hypothesized that these changes were probably driven by unmeasured alterations increases leaf quality due to increased nutrient availability from the non-senescent litter in the debris pulse (Schowalter et al., 2014). However, Schowalter et al. did not document any changes to a folivore species, or to rates of folivory (Schowalter et al., 2014), so the application of these results of changes in arthropods in the canopy to this study are limited. Litter invertebrate communities were also altered by debris addition: certain groups of litter arthropods (coleopterans, millipedes and isopods) were more abundant in plots with intact canopies and debris addition (Richardson et al., 2010).

The debris pulse did not result in changes in leaf production (results of this study) or in the abundances of coqui frogs, one of the dominant predators of invertebrates in this forest (Klawinski et al., 2014). Thus, although neither was measured in this study, I hypothesize that the elevated herbivory observed in non-pioneer plant species in plots where debris was added is likely due to an increase in foliar quality due to higher levels of nutrients available from the non-senescent litter in the debris pulse, and increases in populations of certain herbivore species that feed on non-pioneer species.

4.3. Effects of treatments compared to natural hurricanes

Although herbivory is generally lower after natural hurricanes, such as Hurricane Hugo (Angulo-Sandoval et al., 2004), in this simulated hurricane, it increased likely due to changes in plant communities and non-lethal effects on the herbivore community. The results of this study suggest the effects of hurricanes on herbivory are dependent on a plant species' successional status. The documented reduction in understory herbivory based mainly on

examination of non-pioneer species (only 2 out of the 8 species examined were pioneer species; Angulo-Sandoval et al., 2004). These differences in the species selection may help to explain why these studies did not have congruent results. Additionally, this experiment did not replicate the lethal, direct effects of hurricanes on herbivorous invertebrates (such as the dislodging individuals by wind or mortality from falling debris) that likely contributed to reduced herbivory (Angulo-Sandoval et al., 2004) and the reduced abundance of several invertebrate herbivores (Willig and Camilo, 1991). Lastly, debris addition to the understory or increases in canopy openness would rarely, if ever, be seen occurring independently of one another in nature.

Pre-treatment levels of herbivory (9.5%) were lower in this study than seen before previous hurricanes at this site (16%; Angulo-Sandoval and Aide, 2000a). Some species of common, large phytophagous species have decreased in abundance in the understory after recent hurricanes and did not return to pre-hurricane levels for 5 years post-hurricane (Willig and Camilo, 1991); these suppressed densities may still persist today (Brokaw et al., 2012). The reduction in pre-treatment herbivory may indicate that understory rates have not fully recovered from relatively recent, intense hurricanes (Hurricane Hugo in 1989 and Hurricane Georges in 1998), and if the frequency of hurricanes affecting this forest continues to increase (Scatena et al., 2012), understory herbivory rates could continue on a declining trajectory.

4.4. Links to forest management

Knowing how herbivory responds to disturbance is important for understanding how forests recover from disturbance events because of the significant role that herbivores play in ecosystem functioning globally (Prather et al., 2013). Herbivory from invertebrates affects forest production (Mattson and Addy, 1975; Ritchie et al., 1998; Prather, 2010), decomposition (Chapman et al., 2003; Fonte and Schowalter 2005; Prather 2010), and related nutrient cycling (Ritchie et al., 1998; Stadler et al., 2001; Lovett et al., 2002; Prather, 2010; Schowalter et al., 2011). Herbivory also affects plant community structure through selective feeding by herbivores (Feeley and Terborgh, 2005; Prather 2010), which could tip the balance toward different successional trajectories (Brown, 1985; Mills, 1986; Davidson, 1993; Gandhi and Herms, 2010). Thus, an understanding of alterations to herbivory when a forest is disturbed is crucial to managing forests, especially when managing for particular regeneration or restoration goals after anthropogenic or natural disturbances.

5. Conclusions

The effects of debris addition and canopy opening on understory herbivory in this forest were dependent upon the life history characteristics of the plant species (i.e., whether it is pioneer or non-pioneer). The increase of herbivory in trimmed + no debris plots may in part result from increased density of pioneer plants and a reduction of predators causing a higher abundance of herbivore species that eat pioneer plants. The stimulated herbivory seen in non-pioneer species in plots with intact canopies and where debris was added is likely due to an increase in foliar quality, and increases in the populations of certain herbivore species that feed on non-pioneer species. Future studies might test the potential mechanisms for the increase in herbivory on pioneer and non-pioneer species operating after natural hurricanes by combinations of smaller-scale greenhouse and field mesocosm experiments that manipulate factors likely related to changes in herbivory seen in this experiment (e.g. herbivore feeding choice and performance experiments on pioneer and non-pioneer plants grown with and without increased litter).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.06.040>.

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