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ARTICLE

Special Feature: Tropical Forest Responses to Repeated Large-scale Experimental Hurricane Effects

Disturbance reduces fungal white-rot litter mat cover in a wet subtropical forest

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Abstract

Fungi that bind leaf litter into mats and produce white-rot via degradation of lignin and other aromatic compounds influence forest nutrient cycling and soil fertility. Extent of white-rot litter mats formed by basidiomycete fungi in Puerto Rico decreased in response to disturbances—a simulated hurricane treatment executed by canopy trimming and debris addition in 2014, a drought in 2015, a treefall, and two hurricanes 10 days apart in September 2017. Percent fungal litter mat cover ranged from 0.4% after Hurricanes Irma and Maria to a high of 53% in forest with undisturbed canopy prior to the 2017 hurricanes, with means mostly between 10% and 45% of fungal litter mat cover in undisturbed forest. Drought decreased litter mat cover in both treatments, except in one control plot dominated by a drought-resistant fungus, *Marasmius crinis-equi*. Percent fungal litter mat cover sharply declined after hurricanes, a treefall, and a simulated hurricane treatment. Solar radiation was significantly inversely correlated with relative humidity (RH) and percent litter mat cover within each of the four climatic seasons. Solar radiation was also directly correlated with prior month litterfall, while RH was moderately correlated with throughfall, rain, and litter wetness. However, rainfall was inversely correlated with litter mat cover, possibly due to erosion or saturation during high rainfall events. Canopy opening reduced leaf fall and litter mat cover but these variables were not correlated except in winter. The main factor inhibiting basidiomycete fungi that bind leaf litter into mats was likely lower litter moisture associated with drought and increased solar radiation from canopy opening but secondary compounds in green litterfall may have contributed. Although higher litterfall likely increases fungal mat cover under closed canopy, changes in environmental factors apparently had a stronger inhibitory effect following canopy disturbances. Drought tolerance of some basidiomycete fungal litter mat species provided some resilience to drought.

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KEYWORDS

drought, forest canopy opening, hurricanes, hurricane disturbance, leaf litter decomposition, litter mats, litter wetness, litterfall, resilience, tropical cyclones, solar radiation, Special Feature: Tropical Forest Responses to Repeated Large-scale Experimental Hurricane Effects, tropical forest, white-rot

INTRODUCTION

Differences between white- and brown-rot fungal decomposers have received increasing attention because the products of white- and brown-rot differ, and this has implications for both forest productivity and carbon sequestration (Bai et al., 2017; Osono, 2007). In contrast to brown-rot fungi that are restricted to degrading labile substrates such as cellulose, starch, and sugars, white-rot fungi can degrade acid unhydrolyzable residues (AUR) comprising lignin, lignocellulose, and other aromatic or polyphenolic substances such as cutin, tannin, and humic acids, in addition to using more labile carbon substrates for energy (Klotzbücher et al., 2011; Osono, 2007; Osono et al., 2021). Studies on the effects of white-rot litter decomposers on underlying forest soil, and differential growth stimulation of tree seedlings date back to Hintikka's (1970) work in boreal forest of Finland. Hintikka (1970) observed that humus in patches of litter bleached by white-rot fungi in Finland had different properties from surrounding mor or moder humus, including higher content of readily soluble phosphorus (P) and both available and total nitrogen (N). Further, Hintikka (1970) showed that birch seedlings grew faster in perfusion apparatus containing white-rot litter than those with non-white-rot litter. While Hintikka's (1970) experiment suggested greater soil fertility under white-rot litter decomposers, his experimental design was confounded by the fact that mass loss in litter is accelerated by white-rot (Hintikka, 1970; Lodge et al., 2008; Osono, 2006); faster decomposition could have led to faster nutrient mineralization (Hintikka, 1970).

Ecology of forest litter decomposer basidiomycete fungi has been studied in boreal (Berg & Staff, 1980; Hintikka, 1970; Lindahl & Boberg, 2008), temperate (Frankland et al., 1995; Klotzbücher et al., 2011; Osono, 2006; Osono & Takeda, 2001; Schneider et al., 2012), and tropical forests (Lodge et al., 2008, 2014; Lodge & Asbury, 1988; Osono, 2006; Torres et al., 2005), and colonization of leaves occurred early, late, or in all stages of decomposition depending on carbon to nutrient ratios. Rates of decomposition by a wide range of fungi from boreal to tropical forests varied depending on nutrient availability, substrate quality, and fungal identity (Osono, 2020; Osono et al., 2021). Decomposer agaric fungi (Basidiomycota) in subtropical wet

forest in Puerto Rico were found to colonize abscised leaves with low P concentrations beginning immediately upon reaching the forest floor during the wet season (Lodge et al., 2008; Lodge & Asbury, 1988).

White-rot fungi can be classified as either unit restricted (also known as component-restricted, that is, confined to a single piece of substratum) or unit unrestricted (Osono, 2007). Unit-unrestricted white-rot fungi have effects on ecosystem processes beyond those associated with their rates of decomposition and products, specifically the ability to physically bind litter thereby reducing erosion on steep slopes (Lodge et al., 2008; Lodge & Asbury, 1988), the storage and transfer of limiting nutrients within the litter layer (Lindahl & Boberg, 2008; Lodge et al., 2014), and pulsed release of stored nutrients from litter to soil in response to drying and rewetting cycles (Lodge et al., 1994, 2014). The ability of decomposer basidiomycete fungi to accumulate P in tropical forest leaf litter in Puerto Rico and use it to rapidly colonize and build biomass in freshly fallen leaves that have little P was inferred to contribute to 15%–22% faster rates of decomposition as compared to decomposition by other non-white-rot fungi (Lodge et al., 2008). The amount of P increase in litter was proportional to the number of fungal connections between litter cohorts in Puerto Rico (Lodge et al., 2014).

Litter-binding basidiomycete decomposer fungi were shown to significantly slow the export of leaf litter from steep forest slopes and also protect the underlying soil from erosion caused by rain impact in Puerto Rico (Lodge et al., 2008; Lodge & Asbury, 1988). Despite the importance of litter decomposer basidiomycete fungi in maintaining ecosystem functions, little is known about the extent of non-unit-restricted litter decomposers in tropics (Osono, 2006). A study in subtropical forest by Osono et al. (2021) showed that the unit-restricted ascomycete fungi that bleach litter caused slower mass loss and degraded a selective subset of AUR compared to basidiomycetes. As noted by Osono (2007) in his review of the fate of lignin in decomposing litter, information on the occurrence of bleached litter and humus in nature is still limited, especially in tropical forests, and more studies are needed on the occurrence of bleached litter and humus in nature.

Given the importance of white-rot litter decomposers to nutrient cycling and erosion control at our subtropical

wet forest site in Puerto Rico, we conducted the research reported here on basidiomycete white-rot litter mats to document the extent and response of fungal leaf litter mats to disturbance. Wet forest tropical decomposer basidiomycetes in forest floor litter were found to be sensitive to drying and are thought to depend on a steady supply of fresh leaf litter. Lodge et al. (2008) found that few litter-binding basidiomycete fungi could tolerate high solar radiation and associated drying. The absence of fungal litter mats was previously observed at our site near canopy gaps and hypothesized to be caused by drying (Lodge & Asbury, 1988). This was confirmed in an experiment conducted at our site using litter mats divided in half and placed in either full or partial shade which showed two of the four most drought-tolerant basidiomycete species tested formed significantly fewer attachments to freshly fallen leaves (Lodge et al., 2008). Drying induced by opening the forest canopy was also hypothesized to contribute to a reduction in decomposer fungal root-like structures connecting leaf litter layers following a Canopy Trimming Experiment (CTE) of the Luquillo Long-Term Experimental Research Program (Lodge et al., 2014). Using the second iteration of the CTE initiated in 2014, we measured percent fungal litter mat cover quarterly for 4 years (more frequently during the 2015 drought) beginning before canopy trimming treatment was applied in October 2014 and quarterly thereafter until January 2018. Treatments in the second iteration of CTE were reduced from the original four (canopy trimming and debris addition in all combinations; Shiels et al., 2015) to two: simulated hurricane (canopy trimming with debris added to the forest floor, referred to here as trim + debris) and no-trim (referred to here as the control). In addition to the applied treatments of the CTE, natural disturbance events occurred during the measurement period. An El Niño phase of the ENSO cycle induced a drought that began in March 2015, 3 months after the canopy trimming treatments were applied, and lasted through October of that year. Tropical storm Erika (27 August 2015), a large treefall in the block C control plot, and Hurricanes Irma and Maria (7 and 20 September 2017, respectively) also occurred during the measurement period. We analyzed changes in fungal leaf litter mat cover in relation to the simulated hurricane treatments, natural drought, variation in litterfall inputs, and tropical cyclones. Litterfall is used to measure primary productivity, and it is especially useful in broad-leaved evergreen forests (Bellot et al., 1992; Vitousek, 1982) such as our site. Furthermore, leaf litterfall is the most relevant component of primary production to this study as it is the source of energy and nutrients for leaf decomposer fungi. We further analyzed percent basidiomycete litter mat cover with climate data (relative humidity (RH), throughfall volume,

solar radiation, litter wetness) in addition to litterfall mass. We hypothesized that disturbances that open the forest canopy, either by trimming or natural hurricanes, would reduce fungal litter mat cover via increased solar radiation and decreased humidity and subsequent litterfall, and that drought would similarly reduce litter mat cover.

MATERIALS AND METHODS

Description of the study site

The CTE was established in the El Verde Research Area of the Luquillo Experimental Forest of Puerto Rico (18°20'N, 65°49'W), in three complete replicated blocks on ridges and upper slopes around 350 m elevation. The site is classified as subtropical wet forest in the Holdridge System—an evergreen broad-leaved forest with moderate seasonal variation in rainfall (Ewel & Whitmore, 1973). Mean annual rainfall is 3600 mm and mean annual temperature is 21–25°C (LTER climate data: 11 April 2015; <http://luq.lternet.edu/data/datacatalog>). Soils are classified as ultisols in the Humatus-Cristal-Zarzal series. The most common trees at the site are *Dacryodes excelsa* (Burseraceae), *Prestoea acuminata* var. *montana* (syn. *Prestoea montana*; Arecaceae), *Sloanea berteriana* (Elaeocarpaceae), and *Manilkara bidentata* (Sapotaceae; Shiels et al., 2010).

Treatments

Plots were treated in 30 × 30 m areas with inner 20 × 20 m measurement cores. The measurement area was divided into 16 5 × 5 m subplots, with subplots assigned to particular suites of measurements in a stratified random design to ensure plot coverage. The experiment was designed to disentangle the separate and combined main effects of hurricanes, opening of the canopy and deposition of green leaves and wood on the forest floor. The objective was to determine population and ecosystem responses to increases in frequency of hurricane-like disturbances above background levels (Shiels et al., 2015; Shiels & González, 2014). The original four treatment combinations (a factorial design, with and without canopy trimming and with or without debris addition) were applied from November 2004 through June 2005 (Shiels et al., 2015; Shiels & González, 2014). All non-palm trees that were >15 cm dbh had branches that were <10 cm diameter removed above 3 m height, and palms had their fronds removed. For all non-palm trees 10–15 cm dbh, each tree was trimmed to 3 m height. Debris and wood mass additions were adjusted to

resemble those of Hurricane Hugo which struck the site in 1989. In the second iteration of the CTE, only the trim + debris addition treatment (herein referred to as trim, trimmed, canopy trimming, or Trim + debris) was reapplied from November to December 2014. Only the trim + debris and the no-trim + no debris (control) were monitored intensively through January 2018 including the study described here.

A large treefall occurred in the control plot of block C during the first 2 weeks of June 2016. We observed the treefall when taking quarterly litter mat measurements in early July 2016, as described below.

Measurements

A pre-trim method calibration was conducted using all five designated soil process subplots per plot in June 2014. Based on variance among subplots and the amount of time needed to measure each plot, three of the five subplots designated for soil and litter measurements were subsequently selected based on their proximity to lysimeters. Four parallel 5-m long transect lines were examined for litter mat extent per subplot (beginning 1 m from and parallel to one of the plot edges, and spaced 1 m apart). Length of fungal white-rot litter mats was measured by gently pulling on leaves to determine if they were attached to other leaves and recording the beginning and end of each mat along a meter tape that was used for the transect line. Identity of basidiomes or rhizomorphs was recorded, if present. Sum length (m) of fungal litter mats in each subplot was divided by the 5 m length of each transect line and multiplied by 100 to obtain percent fungal litter mat cover. Mean % litter mat cover was calculated from the four transects in each subplot, and the mean of means and standard error of the mean of means were calculated based on the mean % litter mat cover in the three subplots and graphed.

Litterfall was collected every 2 weeks. The litterfall mass data reported here for each plot represent 1 month of leaf litterfall (g/m^2) prior to litter mat measurement and are comprised of two collections taken 2 weeks apart and ending within 6 days of litter mat measurement date. The 1-month-prior-litterfall cohort was selected because recently fallen leaves are differentially colonized by white-rot fungi at our site. A previous experiment showed reduced fungal attachment of leaves placed on litter mats if leaves were preconditioned to non-white-rot fungi in the forest for more than 2 months (S. Bibbo & D. J. Lodge, personal observation). Total litterfall was collected from 10 baskets, located in a stratified random design (to ensure plot coverage) inside the inner 20×20 m measurement portion of each plot. Baskets were $0.43 \text{ m} \times 0.43 \text{ m}$, and

1 m from the ground (1.85 m^2 total area per plot). The litter was pooled among baskets within plots, oven-dried for at least 2 weeks (to constant weight) at 40°C , then sorted into leaves, wood, reproductive parts (flowers, fruits, and seeds), and miscellaneous material (unidentifiable plant parts, bark, lichens, etc.) and weighed. Only leaf litter mass was used for these analyses as it is the main component of litter mats, basidiomycete fungal decomposers of leaf litter at the site are restricted to leaves and twigs (Lodge, 1993), and leaf litterfall is less variable than other components of litterfall.

Climate variables were throughfall (collected every 2 weeks), and automatic sensor data for rainfall (mm/h, in trim + debris plots only), mean temperature ($^\circ\text{C}$), mean RH, mean solar radiation (W/m^2), and leaf wetness as litter saturation (González et al., 2019). Mean leaf litter saturation fraction (LWmV) was measured by leaf-shaped dielectric leaf wetness sensors (Decagon Devices, Inc.) placed in the litter layer. Placement was made after the trimming treatment. Three sensors were placed, one in each of the three subplots used for fungal litter mat measurements. Data from the automatic sensors were one (daily average of 30-min intervals) measurement at each of the three control and three treatment sites, which we summarize into one 2-week average measurement for the six sites for the 2 weeks prior to litter mat measurement at that site (González & Van Beusekom, 2021).

Statistical analyses

Neither percent fungal leaf litter mat cover nor the microclimate data were normally distributed, precluding the use of analysis of covariance with repeated measures for this longitudinal dataset (Gibbons & Chakraborti, 2014; Ma et al., 2012). We therefore selected generalized estimating equations (GEE; Liang & Zeger, 1986) which are not sensitive to these normality violations. Data were collected in association with two pretreatment samplings (June and October 2014, except leaf litter saturation) and 11 post-treatment dates. GEE models were fit for each of the eight observation datasets. The fungal litter mat observations and leaf litterfall weights (models 1–2) were used to fit Gamma generalized linear models (GLMs) with an inverse link because the data are skewed with many small values and fewer large values. Fungal litter mat cover percentages were used as raw data with an offset of the transect length. Predictor variables were time by days (t) and treatment (T) (a categorical variable with 1 as treatment and 0 as control). The GEE correlation structure was set as autoregressive (depending on the previous observations at the same site).

The GLM part of the Gamma models can be written as (E) expected count, divided by total number with three fitted coefficients, b_0 , b_1_{time} , b_2_{treat} , and $b_3_{timetreat}$, or

$$1/E = b_0 + b_1_{time} \times t + b_2_{treat} \times T + b_3_{timetreat} \times t \times T.$$

A Gaussian GLM model with an identity link was used for plot-based climate observations (models 3–8)

$$E = b_0 + b_1_{time} \times t + b_2_{treat} \times T + b_3_{timetreat} \times t \times T.$$

Wald tests were used to determine which explanatory variables in a model were significant; specifically,

$b_3_{timetreat}$ was examined to determine if there was a significant ($p < 0.05$) time by treatment interaction on percent litter mat cover. Correlations between each of the eight observation types were tested for significance at $p < 0.05$ (average observation by site by day, so six observations times 16 time points). The data were prewhitened (first-differenced and detrended) to remove autocorrelation and seasonality. Then the presence of monotonic relationships between the variables was calculated using the nonparametric Spearman's rank correlation (Gibbons & Chakraborti, 2014). Mann-Whitney U one-sided tests (nonparametric one-sided analysis of variance for two samples, null hypothesis that the two samples do not differ in location versus the alternative that they differ in location, -1 Treatment < Control; $+1$ Treatment > Control)

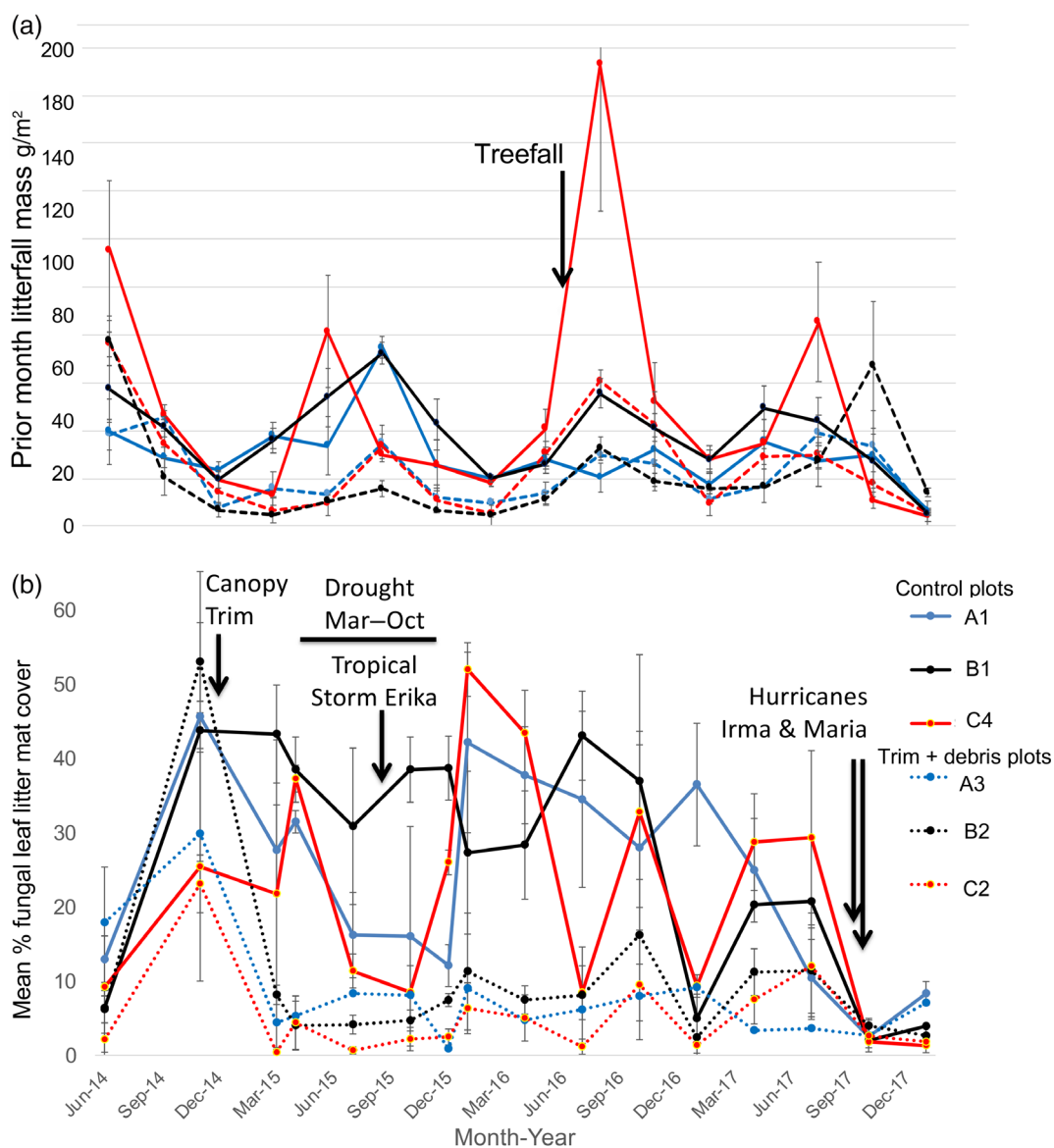


FIGURE 1 (a) Litterfall mass in the month prior to fungal litter mat measurement. (b) Percent basidiomycete fungal leaf litter mat cover in treatment (canopy trim + debris) versus control plots at El Verde, Puerto Rico, from June 2014 to January 2018. Data shown are plot means of subplot means and SD of means

were used on each of the eight variables at each of the 16 sampling times (Mann & Whitney, 1947).

RESULTS

Percent fungal leaf litter mat cover showed a significant reduction in response to the canopy trimming treatment ($b2_{treat} = 0.187$ for Equation (1); Figure 1, Table 1). In addition, there was a significant negative treatment by time interaction ($b3_{timetreat} = -0.0001$) because the effect of treatment decreased over time (Figure 1b, Table 1). The

prior month leaf litterfall weight model (Table 1) showed a significant treatment effect, with less litterfall mass following the canopy trimming treatment than observed in the control (Figure 1, Table 2). Humidity and solar radiation (Figures 2 and 3, Table 1) had significant treatment effects. Humidity decreased and solar radiation increased in trimmed plots relative to control (Figures 2 and 3, Table 2). In addition, solar radiation also had a significant treatment by time interaction of the opposite sign, consistent with a decrease in solar radiation in the trim plots over time (Table 1, $b3_{timetreat} = -0.0618$; Table 2, Figure 3). Relative humidity decreased, whereas solar

TABLE 1 Significant ($p < 0.05$) positive and negative (+/−) treatments and treatment by time interaction effects on % fungal litter mat cover, monthly leaf litterfall mass, and microclimate variables from model tests

Effect	Percentage fungal mat cover ^a	Litterfall ^{a,b}	Temperature	Relative humidity ^c	Solar radiation ^c	Throughfall ^c	Litter wetness ^c
$b2$, canopy treatment	−	−		−	+		
$b3$, treatment × time interaction	+				−		
Time effect per day					+	+	+

Notes: Direction of effects (+/−) is shown only for significant values ($p < 0.05$). Climate variables were means of measurements over 30-min intervals in the prior 2 weeks (González et al., 2021).

^aGamma model used.

^bLitterfall mass in preceding month (g/m^2).

^cGaussian model used.

TABLE 2 Mann–Whitney U tests for pairwise comparisons of canopy treatments for each variable (columns) at each of 16 sample times (rows)

Days after trim	Percentage fungal mat cover	Leaf litterfall ^a	Temperature	Relative humidity	Solar radiation	Throughfall	Litter wetness
−172	+		NA	NA	NA		NA
−23			NA	NA	NA		NA
92	−	−		−	+	+	+
119	−	−		−	+	+	+
213	−	−		−	+		
303	−	−			+		
366	−	−			+		
407	−						
497	−				+		
579	−				+		
668	−	−			+		
776	−	−					
858	−	−			+		
969	−						
(34) 1054		+					
(129) 1148							−

Notes: Days prior to canopy trimming are shown as negative values while days in parentheses are number of days after hurricane Maria.

^aPrior month leaf litterfall mass (g/m^2).

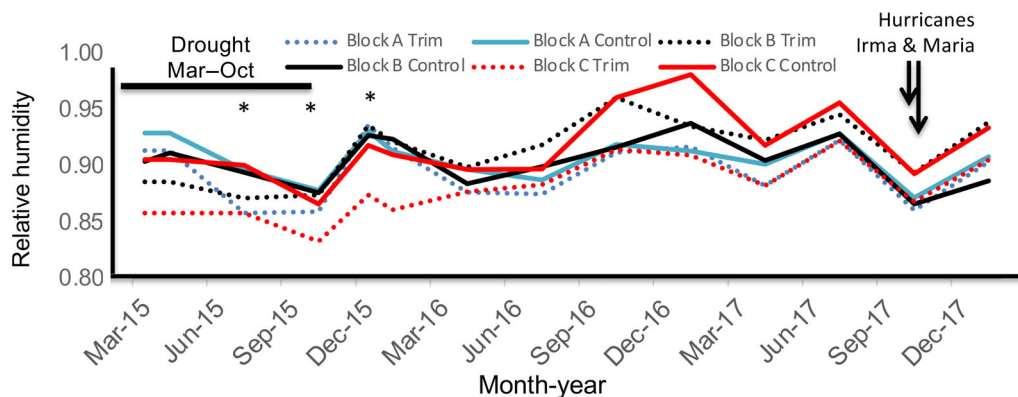


FIGURE 2 Changes in relative humidity (RH) over time in plots with trimmed canopy (dashed lines) and untrimmed (control) plots (solid lines). Asterisks mark sampling dates when RH differed significantly between canopy treatments at $p < 0.05$ according to Mann–Whitney U tests

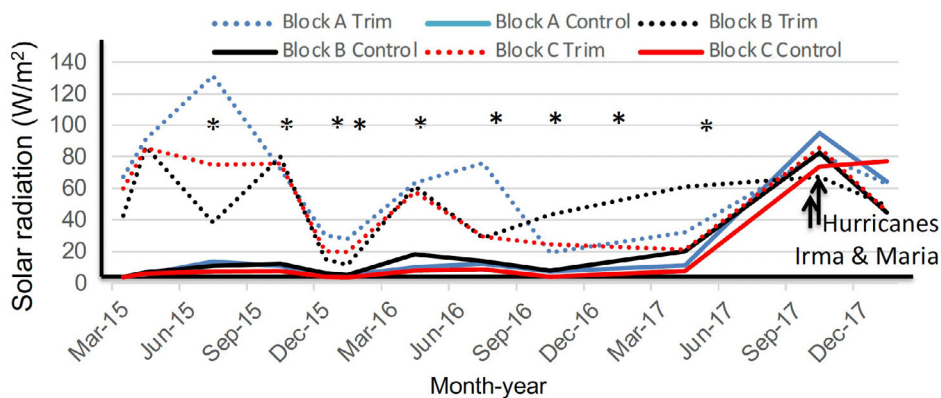


FIGURE 3 Changes in solar radiation over time in plots with trimmed canopy (dashed lines) and untrimmed (control) plots (solid lines). Asterisks mark dates when solar radiation differed significantly between canopy treatments at $p < 0.05$ according to Mann–Whitney U tests

radiation, throughfall, and litter wetness all increased in response to canopy trimming for two or more samplings after treatment (Table 2).

Percent fungal litter mat cover was significantly higher in the trimmed than in control plots during the June 2014 pretreatment measurement, and there were no differences between treatments 1 week prior to trimming (Table 2). Treatment had a significant negative effect on fungal leaf litter mat cover from March 2015 through July 2017 (Figure 1b, Table 2). Percent fungal litter mat cover was only correlated with rainfall after prewhitening to remove seasonal variation, and the relationship was negative rather than the expected positive (Table 3). Nevertheless, solar radiation, which showed a significant treatment effect, was strongly negatively correlated (-0.66 to -0.85) with %litter mat cover within each of the four seasons when data for the two treatments were pooled (Tables 4 and 5, Figure 4). Solar radiation was

inversely correlated with RH and moderately positively correlated with temperature and leaf litterfall in the prior month (Spearman's Rank correlations, $p < 0.05$; Table 3).

An El Niño phase of the Southern Oscillation (ENSO) induced a drought from March to October of 2015 (Figures 1 and 2). Relative humidity was significantly lower in the canopy trimming than in the control treatment when litter mats were measured in April, July, and October of 2015, coinciding with the drought (Figure 2), but no differences in RH were detected afterward. Throughfall was higher in the canopy trimming treatment than in the control plots in April and July of 2015, but not different thereafter (Table 2). Percent fungal litter mat cover decreased in both treatments during the drought from July to October 2015 and differences between treatments remained significant even though the control plot in block B did not show a marked decline, in contrast to the other two blocks (Figure 1b).

TABLE 3 Cross-correlations between variables after removing seasonal variation by prewhitening

Variable	Percentage mat cover	Leaf litterfall	Temperature	Relative humidity	Solar radiation	Throughfall	Rain	Litter wetness
Percentage mat cover	1.000						−0.4942	
Leaf litterfall		1.000	0.6249	−0.5565	0.4036			
Temperature			1.000	−0.4645	0.3914			
Relative humidity				1.000	−0.6694	0.3216	0.4827	0.321
Solar radiation					1.000			
Throughfall						1.000	0.722	
Rain							1.000	
Litter wetness								1.000

Notes: Spearman's rank correlations are given only for those significant at $p < 0.05$. Data from June 2014 (6 months before canopy trimming) to January 2018 (3 months after hurricane Maria) were included. Below diagonal values are the same as those above the diagonal and are not shown.

TABLE 4 Cross-correlations between variables in winter (above the diagonal) and spring (below the diagonal)

Variable	Percentage mat cover	Leaf litterfall ^a	Temperature	Relative humidity	Solar radiation	Throughfall	Rain	Litter wetness
Percentage mat cover	1.000	0.662	−0.632		−0.852		0.714	
Leaf Litterfall		1.000	−0.659		−0.852		0.577	
Temperature			1.000	−0.588	0.819		−0.841	
Relative humidity	0.669			1.000				
Solar radiation	−0.833	−0.618		−0.682	1.000		−0.742	
Throughfall						1.000		
Rain				0.492			1.000	
Litter wetness								1.000

Note: Spearman's rank correlations are shown only if significant ($p < 0.05$).

^aPrevious month leaf litterfall mass (g/m^2).

TABLE 5 Cross-correlations between variables in summer (above the diagonal) and fall (below the diagonal)

Variable	Percentage mat cover	Leaf litterfall ^a	Temperature	Relative humidity	Solar radiation	Throughfall	Rain	Litter wetness
Percentage mat cover	1.000				−0.665			
Leaf litterfall		1.000	−0.76	0.61	−0.685			
Temperature	−0.483	0.490	1.000		0.565			
Relative humidity	0.524	−0.515	−0.845	1.000	−0.543		0.575	
Solar radiation	−0.853		0.624	−0.600	1.000			
Throughfall						1.000	0.886	
Rain						0.525	1.000	
Litter wetness						0.738		1.000

Note: Spearman's rank correlations are shown only if significant ($p < 0.05$).

^aPrevious month leaf litterfall mass (g/m^2).

By January to summer of 2017, fungal leaf litter mat cover and litterfall in the trimmed plots was converging toward that of the control plots (Figure 1a,b), but

differences remained significant between treatments (Table 2). Percent fungal litter mat cover in control plots in summer and fall did not appear to differ significantly

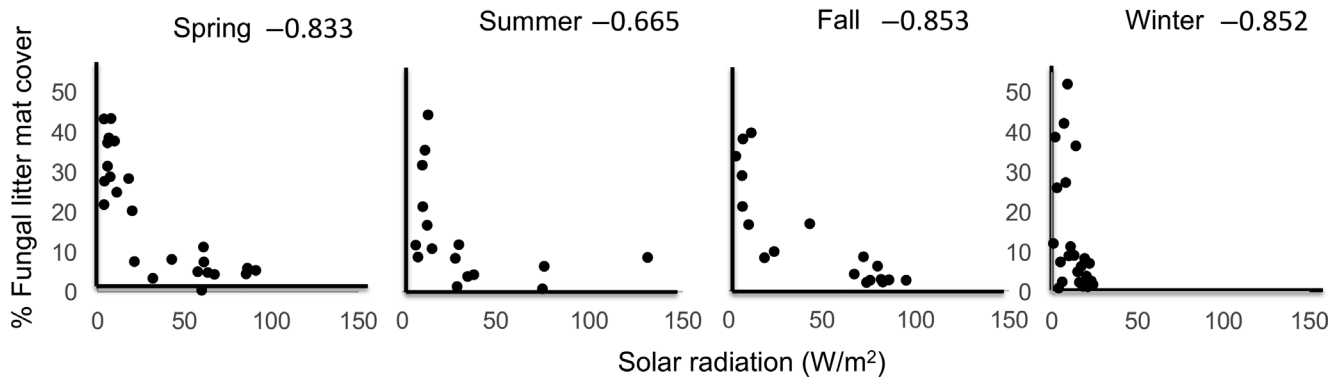


FIGURE 4 Percent fungal litter mat cover versus solar radiation for each sample date and plot, separated by season over the 4-year study. Nonparametric Spearman's rank correlation coefficients are shown ($p < 0.05$)

among years, including the 2015 drought year. The impacts of Hurricanes Irma and Maria 10 days apart in September of 2017, however, was followed by very low levels (0.26%–4%) of % fungal litter mat cover in October 2017 and January 2018 (1.8%–8.4%; Figure 1b).

After detrending to remove seasonal variation and pooling treatments, the only variable significantly correlated with % fungal litter mat cover at $p < 0.05$ was precipitation, with rainfall inversely correlated with fungal litter mat cover (Table 3). As noted above, however, solar radiation was strongly inversely correlated with %fungal litter mat cover within each of the four seasons (Tables 4 and 5, Figure 4). The standardized principal components analysis (PCA) showed that 61% of the variation was explained by the variables, of which 35.3% (axis 1) largely separated observations from the control and trimmed canopy treatments (Figure 5a). Observations from trimmed plots had low cover by fungal litter mats and high solar radiation and low leaf litterfall, whereas control plots had mostly high fungal litter mat cover, low solar radiation, and higher RH. PCA axis 2 separated observations primarily on litter wetness (% saturation) and throughfall, and partially with RH (Figure 5b). A notable feature is a cluster of points in the lower left quadrant that have intermediate % cover by fungal litter mats and at the same time, high litter wetness, throughfall, and RH. The few control treatment points in the lower right quadrant with low % fungal litter mat cover and high throughfall and litter wetness represent post-hurricane (Irma and Maria) observations in October 2017. Solar radiation and leaf litterfall mass in the preceding month are almost completely aligned along axis 1 of the PCA, even though the Spearman's rank correlation coefficient for these two variables was only 0.40 (Figure 5a, Table 3). Among the control plots, a treefall caused a significantly higher peak in litterfall in block C during summer of 2016, concurrent with a significant decline in percent fungal litter mat cover relative to the

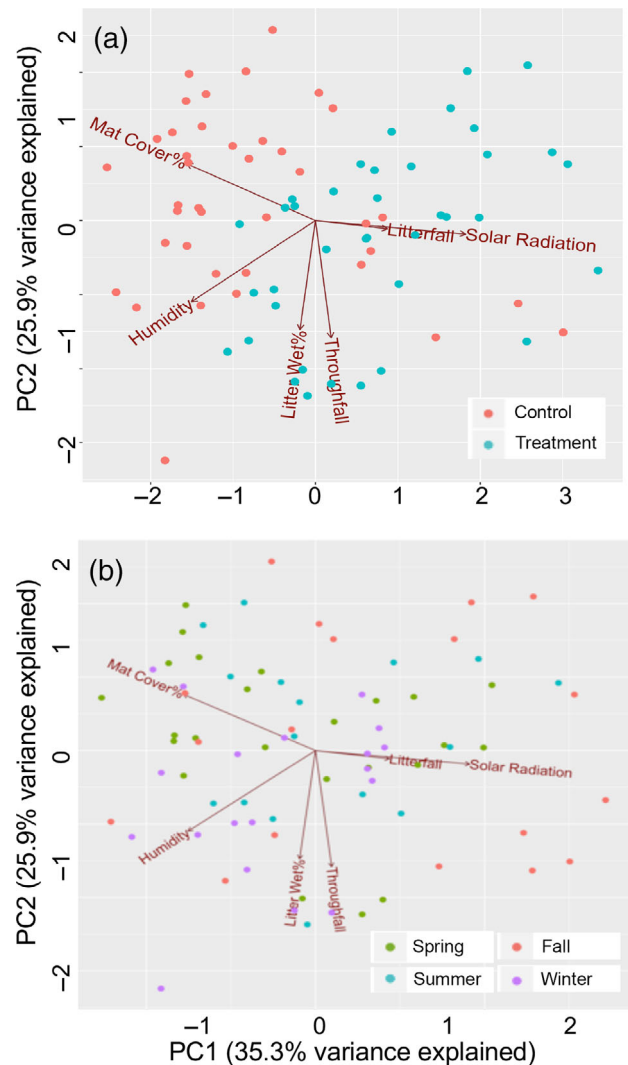


FIGURE 5 Axes 1 and 2 from standardized principal components analysis (PCA) of % fungal litter mat cover in relation to leaf litterfall mass in prior month and climate variables in prior 2 weeks: Relative humidity (RH); litter wetness (%); mean throughfall (ml); and solar radiation (SR). (a) PCA axes 1 and 2, by treatment (trimmed canopy vs. control). (b) PCA axes 1 and 2, by season

other two blocks (Figures 1a,b). The 2-week litterfall collected from that plot on 16 June was 215 g/m² versus 33 and 53 g in control plots of blocks A and B, respectively. Litterfall in the control treatment of block C remained exceptionally high in the next collection on 30 June (258 vs. 26 and 37 g/m² in the other two blocks). Seasonal patterns were not evident for any of the variables in the PCA (Figure 5).

DISCUSSION

Percent fungal litter mat cover in this study ranged from 0.4% after Hurricanes Irma and Maria to a high of 53% in forest with undisturbed canopy prior to the 2017 hurricanes, with means mostly between 10% and 45% in undisturbed forest. These values are in the same range but somewhat higher than in tropical forest of Japan (Osono, 2006; 17.4%), but much higher than those reported from temperate and boreal forests. Bleached humus produced by component-unrestricted basidiomycetes covered 0.4%–11.3% of the total area of the forest floor in boreal forests in Finland (Hintikka, 1970) and temperate broad-leaved forest in Japan (Osono, 2006; 9.8%). The high foliar content of lignin-like polyphenol and lignocellulose content and low concentrations of P found in many tropical forests is likely related to the high abundance of unit-unrestricted white-rot litter mats because types of fungal decay and nutrient translocation during leaf decomposition are influenced by stoichiometry of C:N:P (Klotzbücher et al., 2011; Lodge et al., 2014; Luizão et al., 1998; Osono, 2007).

Does canopy opening reduce percent fungal litter mat cover?

The canopy trimming with debris deposition partial hurricane simulation treatment had a significant negative effect on percent fungal litter mat cover lasting 3 years. Although there was a significant time by treatment interaction, and fungal litter mat cover was converging between treatments in 2017, differences between the trimmed and control treatments remained significant through summer of that year. The time by treatment interaction detected by the GEE model may have been influenced by the hurricane-induced convergence in percent litter mat cover in October 2017. Percent litter mat cover subsequently diverged slightly but not significantly between treatments when measured again after Hurricane Maria in January 2018.

The reduction in percent of the forest floor cover by basidiomycete litter mats in response to canopy opening

resulting from trimming as well as Hurricanes Irma and Maria, and a large treefall gap is consistent with a previous study during the first iteration of the CTE. The results of the previous CTE treatment showed reduced numbers of fungal connections between litter cohorts in response to canopy opening (hyphal strands, cords, and rhizomorphs; Lodge et al., 2014). The previous study also showed reductions in P translocation into the freshly fallen leaf cohort in treatments with canopy trimming, and reduced P content accumulation was correlated with reductions in fungal connectivity between litter cohorts (Lodge et al., 2014).

The impacts of Hurricanes Irma and Maria 10 days apart in September 2017 was similar to the effect of a simulated hurricane treatment (canopy trimming with debris deposition) in the second iteration of the CTE initiated in November–December 2014. The real and the simulated hurricane treatment as well as a large treefall in the control plot of block C induced sharp declines in percent fungal litter mat cover. The slow recovery of fungal litter mat cover in the trimmed plots in this study, which was still significantly below that of control plots after 3 years, might be attributable to drying effects of increased solar radiation and reduced leaf litterfall inputs. The opening of the canopy in the previous iteration of the CTE was associated with decreased litter moisture, rates of litterfall, fungal connectivity in the litter—a measure of unit-unrestricted fungi—and an increase in fungivorous invertebrates that prefer to feed on microfungi rather than Basidiomycota (Richardson et al., 2010; Shiels et al., 2015; Silver et al., 2014). Furthermore, another study at our site found significantly lower rates of attachment to freshly fallen leaves that were placed on replicate (divided and relocated) fungal litter mats placed in partial than those placed in full shade for two of the drought-tolerant basidiomycete fungi tested (Lodge et al., 2008). In that study, the partial shade plots had triple the evaporative potential of the full shade plots; it is likely that the fungal response to solar radiation is largely mediated by evaporation from the litter layer but might also be influenced indirectly by changes in litter arthropod density and diversity in response to UV radiation (Huang et al., 2020). In CTE1, Richardson et al. (2010) found changes in fungivorous arthropod composition in litter were associated with canopy opening. An interesting cluster of points in the lower left quadrant of the PCA representing trimmed plots suggests that moderate levels of fungal litter mat cover were contingent upon higher levels of RH and lower solar radiation, likely observations from subplots located near the plot border that were partly shaded by the surrounding forest.

Do high solar radiation and low humidity reduce fungal litter mat cover?

Solar radiation increased significantly in the trimmed plots and was strongly inversely correlated with percent litter mat cover within each of the four seasons and also the first axis of the PCA. Solar radiation is an indication of moisture as it was strongly inversely correlated with RH. Litter fungi in wet tropical forest in Puerto Rico were previously shown to be sensitive to drying (Lodge, 1993; Lodge et al., 2008). At the same site as this study, fungal biovolume in leaf litter declined by half during 2-week intervals that frequently lacked sufficient rain to reach the forest floor as throughfall for 3 consecutive days (Lodge, 1993), and the dominant basidiomycete leaf decomposer, *Gymnopus johnstonii*, became locally extinct on ridges after the canopy was opened by hurricane Hugo in 1989, which was preceded and followed by drought (Lodge & Cantrell, 1995). In addition, a litter basket decomposition experiment during the first iteration of the CTE showed that addition of green leaves buffered the underlying senesced litter from moisture loss and ameliorated the negative effect of canopy opening on fungal connectivity to the senesced litter cohort below (Lodge et al., 2014). It was therefore surprising to find a significant negative rather than a positive correlation between rainfall and percent fungal litter mat cover. A previous test of drought tolerance at our site using four of the least drought-sensitive litter mat basidiomycete species was conducted to determine if they could reduce soil erosion on a steep road embankment (Lodge et al., 2008). Half of each litter mat was placed in full shade or partial shade to quantify their rates of attachment to freshly fallen leaves (Lodge et al., 2008). Two of the four fungal species formed more attachments in full shade that had one third the evaporative potential of the partial shade site, one species (*Marasmius guyanensis*) formed more attachments in partial than full shade, and the fourth species, *Marasmius crinis-equi*, formed the greatest number of attachments in both full and partial shade. It may be significant that *M. crinis-equi* was the dominant litter decomposer basidiomycete recorded in the control plot of block B, which was the only plot that did not show a significant decline in percent fungal litter mat cover during the 2015 drought. Data on percent fungal litter mat cover in the control plots were examined to determine if there were obvious direct inhibitory effects of 2015 March–October drought when compared to normal years (2014 and 2015–2017; Figure 2). Looking across years within seasons, however, there were no obvious patterns of lower fungal litter mat cover in 2015 relative to the drier season in other years.

Do high rainfall events reduce fungal litter mat cover?

Both low and high rainfall may have negative impacts on white-rot litter mat cover. Although high RH was positively related to fungal litter mat cover, and RH is positively related to rainfall, extremely high rainfall events may have a negative impact. Lodge et al. (2008) found that overland flow from a high rainfall event disrupted some fungal litter mats, and that rain impact without overland flow caused significant losses of both litter and soil from steep slopes that lacked litter-binding fungi. Hurricane Maria was a high rainfall event (ca. 1500 mm over 3 days at El Verde; Hall et al., 2020) and was associated with a sudden reduction in fungal litter mat cover in this study. There is tremendous energy represented by this level of rain force (Lugo, 2020; Van Beusekom et al., 2018) and Hall et al. (2020) found that hurricane-induced rainfall was a better predictor of forest damage in Puerto Rico than maximum wind speed. Thus, extreme rainfall events may represent too much of a good thing. Our hypothesis that Hurricane Maria rainfall damaged the fungal litter mats is concordant with the surprising and significant negative correlation (-0.4942) between fungal litter mat cover and rain after removal of seasonal variation. However, a similar crash in litter mat extent was found after canopy trimming without an associated extreme rainfall event.

Does litterfall affect fungal litter mat cover?

We expected higher litterfall to have a positive effect on basidiomycete fungal litter mat cover based on previous studies of their ecology (Lodge, 1993; Lodge et al., 2008, 2014). The basidiomycete litter decomposers at our site in Puerto Rico accumulate nutrients from partly decomposed leaves and use these reserves to capture and quickly build biomass in freshly fallen leaves (Lodge et al., 1994, 2008, 2014; Lodge & Asbury, 1988). Frankland et al. (1995) previously described similar “sit-and-wait” behavior of a basidiomycete decomposer fungus, *Mycena galopus*, in using nutrients from decomposed litter to rapidly colonize fallen conifer litter in the United Kingdom, consistent with the model of Klotzbücher et al. (2011). Lodge et al. (2008) showed that fungal mats at our site in Puerto Rico differentially migrated uphill on steep slopes because fresh litter tumbling downslope accumulated on their uphill sides. It was therefore surprising to find that higher percent litter mat cover corresponded with low litterfall mass in the PCA and no relationship between these variables using

Spearman's rank correlation. This anomaly is best explained by the positive correlation between leaf litterfall mass in the prior month and solar radiation (0.4036 Spearman's rank correlation) since solar radiation (and hence, evaporative potential, Lodge et al., 2008) was strongly inversely correlated with fungal litter mat cover within each of the four seasons as well as in the PCA. Litterfall mass was highest in summer and also in fall during the 2015 drought when percent litter mat cover was generally lowest. Notably, litterfall mass was not significantly correlated with percent litter mat cover after prewhitening to remove seasonal variation.

Consistent with the observation above of an inverse relationship between high senesced leaf litterfall and percent fungal litter mat cover, high green leaf litter inputs from canopy disturbances were also strongly inversely correlated with litter mat cover. The high litterfall caused by a treefall in the block C control plot in summer of 2016 corresponded to a significant decline in percent litter mat cover rather than an increase. A similar decrease in litter mat cover was observed in all plots and both canopy treatments immediately following Hurricane Maria in 2017 despite massive inputs of green leaf litter. The deposition of green leaves from disturbances that open the forest canopy, however, is confounded with higher solar radiation. These observations together with an absence of significant correlation between prior month litterfall and percent litter mat cover during this study (except in winter) suggest litterfall mass is not the dominant factor determining litter mat cover soon after disturbances that open the canopy. Other components of primary production such as fine roots and root exudates are unlikely to have strongly influenced our results as tree root mats were absent from litter under closed canopy during much of our study as a result of drought and hurricanes. Surface root mats on ridges and upper slopes at our site in summer 2016 were limited in extent and were formed mostly by roots of *D. excelsa* and *M. bidentata* trees (M. Sánchez-Julia & D. J. Lodge, personal observations).

The previous iteration of the CTE indicated that green leaf litter increased moisture in the litter cohorts below and partly ameliorated the unfavorable drying effects of canopy opening on fungal connectivity (Lodge et al., 2014; Shiels et al., 2015). It was therefore surprising that fungal litter mat cover decreased to near zero following canopy trimming with addition of green debris in the second iteration of the CTE as well as following a treefall and Hurricanes Irma and Maria despite large inputs of green leaf litter. This pattern might indicate that addition of large masses of green leaves may be inhibitory to litter mat decomposer basidiomycetes, as suggested by a study in Puerto Rico that found slower decomposition of

senesced leaf litter when mixed with green hurricane litter, perhaps caused by secondary compounds leached from the green leaves (Silver, unpublished data cited in Willig et al., 2015). That hypothesis is consistent with the very low fungal litter mat cover in July 2016 following high green litterfall from a large treefall in the control plot in block C relative to control plots in the other two blocks. In contrast, prior results from our site that showed that application of fresh green leaves increased rather than decreased both fungal connectivity and decomposition rates in underlying senesced litter cohorts (Lodge et al., 2014). The abundance and quality of plant secondary compounds likely differed, however, between the previous study (Lodge et al., 2014) that used a composite of green leaves from three co-dominant trees comprising 40% of annual litterfall in these plots and the 30 other plant species comprising the remaining 60% of leaf fall (Zalamea & González, 2008). Plant secondary compounds are known to vary among tree species and their production responds to both biotic and abiotic stress (Simon & Adamczyk, 2019). Łukowski et al. (2021) found that faster decaying leaf litter had a lower content of defensive compounds. Therefore, inhibition of decomposer fungi by secondary plant compounds in green leaf litter remains a viable hypothesis for explaining our results. The significant decreases rather than the expected increases in fungal litter mat cover in response to large inputs of green leaf litter in the CTE trim + debris treatment, the large treefall in block C control and Hurricanes Irma and Maria are most consistent with drying associated with higher solar radiation resulting from the large canopy gaps rather than litterfall mass. In addition, it may be significant that Hurricane Maria was an exceptionally wet event, which as noted above, may have contributed to the post-hurricane depression of fungal litter mat cover.

How might changes in fungal litter mat cover affect ecosystem processes?

Given that the products of white-rot decomposition have been shown to differ from other types of rot, reductions in fungal litter mat cover might induce changes in carbon sequestration and nutrient cycling (Bai et al., 2017; Osono, 2007). Based on studies of changes in soil under white-rot leaf litter in Finland (Hintikka, 1970), wood decomposed by white-rot at our site in Puerto Rico (Lodge et al., 2016), and slowed leaf decomposition in the trim + debris treatment of the first iteration of the CTE associated with shifts from mat-forming basidiomycete fungi that cause white-rot of litter to unit-restricted microfungi (González et al., 2014; Lodge et al., 2014;

Shiels et al., 2015) we would expect decreased white-rot litter mat cover after canopy opening to correspond to delayed N flux to soil. Instead, Moreno et al. (2019, unpublished manuscript) found faster and greater N flux in the trim + debris treatment associated with an increase in leaf-shredding arthropods. In the first iteration of the CTE, a combination of reduced canopy tree uptake and increased litterfall N concentrations led to a delayed accumulation of soil N that stimulated bacterial conversion of NH_4 to the leachable nitrate form which was subsequently detected in groundwater 9–12 months after the simulated hurricane treatment (McDowell & Liptzin, 2014; Shiels et al., 2015; Silver et al., 2014).

In addition to changes in N cycling, we might also expect a more rapid flux of P from litter in the canopy trimming treatment based on previous studies at our site and other neotropical forests (Cleveland et al., 2006; Lodge et al., 2008, 2014; Schreag et al., 2013). Moreno et al. (2019), Cantrell et al. (2021) did find greater P flux from litter to soil after 35 days of green leaf decomposition in litter bags during the second iteration of the CTE. Studies by Cleveland et al. (2006) and Schreag et al. (2013) showed in Central American forests that large early fluxes of P from leaf litter were from leaching of organic and inorganic P forms and the processes were non-biological, while Lodge et al. (2014) in Puerto Rico and Luizão et al. (1998) in Brazil showed that retention and accumulation of P above 100% of initial content in decomposing rain forest litter was attributable to fungal and microbial immobilization of P. Lodge et al. (1994, 2008) hypothesized that recycling of P within the litter layer by fungi followed by pulsed release in response to drying and rewetting results in proportionately higher P availability to tree roots in P-fixing clay soils with high iron and aluminum content. Whether internal recycling of P within the litter layer by unit-unrestricted basidiomycete fungi results in greater P availability to plant uptake and growth following a disturbance event may be contingent on climatic conditions preceding and following the disturbance that determine whether nutrient release is synchronous or asynchronous with fine root uptake (Silver & Vogt, 1993). For example, Hurricane Hugo in 1989 was preceded and followed by a drought that killed most fine roots (Silver & Vogt, 1993), thereby reducing the ability of canopy trees to capture N, P, and K (potassium) leached from debris. The 2015 drought resulted in disappearance of fine root mats in leaf litter on ridges and upper slopes at El Verde after Hurricane Hugo as well as from early 2015 till summer 2016 (D. J. Lodge & M. Sánchez-Julia, personal observations).

The effects of reduced white-rot litter mat cover on soil carbon and nutrients following hurricane disturbance are difficult to predict because of contingencies such as the

one noted above, conflicting results from different studies, as well as the comparatively massive carbon and nutrient inputs from large woody debris (Sanford et al., 1991). Most studies on the effects of white-rot on underlying soil has been conducted on decaying wood rather than on leaf litter. Although Stutz et al. (2017) found less exchangeable Ca^{2+} and Mg^{2+} in soil under white-rotted logs in Austria, Zalamea et al. (2016) found higher availability of cations (Ca^{2+} , K^+ , and Mg^{2+}) associated with 7-year decayed white-rotted logs at a different wet forest site in the Luquillo Mountains of Puerto Rico. Bai et al. (2017) in China and Stutz et al. (2017) in Austria found that soil under white-rotted logs had less C and N than soil under brown-rotted logs while Lodge et al. (2016) in Puerto Rico found greater soil accumulation of C and N under white-rotted logs of two ages (hurricane cohorts) than soil away from the logs. However, Lodge et al. (2016) found changes in total soil C whereas Stutz et al. (2017) detected difference in water extractable organic C. Both Zalamea et al. (2007) in Puerto Rico and Stutz et al. (2017) in Austria found greater aromaticity of soil carbon under logs decayed by white-rot fungi. The accumulation of aromatic compounds from white-rot of primarily woody debris may have contributed to the 10-year accumulation of carbon in soil found in CTE plots with debris addition without canopy trimming, especially the heavy soil carbon fraction that was strongly correlated with iron concentration (Gutiérrez del Arroyo & Silver, 2018). While the large mass of woody debris relative to leaf litter resulting from hurricane damage is thought to have a dominant effect of increasing P availability in soil with high iron content based on Century modeling calibrated with hurricane data (Sanford et al., 1991), the importance of nutrient cycling via fine litter cannot be discounted, however. Gutiérrez del Arroyo and Silver (2018) found significant accumulation of extractable P in soil 10 years after debris addition under closed canopy, but not in the trim + debris treatment, and hypothesized that reduced litterfall after canopy opening had muted the positive effect of debris deposition on P availability. Lodge et al. (2016) showed that while soil beneath decaying logs at our site in Puerto Rico had more C and N than soil from paired cores taken within 50 cm away from the logs, fine roots foraged differentially for nutrients by proliferating under the logs only in the wetter seasons, and away from logs under freshly fallen litter in the drier season. Two studies at our site in Puerto Rico showed that logs, rocks, and large surface roots act as debris dams on steep forest slopes that lead to long-term accumulation of leaf litter on the upslope side, and deprivation of litter to the downslope side results in differential carbon and nutrient accumulation in soil on the upslope side of obstructions (Lodge et al., 2016). An experiment in a tropical forest in Panama (Vincent et al., 2010) showed

that 3 years of fine litter removal resulted in a 23% decrease in P, whereas 3 years of litter addition resulted in a 16% increase in P in the upper 2 cm of soil (Vincent et al., 2010), and the organic P in the upper 2 cm of soil could supply a fifth of the P needs of forest trees.

CONCLUSIONS

This study supports previous research showing greater abundance of fungal white-rot litter mats in tropical forests compared to studies in temperate and boreal forests. These litter mats, which are bound together by unit-unrestricted basidiomycete fungi, had similar negative responses to canopy opening from both a simulated hurricane trimming experiment and real hurricanes. The negative impacts of canopy opening on percent cover by fungal litter mats was most closely correlated with increased solar radiation and associated reduction in RH though changes in litterfall may have played a role. Increased solar radiation was previously shown to result in greater evaporative potential and lower rates of fungal attachment to senesced leaves placed on litter mats. Based on previous studies, there might have been a positive relationship between litterfall mass and percent fungal litter mat cover under closed canopy despite absence of significant correlations in most comparisons in this study. In contrast to a previous study at our site showing the application of green leaf litter stimulated fungal connectivity and decomposition in the litter layer, large inputs of green leaves from the simulated and actual hurricanes and a large treefall in this study were associated with a crash rather than an increase in fungal litter mat cover. Green leaf deposition from disturbances that open the forest canopy, however, is confounded with higher solar radiation, as we observed in block C following a large treefall and also in all plots after Hurricanes Irma and Maria. We infer from the results of this study, which contrast with those of a previous study showing addition of green leaves increased rather than decreased fungal connectivity in the litter layer, together with a previous experiment that showed reduced rates of fungal incorporation of senesced leaves by basidiomycete fungi into litter mats exposed to partial versus full shade, that the main effect of forest canopy disturbances results from canopy opening and the associated higher solar radiation and evaporative potential though inhibitory effects of secondary compounds from green leaf deposition could have been a contributing factor. High moisture may partly compensate for increased drying from high solar radiation, and variation in drought tolerance among the agaric fungi that bind litter together in mats may provide some resilience under increasing frequency of hurricanes and other disturbances that open the forest canopy. However, high

rainfall events such as Hurricane Maria may disrupt fungal litter mats.

Biogeochemical and nutrient cycling changes resulting from decreased abundance of white-rot litter decomposers following disturbances that open the canopy and deposit debris on the forest floor are difficult to predict other than changes in nutrient fluxes from litter to soil and possible decreases in aromaticity of soil carbon derived from non-white-rot litter decomposition based on previous studies on wood decomposition. Reductions in aromatic carbon compounds from leaf decomposition following hurricane damage to forest canopies and similar anthropogenic disturbances, however, are likely to be offset by decay products from the much greater mass of large woody debris in which white-rot fungi are more buffered from the microclimate changes associated with canopy opening. Nevertheless, nutrient cycling in fine litter is an important source of nutrients for trees in wet tropical forests and the white-rot litter decomposers that are abundant and play key roles in undisturbed forest are sensitive to the effects of canopy opening.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

In addition to datasets cited herein (González & Van Beusekom, 2021; González et al., 2019), fungal litter mat data (Lodge, 2021) are available from the Environmental Data Initiative: <https://doi.org/10.6073/pasta/131095b53ce38db265e94d58fc335e95>.

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