DOI: 10.1002/ecs2.4084

#### ARTICLE

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

Revised: 13 January 2022

## Canopy opening increases leaf-shredding arthropods and nutrient mineralization but not mass loss in wet tropical forest

Ivia I. Moreno<sup>1</sup> | Maria F. Barberena-Arias<sup>1</sup> | Grizelle González<sup>2</sup> | D. Jean Lodge<sup>3</sup> | Sharon A. Cantrell<sup>1</sup>

<sup>1</sup>Department of Biology, Universidad Ana G Méndez, Gurabo Campus, Gurabo, Puerto Rico

<sup>2</sup>USDA Forest Service International Institute of Tropical Forestry, Río Piedras, Puerto Rico

<sup>3</sup>USDA Forest Service, Northern Research Station, Luquillo, Puerto Rico

**Correspondence** Ivia I. Moreno Email: iviapr@gmail.com

#### Present address

Maria F. Barberena-Arias, Department of Science and Technology, Universidad Interamericana, Metro Campus, San Juan, Puerto Rico

D. Jean Lodge, Odum School of Ecology and Department of Plant Pathology, University of Georgia, Athens, Georgia, USA

#### Funding information

International Institute of Tropical Forestry USDA Forest Service; Universidad de Puerto Rico; US National Science Foundation, Grant/Award Numbers: DEB-0620910, DEB-0218039; National Science Foundation LTER Grant, Grant/ Award Number: NSF DEB 1239764

Handling Editor: Aaron B. Shiels

#### Abstract

Hurricanes alter forest habitat by opening the canopy and depositing fresh wood and leaves. The objectives of this study were to evaluate the effects of hurricane and drought-driven changes to forests on green litter decomposition, invertebrate communities, and nutrient mineralization over a short period (6 months) after disturbance. We used three complete replicated blocks with two canopy treatments: control and trim + detritus. Green leaves were enclosed in litterbags of three different mesh sizes to determine the effect of soil fauna of varying body sizes. Litterbags were retrieved from the field after 21, 35, 84, and 168 days and transported to the laboratory in individually sealed plastic bags. We extracted and identified invertebrates, measured leached and mineralized litter nutrients using ion resin membranes placed for 1 week under the leaves inside the litterbags, and determined litter mass loss. Additional resin membranes were placed in the lowest litter layer above the mineral soil. The number of arthropod taxonomic groups and nutrient mineralization differed significantly between control and trim + detritus. Regardless of mesh size, bags in control plots had consistently higher invertebrate richness than in trim + detritus plots. Nitrogen mineralization and phosphorous mineralization were significantly higher in trim + detritus in large mesh size, and decomposer arthropod abundance was highest in large-sized mesh bags. These data suggest that within functional categories, variations in feeding behavior among arthropod orders may affect the release of nutrients from organic matter. Percent mass loss did not differ between canopy treatments or litterbag mesh sizes, but instead decreased during drought. Invertebrate composition, but not abundance, differed significantly between canopy treatments with greater dominance by shredders (Lepidoptera and Diptera larvae) in trim + detritus, which corresponded to higher rates of nutrient mineralization from green leaves. These results suggest that regional drought dominated the

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

FCOSPHERE

AN ESA OPEN ACCESS JOURNAL

2 of 20

mesoclimate surpassing any microclimate variation in response to canopy treatments. Since mass loss did not differ between canopy treatments or litterbag mesh sizes, our results suggest that differences in short-term nutrient fluxes from green litter are mostly related to changes in the litter invertebrate food web rather than rates of decomposition.

#### K E Y W O R D S

arthropods, canopy opening, green litter, hurricane disturbance, litter decomposition, Luquillo Mountains, mass loss, nutrient mineralization, Special Feature: Tropical Forest Responses to Repeated Large-Scale Experimental Hurricane Effects, tropical forest

#### INTRODUCTION

Leaf litter supplies limiting nutrients for plant growth via leaching and nutrient mineralization, while the availability of soil nutrients to plants is augmented through decomposition, which increases soil organic matter via recalcitrant residues (Denslow et al., 1998; Lodge et al., 1991). Leaf litterfall is an important source of organic phosphorus (P) via nutrient cycling in undisturbed humid tropical forests (Clark et al., 2001; Raich & Tufekciogul, 2000; Silver et al., 2014; Tanner et al., 1998; Vincent et al., 2010). Although litter decomposition is mainly the result of microbial activities, invertebrates are important for conditioning the litter and influencing microbial biomass, both ultimately altering the activity of the microbial community and thus decomposition and mineralized nutrients (Coleman et al., 2004; González et al., 2001). For example, arthropods that fragment litter directly modulate decomposition as they feed on large pieces of litter transforming them into smaller pieces with a larger surface area, thereby stimulating the activity of decomposer microorganisms. On the contrary, grazing arthropods can selectively feed on decomposer fungi, thereby reducing their biomass, altering their community composition, and increasing nutrient mineralization (Barberena-Arias & Cuevas, 2018; Wardle & Lavelle, 1997). The effects of organisms on decomposition rates are considered to occur at smaller scales in comparison with other factors (resource quality and physicochemical conditions) and are often not explicitly included in decomposition studies (González, 2002; Wall et al., 2008). This may be partly because quantifying the influence of fauna on litter decomposition and nutrient mineralization is more difficult than that of microorganisms given their indirect effect via regulation of bacterial and fungal biomass (González, 2002). Most studies addressing the roles of different groups of soil fauna on decomposition use litterbags with different mesh sizes to exclude specific groups (microfauna, mesofauna, and macrofauna) (Bokhorst & Wardle, 2013; Bradford et al., 2002). The mesofauna has received the most attention because it contains two groups of abundant and diverse arthropods, the Collembola (springtails) and Acari (mites) (primarily grazers), together with less abundant groups such as Protura, Diplura, pseudoscorpions, Symphyla, and Pauropoda. Soil fauna can account for up to 66% of the total decomposition in the tropical wet forest in Puerto Rico (González et al., 2001). Disturbances such as hurricanes can radically alter patterns of litter decomposition and nutrient cycling (González et al., 2014; Lodge et al., 2014; Ostertag et al., 2003; Richardson et al., 2010). For example, soil nitrogen (N) availability decreased after Hurricane Hugo in Puerto Rico in response to increased nutrient immobilization by soil microbial biomass, resulting in slowed canopy closure (Lodge et al., 1994; Zimmerman et al., 1995). Nitrogen is not typically a limiting nutrient in humid tropical forests, except at high elevations where N and P are often colimiting, whereas soil P is thought to be the primary limiting factor for wet tropical ecosystem processes including forest productivity and litter decomposition because there is low availability of P in most highly weathered soils (Cleveland et al., 2006; Dalling et al., 2016; Lodge et al., 2014; Tanner et al., 1998; Vincent et al., 2010; Vitousek & Sanford Jr, 1986). Availability and fate of soil N and P in tropical ecosystems differ nonlinearly in response to pulsed versus chronic inputs, as well as timing of pulsed releases in relation to relative biomass of microbes and fine roots (Lodge et al., 1994).

Arthropod community responses to disturbances such as hurricanes are highly variable because heterogeneous changes in a habitat associated with landslides, floods, large amounts of fallen wood, green leaves, and canopy opening may increase resources for some species and reduce it for others (Barberena-Arias & Aide, 2002; Walker et al., 1996). Hurricane disturbance alters the physical structure of the forests by creating canopy openings that increase solar radiation reaching the forest floor, thereby increasing temperature and decreasing moisture in litter on the forest floor (Richardson et al., 2010; Shiels et al., 2015; Van Beusekom et al., 2020). Therefore, the combination of detritus and opening of the canopy, increasing light levels, decreasing humidity, and changing nutrient inputs and recycling of N and P in the soil are factors that influence the trophic dynamics in soil and forest litter (Rivera, 2008; Silver et al., 2014).

Responses in the detrital food web and nutrient cycling in a subtropical wet forest in Puerto Rico have been a major focus of a large-scale manipulation to simulate the canopy opening and detritus deposition effects associated with strong hurricane impacts, which are predicted to occur with increased frequencies (Knutson et al., 2015; Zhao & Held, 2012). In the first iteration of a replicated canopy trimming experiment (CTE) at our site, mass loss and N mineralization from both green and senesced leaves were significantly slowed by canopy opening, which was attributed to drying of the litter layer and changes in arthropod community composition (González et al., 2014; Richardson et al., 2010). Those studies also found slower mass loss in litterbags with small mesh size, which corresponded to a lower Margalef diversity and a simplified functional complexity in the detrital food web. In the same experiment, canopy opening reduced fungal connectivity between litter cohorts by basidiomycete macrofungi that can degrade lignin (Lodge et al., 2014; Lodge et al., 2022)—a result that was consistent with invertebrate data from Richardson et al. (2010) who found a shift from invertebrate consumers of macrofungi to those that prefer microfungi in the open canopy treatments (Shiels et al., 2015). Significantly, Lodge et al. (2014) also found decreased P immobilization and translocation in response to canopy opening and reduced fungal connectivity.

Our objectives were to determine how canopy opening with detritus deposition and size-based litter arthropod functional groups affected litter invertebrate abundance and composition, and mass and nutrient loss from green leaf litter. This study occurred within the second iteration of a replicated CTE comprised of a simulated hurricane treatment (canopy trimming with detritus deposition) and matched control (unmanipulated) plots. We used litterbags of three mesh sizes to separate the effects of these arthropod size groups, using animal size to approximate the three functional groups: microarthropods, litter transformers, and ecosystem engineers. Litter transformers are predominantly meso- and macrofauna that fragment litter, thereby increasing residue surface area, while ecosystem engineers are macrofauna such as ants and termites, and megafauna such as earthworms and vertebrates that physically transform the environment in ways that modify the resources for other organisms (Jones et al., 1994; Zhang et al., 2012). In addition, we placed cation and anion exchange resin membranes beneath the leaves inside the litterbags to determine relative rates of leaching plus mineralization. We also placed ion exchange resin membranes at the litter-soil interface more frequently during the early part of our experiment to determine whether peak nutrient fluxes from the

litterbags coincided with peak fluxes into soil. Turner et al. (2018) previously showed that resin-exchangeable P was a good measure of P availability along a soil P gradient in Panama and that forest productivity as measured by tree growth increased with available P. We expected that arthropod functional groups would influence both mass and nutrient loss from the green leaf litter and that mass loss would be slower in the open canopy treatment.

#### MATERIALS AND METHODS

#### Study site

This study was performed in the Luquillo Experimental Forest (LEF) (Figure 1), located in northeastern (18.33080, -65.82320, World Geodetic System 84) Puerto Rico. The LEF is composed of four life zones that result from changes in elevation, climate, and soil characteristics (García-Martinó et al., 1996; Willig et al., 1996). The study was specifically located within the tabonuco forest (Dacryodes excelsa), which is classified as subtropical lower montane wet forest with average monthly temperature of 21°C in January and 25°C in September (Brown et al., 1983; Gould et al., 2008). Total annual precipitation is approximately 3.5 m (García-Martinó et al., 1996), with approximately 97 rainless days per year. In this forest, rainfall is weakly seasonal and has a drier season between December and March (most commonly March) (http://lternet.edu/data/lterdb14/data/). Litterfall is seasonal, with a main peak from March to June, a secondary peak in September, and minima from December to February (Lawrence, 1996; Richardson et al., 2010; Zalamea & González, 2008; Zou et al., 1995).

#### Field study design

This study is part of a second iteration of the CTE performed by the Luquillo Long-Term Ecological Research Program (LTER) near El Verde Field Station (Figure 1). Three ridge sites in tabonuco forest, designated blocks A, B, and C, were used, each having two  $30 \times 30$ -m treatment plots with central  $20 \times 20$ -m measurement areas, of which one plot was control and the other was experimental (herein trim + detritus) (Richardson et al., 2010; Shiels & González, 2014; Shiels et al., 2010). The canopy was trimmed by arborists, and detritus was deposited on the ground in the trim + detritus plot, simulating the impact that a hurricane has in this forest. Each plot was subdivided into 16 subplots, and 3 of the 5 randomly selected decomposition subplots (5  $\times$  5 m) were chosen based on proximity to lysimeters. In each subplot,



El Verde Field Research Station, Luquillo Experimental Forest, northeastern Puerto Rico (maps taken from https://data.fs.usda.gov)

FIGURE 1 El Verde Field Research Station, Luquillo Experimental Forest, northeastern Puerto Rico (Quiñones et al., 2018)

litterbags with different mesh sizes were placed to be collected at four specific times. Litterbags (one per subplot) were retrieved at 21, 35, 84, and 168 days after trimming. The start dates were different, coinciding with completion of the canopy treatment in each block (A—16 December 2014; B—14 November 2014; and C—10 December 2014). This experimental design represents 3 blocks  $\times$  2 plots/block (1 trim + detritus/1 control)  $\times$  3 subplots  $\times$  3 litterbag mesh sizes  $\times$  4 collecting times, for a total of 216 litterbags. The experiment was performed

between October 2014 and May 2015, which encompasses months typically considered wetter and drier, respectively, including a drought from March through October 2015.

## Litterbags

Three of the most common plant species in the tabonuco forest were selected to represent typical litter quality, Manilkara bidentata (ausubo), D. excelsa (tabonuco), and Prestoea acuminata var montana (palma de sierra) (Richardson et al., 2010; Zalamea & González, 2008; Zimmerman et al., 2014). Litterbags were made with Velcro (Figure 2), which allowed for the easy handling to fill with equal proportions of air-dried green leaves from each (5 g) of these three species (total 15 g per bag). Litterbag mesh sizes were selected to exclude decomposer food web functional groups (Wardle, 2002), using animal body width (Swift et al., 1979) as a proxy. Small mesh (Figure 2a) had a pore size of 0.003-mm<sup>2</sup> mesh—allowing only microfood web organisms (Wardle, 2002) to enter, which include microbes and micropredators (e.g., nematodes and protozoans) that feed upon the microbes (e.g., bacteria-Wardle, 2002); medium mesh (Figure 2b) had a pore size of 0.4 mm<sup>2</sup>—that allowed microfood web organisms, and mesofauna such as fungal grazers like collembolans and some mites; and large mesh (Figure 2c) had a pore size of 3 mm<sup>2</sup>—that allowed all the above plus macrofauna, which includes most components of the decomposition food web to enter the bag including litter shredders (i.e., transformers) such as Diplopoda (e.g., small diplopods) that break litter into smaller pieces that promotes microbial growth (Wardle, 2002), but excluding megafauna (i.e., large animals) such as earthworms (ecosystem engineers) and large diplopods. From now on, litterbags with small mesh size will be called small, medium mesh size will be called medium, and large mesh size will be called large. The use of litterbags with different mesh sizes allowed three different decomposer functional groups to enter the bags and us to evaluate how they differentially affect mass loss and leached/mineralized nutrients. Litterbags were collected (between October 2014 and May 2015) for 6 months (168 days) after canopy trimming occurred.

#### Nutrients

Nutrient fluxes were quantified using ion exchange resin membranes (PRS<sup>TM</sup> probes) placed under the leaves inside the litterbags to adsorb nutrients leaching from the decomposing leaves. One week prior to collection, two pairs of each membrane (two anionic and two cationic) were placed under the litter inside the litterbags assigned to be collected (Figure 3). The PRS<sup>TM</sup> probes were placed inside litterbags beginning at 2 weeks, incubated for 7 days and collected at 3 weeks, 3 months, and 6 months (35, 64, and 168 days, respectively) after canopy trimming occurred, rinsed with deionized water, and then sent to Western Ag Innovations for nutrient analyses. Additional PRS<sup>TM</sup> probes were similarly placed in the fermentation layer of the standing litter at the litter-soil interface beginning 2-5 weeks before trimming, 0-5 days after litter was redistributed on the trimmed plots, and at 1-week intervals for the first month, and again at 3 and 6 months. Litter-to-soil fluxes were compared graphically between treatments within blocks to account for the staggered start times among blocks, and because microbial communities were previously found to differ significantly among blocks (Cantrell et al., 2014). We used two different membrane types-anion probes (orange) that have a positively charged membrane to adsorb all negatively charged anions (nitrate, phosphate, and



**FIGURE 2** Photograph of differences among mesh sizes: (a) small, (b) medium, and (c) large. All photographs were taken at the same magnification  $(40\times)$  under a dissecting microscope.



**FIGURE 3** Two pairs of each PRS<sup>TM</sup> probe (two anionic and two cationic resin exchange membranes) were buried inside litterbags 1 week prior to sampling.

sulfate) and cation probes (purple) that have negatively charged membrane to adsorb all positively charged cations (ammonium, potassium, calcium, and magnesium). These probes bearing resin membranes are used for quantifying spatial and temporal variations in nutrient rates for all ions (Quian & Schoneau, 2002). After 1 week inside decomposition bags or incubation at the litter–soil interface, probes were retrieved, placed in ziplock bags, rinsed in deionized water, and sent to Western Ag for analyses.

#### Arthropod extraction and classification

Litterbags retrieved from the field were placed individually in sealed plastic bags for transport to the laboratory. The contents of each retrieved litterbag were placed in Berlese funnels for 1 week for arthropod extraction (Barberena-Arias, González, & Cuevas, 2012; Barberena-Arias, Ortiz-Zayas, et al., 2012; Walter, 1987). The Berlese-Tullgren funnel (Walter, 1987) uses a light source to force organisms out of the sample as the sample dries (Sandler et al., 2010). Collected arthropods were counted and identified to order and family using a dissecting microscope  $(20-40\times)$ , assigned to a trophic category based on their life stage and feeding habits (Triplehorn & Johnson, 2005), and the abundance was standardized to individuals per gram of dry litter.

## Mass loss

Litter samples used to determine mass loss were also used for arthropod extraction. Therefore, before arthropod extraction, litter samples were weighed (wet weight) and then oven-dried at 60°C for 1 week after arthropod extraction and reweighed to obtain dry weight. To calculate mass loss, a simple exponential decay function model was used as proposed by Jenny et al. (1949) and discussed by Olson (1963). This model proposes that the decomposition follows a unique pattern:  $X_t = X_0 e^{-kt}$ , where  $X_t$  is the fraction of leaf litter remaining at time *t* (days),  $X_0$  is the initial amount of litter, and *k* is the decomposition constant.

#### Data analysis

We tested for differences (p < 0.05) in percent mass remaining and nutrient fluxes from the litter (nutrient concentration [in micrograms per 10 cm<sup>2</sup> per week]) in response to canopy treatments, litterbag mesh sizes, and time using the generalized linear model (GLM): univariate analysis of variance using IBM Statistical Package for the Social Sciences (SPSS 20). GLM was also used to determine the effects of canopy treatment, litterbag mesh size, and time on arthropod abundance and richness. In addition, we used principal components analysis (PCA, Paleontological Statistics [PAST]) to evaluate the strongest covariation among NO<sub>3</sub>-N, NH<sub>4</sub>-N, P, K, and arthropod richness in litterbags with different mesh sizes (therefore different arthropod communities) and control and trim + detritus. We assumed linear relationships among these variables for a variance-covariance matrix, and we interpreted the first two axes (McCune & Grace, 2002). For the arthropod community, a multiresponse permutation procedure (MRPP; PC-ORD)) was used to compare the species composition of arthropods among mesh sizes, treatments, and time, based on

Sorensen's coefficient dissimilarity index (CCs = 2c/S1 + S2), where CCs is Sorensen's coefficient, *c* the number of species common to both communities, S1 the number of species in Community 1, and S2 the number of species in Community 2 (McCune & Grace, 2002). Sorensen's coefficient is based on the presence and absence, and MRPP was used to determine differences in species composition between treatments, among mesh sizes, and through time.

#### RESULTS

#### Mass loss

Percent mass remaining decreased in both the control and trim + detritus treatments over time and followed the same pattern (Figure 4). In addition, we observed that changes in mass loss over time were significant ( $p \le 0.05$ ) but there were no differences in the rate of mass loss between canopy treatments or litterbag mesh sizes (Table 1). There were no significant interactions between canopy treatment, litterbag mesh size, and time. Furthermore, the mass loss was initially rapid, decreasing by 40%

during the first 21 days in both treatments, and then, it slowed. At the beginning of the experiment, 14 days of precipitation showed a wet period that corresponded to the rapid mass loss observed during the first 21 days of the experiment (Figure 5). However, after December 2014, 14-day cumulative rain showed recurring occurrences of dry days/weeks corresponding to the slower mass loss during the subsequent 168 days in both canopy treatments (Figure 5). Moreover, the Climate Prediction Center (2014) classified the time between September 2014 and May 2016, as a warm period. Warm periods are associated with decreased precipitation in Puerto Rico. Correspondingly, the Drought Monitor Reports stated that by May 2015 >50% of the land area in Puerto Rico was abnormally dry or under moderate drought (U.S. Drought Monitor, 2018).

## Rainfall

During the study period, precipitation varied from the usual pattern resulting in days with cumulative rain lower than the norm. For example, October had 7 days with 14-day cumulative rain lower than 33.9 mm, which are considered dry. In addition, January had 5 days, March



**FIGURE 4** Mean ( $\pm$ SE) percentage mass remaining in each mesh size of litterbag and for control (a) and trim + detritus (b) treatments over time after canopy trimming

**TABLE 1** Generalized linear model: Univariate analysis of variance for the effect of canopy trimming treatment, litterbag mesh size, and time on percent mass remaining (%)

		Mass remaining (%)		
Effect	df	F	р	
Treatment	1	1.911	0.168	
Size	2	1.021	0.362	
Time	3	83.08	<0.001	
$Treatment \times size$	2	0.840	0.433	
$Treatment \times time$	3	1.126	0.340	
Size $\times$ time	6	0.385	0.888	
$Treatment \times size \times time$	6	0.655	0.686	

*Note:* The significance of bold format is about p values significant (p < 0.05)



**FIGURE 5** Precipitation for 1 year (2014–2015) at 21 days, 35 days, 84 days, and 168 days during 6 months (168 days) following canopy trimming in the Luquillo Experimental Forest in El Verde Field Station located in northeastern Puerto Rico (18.33080, –65.82320, World Geodetic System 84)

had 6 days, April had 5 days, and May had 19 dry days. Consequently, during the study period, 5 of 8 months had consecutive dry days that lasted about a week or more. On the contrary, November had 7 wet days (Figure 5).

#### Arthropod abundance

There was no significant difference in arthropod abundance between treatments or among mesh sizes (Figure 6c). Abundance varied between 2 and 1 individuals  $g^{-1}$  dry litter (Figure 6a) in both treatments and among mesh sizes, with a trend for higher abundance in medium mesh size. A total of 1804 individuals were collected representing 14 taxonomic groups. Medium-sized mesh bags had more arthropods in the trim + detritus, whereas large-sized mesh bags had more invertebrates in the undisturbed canopy control treatment, but the interaction between canopy treatment and mesh size was not significant (Table 2). Therefore, canopy disturbance with detritus deposition did not alter arthropod abundance relative to control (Figure 6). Arthropod abundance changed significantly over time (Table 2), reaching a peak after 84 days in the field (Figure 6). Through time, abundance showed a similar pattern in both control and trim + detritus.

#### **Arthropod composition**

The total number of arthropod orders was significantly higher in control than in trim plots, and higher in large than in medium and small mesh size. Overall, in control plots, small mesh bags had 9 orders, medium had 7 orders, and large had 13 orders, while in trim + detritus plots, small had 4 orders, medium had 6 orders, and large had 10 orders. Arthropod richness significantly varied through time (Table 2), progressively decreasing (Figure 6). Moreover, our experiment showed that richness decreased through time as did remaining mass.

Arthropod community composition was significantly different (MRPP; p = 0.0084) between treatments, mesh sizes, and time. The test statistic (T) shows separation between treatments (control and trim + detritus) (T = -3.328) and among litterbag sizes (T = -5.185)(small, medium, and large), and a greater separation (T = -16.141) between times (after 21, 35, 84, and 168 days in the field). Furthermore, the agreement statistic (A) shows heterogeneity to be equal within groups in litterbag sizes (A = 0.015), treatments (A = 0.007), and time (A = 0.056). These results suggest that identities of arthropod groups associated with decomposing litter vary between environmental conditions (control and trim + detritus), among decomposing functional groups (mesh sizes), and through time, with arthropod functional groups having a stronger effect than the canopy treatment (Table 3). Notably, large mesh litterbags in the trim + detritus treatment had 10 Lepidoptera larvae per gram of dry litter versus 1 in control plots (Table 4).



**FIGURE 6** Arthropod abundance and richness (number of taxonomic group): (a) abundance in treatments (control and trim + detritus); (b) richness in treatment (control and trim + detritus); (c) abundance in mesh sizes (small, medium, and large); (d) richness in mesh size (small, medium, and large); (e) abundance through time (21, 35, 84, and 168 days); and (f) richness through time (21, 35, 84, and 168 days in the field). Bars represent standard error.

Acari, Coleoptera, and Diptera were found in both treatments and all mesh sizes; Acari were the most abundant order. However, the composition of the arthropod community significantly differed between control and trim + detritus plots, among mesh sizes, and through time. For example, the large mesh bags in trim + detritus

		Abundance		Richness	
Effect	df	F	p	F	р
Treatment	1	1.39	0.240	10.286	0.002
Size	2	1.425	0.243	29.696	<0.001
Time	3	7.401	<0.001	26.083	<0.001
Treatment × size	2	1.361	0.259	4.071	0.019
Treatment × time	3	1.059	0.368	0.655	0.581
Size $\times$ time	6	0.45	0.844	1.798	0.101
Treatment $\times$ size $\times$ time	6	0.581	0.745	0.601	0.729

**TABLE 2** Generalized linear model: Univariate analysis of variance for the effects of canopy treatment, litterbag mesh size, and incubation time on the arthropod abundance and richness

*Note*: The *p* values in bold are significant at <0.05.

**TABLE 3** Summary statistics for multiresponse permutation procedure to compare diversity patterns and species composition of arthropods. Results of taxonomic group Sorensen's distance, comparing three different factors: treatment, litterbag size, and time (days) (*T*, test statistic and *A*, agreement statistic).

Factor	Observed	Expected	Variance	Skewness	Т	р	A
Treatment	0.735	0.740	0.000	-1.276	-3.328	0.008	0.007
Litterbag size	0.729	0.740	0.000	-0.903	-5.185	0.000	0.015
Time (days)	0.699	0.740	0.000	-0.737	-16.141	0.000	0.056

*Note:* The significance of bold format is about *p* values significant (p < 0.05)

**TABLE 4** Abundance of arthropods by taxonomic group (*O*, order; *C*, class) across canopy treatments (control vs. trim) and litterbag mesh sizes. Numbers of individuals were standardized per gram of dry litter followed by SE in parentheses

Treatment/taxon	Control S <sup>a</sup>	Control M <sup>b</sup>	Control L <sup>c</sup>	Trim S	Trim M	Trim L
Acari (O)	58 (±3)	108 (±2)	107 (±3)	31 (±10)	98 (±3)	115 (±3)
Coleoptera (O)	1 (±0)	1 (土0)	6 (±0)	$1(\pm 1)$	16 (±1)	9 (±1)
Diptera (O)	11 (±0)	14 (±1)	17 (±0)	4 (±1)	21 (±1)	35 (±1)
Collembola (O)	50 (±13)	14 (±1)	11 (±0)	40 (±7)	20 (±3)	4 (±1)
Blattodea (O)	1 (±0)		2 (±0)			1 (±0)
Thysanura (O)	$1(\pm 0)$					1 (±0)
Homoptera (O)			$1(\pm 0)$			
Hymenoptera (O)	5 (±1)	65 (±9)	12 (±2)		8 (±4)	1 (±0)
Lepidoptera (O)			$1(\pm 0)$		2 (±0)	10 (±1)
Pseudoscorpion (O)		1 (土0)	3 (±0)			1 (±0)
Isopoda (O)			$1(\pm 0)$			
Aranae (O)			2 (±0)			
Diplopoda (C)	$1 (\pm 0)$		4 (±1)			$1 (\pm 0)$
Chilopoda (C)	$1(\pm 0)$		$1  (\pm 0)$			
Plecoptera (O)		1				

<sup>a</sup>S, small mesh litterbags.

<sup>b</sup>M, medium mesh litterbags.

<sup>c</sup>L, large mesh litterbags.

treatment (Table 3), particularly at 21 days, had a high abundance of Lepidoptera larvae, which were absent from control. In contrast, orders that were unique to control

include Homoptera, predaceous Pseudoscorpions, and Chilopoda, and litter transformers such as Blattodea, Isopoda, and Diplopoda. Therefore, our results showed that

		NH4-N		Р		К	
Effect	df	F	р	F	р	F	р
Treatment	1	8.12	0.01	0.05	0.83	6.62	0.01
Size	2	11.35	0.00	5.81	0.00	4.38	0.01
Time	3	17.63	0.00	4.06	0.01	53.38	0.00
Treatment $\times$ size	2	5.79	0.00	0.00	1.00	1.56	0.21
$Treatment \times time$	3	2.56	0.06	0.28	0.84	2.14	0.10
Size $\times$ time	6	3.26	0.01	4.43	0.00	0.43	0.86
$Treatment \times size \times time$	6	1.91	0.08	0.15	0.99	1.32	0.25

**TABLE 5** Generalized linear model: Univariate analysis of variance for the effects of treatment, litterbag mesh size, and time on weekly nutrient fluxes (NH<sub>4</sub>-N, P, and K) from decomposing green leaves

*Note*: The *p* values in bold are significant at <0.05.



**FIGURE 7** Mean (±SE) weekly nutrient fluxes of nutrients from litterbags of three mesh sizes under two canopy treatments. (a, b) Nitrogen (NH4-N). (c, d) Phosphorus (P). (e, f) Potassium (K), in two canopy treatments: control (a, c, and e) and trim + detritus (b, d, and f)

the litter arthropod community in the trim + detritus treatment was a subset of those in the control treatment, except for Lepidoptera larvae.

#### Nutrient fluxes from decomposing leaves

NH<sub>4</sub>-N and potassium (K) (but not P) fluxes from decomposing leaves differed significantly between the canopy treatments (Table 5). Moreover, litterbag mesh sizes significantly affected fluxes of all three nutrients (Table 5). For example, N and P fluxes were greatest in large mesh, intermediate in medium mesh, and smallest in small mesh litterbags (Figure 7). The higher N and P fluxes in the large mesh bags corresponded to the presence of Isopoda, Diplopoda, and Chilopoda in control plots and Lepidoptera larvae in trim + detritus plots. Fluxes of P only differed between mesh sizes at 168 days in the control canopy treatment but differed at both 35 and 168 days in the trim + detritus canopy treatment and were higher in large mesh than in the other two mesh sizes (Table 5). These results showed the early peak at 35 days in N and P fluxes in the litterbags was concordant with peak capture of leached and mineralized nutrients adsorbed by probes at the litter-soil interface in which a significant difference in N and P occurred between control and trim + detritus canopy treatments (Figure 8). Therefore, nutrient fluxes changed significantly over time for all three nutrients, generally increasing and then decreasing (Table 4, Figure 7). These results showed there were significant mesh sizeby-time interactions for fluxes of both NH<sub>4</sub>-N and P, but not K (Table 5). There was a significantly greater flux of P and K across the litter-soil interface in the trimmed plot in block C, including during the first week after trimming (Figure 8).

Our experiment showed all bag clusters follow the same general pattern regardless of size or treatment. Only the bags with the full arthropod community (large mesh) in the trim + detritus treatment differed from all others, particularly at the beginning of the experiment (Figure 9). Also, canopy openness with debris addition (trim + detritus) may play a role for a different arthropod community to develop, which are related to high K that decrease through time (Axis 1) and high NH<sub>4</sub>-N that peaked at 35 days (Axis 2) (Figure 9).

#### DISCUSSION

We found greater nutrient fluxes from green leaf litter in a simulated hurricane treatment compared with the control, and fluxes in the hurricane treatment were greater in large mesh bags with the full arthropod community than in the medium and small mesh bags. The number of arthropod taxonomic groups was significantly higher in control than in trim + detritus, while decomposer arthropod abundance was highest in large-sized mesh bags in the control. The early abundance of Lepidoptera larvae feeding on green leaves in large mesh bags in the trim + detritus treatment and their absence from the control treatment, however, may have contributed to high nutrient fluxes in the trim + detritus treatment. Another significant factor could be the decrease in macromycete litter decomposer fungi found in these same trimmed plots in response to canopy opening (Lodge et al., in press). Macromycete fungi were previously found to recycle and conserve limiting nutrients under closed canopy (Lodge et al., 1994, 2008, 2014). Changes in fungal decomposers and shifts in invertebrates that differentially feed on microfungi rather than macrofungi were also observed during the first iteration of the CTE (Lodge et al., 2014; Richardson et al., 2010).

#### Mass loss

Although we did not find differences in green leaf litter mass loss between canopy treatments or among litterbag mesh sizes, nutrient fluxes are not always strictly correlated with leaf litter decomposition (Bragazza et al., 2008; Hangs et al., 2014). The lack of differences in mass loss does not appear to be related to the short (6-month) duration of this study. Decomposition is rapid in wet tropical forests occurring in about 9-18 months. Mass loss diverged significantly among treatments (senesced vs. green leaves and trim + debris vs. no trim no debris) beginning 2 months after placement during the first iteration of the CTE (González et al., 2014). In this study, about 20% mass remaining was attained at 6 months as compared to 12-18 months in the first iteration of the CTE (González et al., 2014). Ostertag et al. (2022) found in a pantropical leaf decomposition experiment in montane and lowland forests that differences in mass loss between litterbag mesh sizes were highly significant using either the mean data from 3and 7-month incubation or the 7-month data alone. As noted previously, litter arthropods have largely indirect effects on litter decomposition via regulation of bacterial and fungal populations.

## Nutrient fluxes

The timing and magnitude of nutrient fluxes from leaf litter to soil have significant effects on structure and functioning of plant communities (Aerts et al., 1999; Bragazza



Nutrient capture time (weeks after trimming)

FIGURE 8 Weekly nutrient litter-soil interface fluxes of N (a), P (b), and K (c) in two canopy treatments: control and trim + detritus

et al., 2008; Lavelle et al., 1993; Lodge et al., 1994, 2014). In forests recovering from canopy disturbance, as in this study, the timing and magnitude of nutrient fluxes interacting with environmental factors influence nutrient fate in terms of the proportion incorporated by vegetation versus lost from the ecosystem via fluxes to the atmosphere or leached and exported by streams (Lodge et al., 1994; Lodge & McDowell, 1991; McDowell et al., 1996; McDowell & Liptzin, 2014; Shiels et al., 2015; Steudler et al., 1991; Zimmerman et al., 1995). Sun et al. (2022) showed N and P export from the Rio Grande watershed, which includes our site, increased about 300% during Hurricane Maria, and took nearly a year to return to background levels. In this study, nutrient fluxes from green litter differed significantly between canopy treatments and litterbag mesh sizes, and these differences corresponded to changes in arthropod community composition. We found N and P fluxes from green litter to soil were highest in bags with large mesh size in the trim + detritus treatment. Correspondingly, McDowell (in press) found in lysimeters located nearest our litterbags that nitrate accumulated more in groundwater in the trim + detritus than in the control



**FIGURE 9** Principal components analysis (PCA) of the green leaf litter arthropod. Control treatment (a) and trim + detritus (b). Axis 1 with 89.7% of variability and Axis 2 with 9.9% of variability. Solid triangles, small; open diamonds, medium; and solid circles, large

treatment. The occurrence of a significant drought during this study could have uncoupled nutrient mineralization and root uptake, as observed previously following Hurricane Hugo (Lodge et al., 1994; McDowell et al., 1996). In contrast, González et al. (2014) found slower N mineralization along with slower mass loss in response to canopy trimming.

The trim + detritus plot in block C had significantly greater fluxes of P and K across the litter-soil interface, but this occurred too soon after canopy trimming to be attributed to invertebrates. Both P and K are known to be highly leachable soon after leaf fall (Schreeg et al., 2013). Because trimming of the blocks was staggered, higher rainfall could potentially lead to greater initial leaching of nutrients. However, cumulative 7-day rainfall (Ramírez, 2021) during ion resin membrane exposure immediately following trimming was similarly high (332–354 mm) in blocks A and C but low (52 mm) in block B; thus, leaching potential does not explain the

high rate of leaching of P and K during the first week only in the trimmed plot in block C. Instead, litterfall mass in the preceding month and fungal litter mat abundance (Lodge et al., in press) were related to the differences in fluxes of P and K at the litter-soil interface. Litterfall mass was higher in block C than in blocks A and B just prior to the trim and could have contributed to greater P and K being leached from the litter layer. However, the abundance of fungal litter mats was most closely correlated with the disparity in leaching of P and K among plots and treatments. Block C had the lowest percent fungal litter mat cover prior to the trim. Following the trim, the control plot in block C maintained its fungal litter mat cover and had lower nutrient fluxes to soil, whereas fungal mats completely disappeared from the trimmed plot in block C in response to canopy opening, corresponding to high fluxes of P and K. This result agrees with that of Lodge et al. (2014) who found that P leached from litterfall during the previous iteration of the CTE was immobilized by fungi in the lower litter layers. We hypothesize that active fungal litter mats are important in immobilizing and recycling nutrients in the litter layer, as previously shown for P by Lodge et al. (1994, 2014).

#### Drought

Drought following canopy disturbance to forests may contribute to losses of nutrients from the ecosystem if it causes asynchrony between nutrient release and plant uptake. For example, the effects of canopy loss and debris deposition at our site from both Hurricane Hugo in 1989 and the previous iteration of the CTE led to an accumulation of soil ammonium that stimulated microbial conversion to nitrate that then leached into the groundwater and was exported via streams (McDowell et al., 1996; McDowell & Liptzin, 2014). Hurricane Hugo was preceded by a drought that caused mass mortality of fine roots and microbial biomass resulting in asynchrony between N mineralization and root uptake and losses of N from the ecosystem in streamwater (Lodge et al., 1994; McDowell et al., 1996; Shiels et al., 2015). Additional N was lost from the ecosystem to the atmosphere after Hurricane Hugo via denitrification (Lodge et al., 1994; Steudler et al., 1991).

The decreased rate of decomposition toward the end of our experiment can be attributed to drought, which is known to slow decomposition (Sanaullah et al., 2012). Canopy trimming resulted in abiotic changes: increased throughfall, higher soil moisture, higher solar radiation, and decreased litter moisture (Shiels et al., 2015; Van Beusekom et al., 2020). These results suggest that regional drought dominated the mesoclimate surpassing any microclimate variation that the experiment manipulation might have created. This may explain the similar pattern in mass loss we observed in trimmed and control plots in the presence of drought, in contrast to the first iteration of the CTE in which canopy treatments differed in the absence of drought (González et al., 2014; Richardson et al., 2010). A pretreatment drought occurred in 2002 before the first canopy trimming and the litterbag decomposition experiment in 2004, leading to pre- versus post-treatment differences in microbial communities within the control treatment, but rainfall had returned to normal before canopy treatment and the decomposition experiment (Cantrell et al., 2014; González & Lodge, 2017; González et al., 2014). In their pantropical leaf decomposition experiment in montane and lowland forests, Ostertag et al. (2022) showed hierarchical control of leaf litter mass loss with climate having a stronger effect on leaf litter mass loss than biotic factors including invertebrate size class.

#### Arthropod community composition

Canopy opening is a major determinant of community change by reducing arthropod diversity and biomass (decrease detritivores; e.g., Coleoptera and Diplopoda) and changes in fungivores (e.g., Collembola and Mites) (Richardson et al., 2010). We predicted that arthropod diversity and abundance in green leaf litter would vary among the three mesh sizes in the control and trim + detritus treatment. We confirmed that arthropod diversity and community composition were associated with canopy trimming and its interaction with mesh size. Arthropod abundance, however, was not affected by either mesh size or canopy treatment. The changes in habitat caused by disturbances (e.g., hurricane) affect the composition of arthropod communities since changes in abundance and distribution of resources can modify the microhabitat used by arthropods (Barberena-Arias, González, & Cuevas, 2012; Barberena-Arias, Ortiz-Zayas, et al., 2012). In addition, canopy opening with detritus deposition (trim + detritus treatment) provides more organic matter for arthropods, which stimulates the activity of soil organisms. For decomposer arthropods, litter represents habitat and food either directly or indirectly through microbial biomass; therefore, more litter represents higher resource availability, which can in turn promote both abundance (Sayer et al., 2010) and richness (Richardson et al., 2010). Although one might expect increased abundance or richness of arthropods in response to debris deposition in the CTE based on results of a litter addition and removal experiment in Panama by Sayer et al. (2015), that study was conducted under an undisturbed canopy, whereas the CTE combined canopy opening with debris addition. During this experiment, both arthropods and remaining mass decreased through time suggesting a

positive relationship, as previously found by Barberena-Arias and Aide (2003). Counterintuitively, regardless of mesh size, bags in our control plots had consistently higher richness than in trim + detritus plots most likely from the environmental effects of canopy opening. This result is consistent with that from the first iteration of the CTE in which Margalef index of diversity for litter arthropods was positively related to mass loss (González et al., 2014).

In this study, Acari was the most abundant order and common in both canopy treatments, while the number of taxonomic groups was higher in control than in trim + detritus and soon after disturbance (21 days after trim) in large mesh bags. These results showed a pattern of a higher number of orders in the control treatment than in trim + detritus and that the composition of the latter was mostly a subgroup of that in the control. The simulated hurricane treatment affected the number of orders in trim + detritus in all mesh sizes. Furthermore, the abundance of arthropods and richness showed a similar pattern among mesh sizes in both treatments. Though not significant, the abundance in small-sized mesh bags was always lowest and that in large-sized mesh bags was always highest, while that in medium-sized mesh bags was intermediate for both canopy treatments. In addition, abundance results showed a peak at 84 days after trim, whereas richness decreased at the same time. These data suggest that abundance and richness of arthropods are affected differently by the canopy treatments, and it also suggests that the biodiversity of trim + detritus is mostly a subgroup of control and the effects of the hurricane affect the number of orders in trim + detritus in all sizes of mesh.

# Arthropod community and nutrient mineralization

We found significantly higher mineralization of N and K (but not P) in bags with large mesh size in the trim + detritus treatment with rates of N mineralization higher than in previous studies. The green leaf litter mixture we used had a higher quality than in the previous CTE experiments because one third was comprised of higher nutrient palm leaves (Richardson et al., 2005). Although the green leaf mix used in this study had higher quality (lower C:N and C:P) than used in the previous CTE experiments (González et al., 2014; Harris & Medina, 2013; Lodge et al., 2014; C:N ratio of 34 based on green lower leaves in Harris & Medina, 2013 versus 38-41 in Lodge et al., 2014), this cannot explain the higher rate of N mineralization found in this study. Instead, a key difference between the two CTE experiments is that the green leaf mass in the previous CTE was stored for several

months outside of the plots before being applied to the plots and was consumed by Lepidoptera and other arthropods prior to deposition as frass (Richardson et al., 2010), whereas green litter was applied to the plots within a week to 10 days after trimming in this experiment. Furthermore, we found significant differences in arthropod communities in the large mesh bags in trim + detritus treatment (Table 3) and particularly at 21 days where bags with large mesh size in trim + detritus were strikingly different (Figure 7). These bags had high abundance of Lepidoptera larvae per gram of dry litter presumably feeding on the green leaves deposited on the ground, while the control plots had only one Lepidoptera larva per gram (Moreno, 2019; Table 4). Lepidopteran adults are opportunistic and rapidly respond to increased availability of new leaves (Torres, 1992); therefore, the detritus deposited on these plots may have contributed to an outbreak of lepidopteran larvae that then were able to colonize litterbags with large mesh size.

The comminution that resulted from the feeding of these chewing Lepidoptera larvae may have resulted in higher leaching/mineralization of N, P, and K from these bags (Figure 7). The peak of nutrient mineralization after 4 weeks in both the large mesh litterbags and at litter-soil interface suggests that processes in the large-sized mesh bags were comparable to those in the green litter that was applied to the plots in the trim + debris treatment (Figure 8), while trim + detritus and control large mesh bags also differed in the kinds of detritivores (Moreno, 2019) which include arthropods feeding on organic matter and/or associated organisms such as fungi, bacteria, and algae (Moreno, 2019). In control bags, 64% were adults of mostly oribatid mites (54%), while in trim + detritus bags, 65% were larvae of mostly dipterans (50%) from the families Chironomidae and Psychodidae. Oribatids with closed genital plates feed mainly on fungi/algae growing on decomposing organic matter (https://www.zoology.ubc.ca/ ~srivast/mites/group.html), while dipterans such as Chironomids are semiaquatic larvae that may colonize moist soil or vegetation and feed on detritus and associated microbes (Delettre, 2000). We hypothesize that the rapid application of fresh green leaves to the trim + detritus plots in this experiment created a greater abundance of Lepidoptera and other medium-sized arthropods, which then increased shredding of green leaf litter in our large mesh litterbags, thereby stimulating nutrient mineralization (Walker et al., 1996). Together, these results suggest that relative differences in nutrient fluxes from green leaf litter were related to changes in the litter invertebrate food web rather than rates of decomposition. In addition, the higher N flux from green leaves in the trim + detritus treatment was unexpected. Our results also contrast with those from the first iteration of the CTE by González

et al. (2014) who found slower N mineralization with canopy opening. Furthermore, arthropod food web community complexity was reduced under open canopy in this study, and previous literature reviews and syntheses (David, 2014; Wardle, 1999) suggested that both macro- and microarthropods stimulate N mineralization. However, as noted by González and Seastedt (2001), the interactive effects of fauna and microbes on nutrient mineralization depend on the specific feeding behavior of the fauna and the microbial community. The study by Lodge et al. (2022) found that basidiomycete leaf litter mat cover was significantly higher in the control than in the trim + detritus treatment, and these macrofungi are known to conserve and recycle nutrients in the litter layer (Lodge et al., 2014, 2022), which is consistent with our results. The previous studies (González et al., 2014; Lodge et al., 2014), however, indicated more mineralization of P but not N in trimmed plots, whereas this study found greater mineralization of N but not P in the trimmed plots. On the contrary, undisturbed communities, such as those present in control plots, were dominated by adult mites and nutrient leaching/mineralization resulted like all other mesh sizes that lepidopterans and dipterans were unable to colonize. These data suggest that within functional categories, variations in the specific feeding behavior among arthropod orders may affect the release of nutrients from organic matter; in this case, the feeding behavior of mandibulate Lepidoptera and Diptera larvae seem to enhance microbial activity that possibly resulted in increased leaching/ mineralization in large mesh litterbags in trimmed plots.

#### CONCLUSIONS

In this study, we predicted that arthropod diversity of green leaf litter would vary among the three mesh sizes and between the control and trim + detritus treatments. However, we found arthropod diversity and community composition were affected by the canopy and mesh size treatments, whereas arthropod abundance was not affected. In addition, we found that litterbag mesh size significantly affected mineralization of nutrients from the green leaves in the trimmed plots. We hypothesize that the effect of canopy opening and detritus (trim + detritus treatment) provided more organic matter for arthropods that stimulated the activity of lepidopteran larvae soon after the trim, resulting in higher nutrient fluxes from green litter. We hypothesize that drought had a stronger effect on mass loss and nutrient mineralization than the canopy treatments and litterbag mesh size. Our results are consistent with previous support for hierarchical control of litter decomposition and mineralization (Djukic et al., 2018; Ostertag

et al., 2022). The effect of arthropods on leaf litter decomposition occurs on a smaller scale, not on a mesoscale. Therefore, our results are aligned with previous studies showing that at the mesoscale level, the predominant factors in litter decomposition are resource quality and environmental conditions (Djukic et al., 2018; Ostertag et al., 2022). Based on evidence from multisite experiments at regional and global scales, while soil animals are considered key regulators of decomposition at local scales, their role at larger scales is still unresolved (Wall et al., 2008).

#### ACKNOWLEDGMENTS

A special thanks to the team and volunteers at the Microbial Ecology and Biotechnology Research Lab at Universidad Ana G. Méndez, Gurabo, and the team at the El Verde Field Research Station. Also, thanks to LTER 5: Understanding Environmental Change in Northeast Puerto Rico by the National Science Foundation LTER Grant (NSF DEB 1239764) and principal investigator Dr Jess Zimmerman for sponsoring research by the first author. Additional support was provided by the USDA Forest Service, International Institute of Tropical Forestry, and the University of Puerto Rico, Río Piedras Campus.

#### **CONFLICT OF INTEREST**

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Nutrient flux data (Cantrell et al., 2021) and invertebrate data (Moreno et al., 2022), respectively, are available from the EDI Data Portal: https://doi.org/10.6073/pasta/f27efaa8fa45f1f2c55e496c53d800ff and https://doi.org/10. 6073/pasta/facc2b533a70e205c5af112482bc437f.

#### ORCID

*Ivia I. Moreno* https://orcid.org/0000-0003-0911-4437 *Grizelle González* https://orcid.org/0000-0003-3007-5540

D. Jean Lodge D https://orcid.org/0000-0003-4807-348X

#### REFERENCES

- Aerts, R., J. T. A. Verhoeven, and D. F. Whigham. 1999. "Plant-Mediated Controls on Nutrient Cycling in Temperate Fens and Bogs." *Ecology* 80: 2170–81.
- Barberena-Arias, M. F., and T. M. Aide. 2002. "Variation in Species and Trophic Composition of Insect Communities in Puerto Rico 1." *Biotropica* 34: 357–67.
- Barberena-Arias, M. F., and T. M. Aide. 2003. "Species Diversity and Trophic Composition of Litter Insects during Plant Secondary Succession." *Caribbean Journal of Science* 39: 161–9.
- Barberena-Arias, M. F., and E. Cuevas. 2018. "Physicochemical Foliar Traits Predict Assemblages of Litter/Humus Detritivore Arthropods." In *Tropical Forests*, edited by P. Sudarshana, M. Nageswara-Rao, and J. Soneji, 1–19. London: Intech.

- Barberena-Arias, M. F., G. González, and E. Cuevas. 2012. "Quantifying Variation of Soil Arthropods Using Different Sampling Protocols: Is Diversity Affected?" *Tropical Forests* 14: 51–70.
- Barberena-Arias, M. F., J. Ortiz-Zayas, C. Abad, G. Almodóvar, E. López, M. Rodríguez, and L. Troche. 2012. "Comparación de la fauna de artrópodos terrestres entre pastizales y bosques dominados por el tulipán africano (*Spathodea campanulata*), en tres zonas del carso norteño en Puerto Rico." Acta Científica 26: 68–79.
- Bokhorst, S., and D. A. Wardle. 2013. "Microclimate within Litter Bags of Different Mesh Size: Implications for the 'Arthropod Effect' on Litter Decomposition." Soil Biology and Biochemistry 58: 147–52. https://doi.org/10.1016/j. soilbio.2012.12.001.
- Bradford, M. A., G. M. Tordoff, T. Eggers, T. H. Jones, and J. E. Newington. 2002. "Microbiota, Fauna, and Mesh Size Interactions in Litter Decomposition." *Oikos* 99: 317–23.
- Bragazza, L., A. Buttler, A. Siegenthaler, and E. A. D. Mitchell. 2008. "Plant Litter Decomposition and Nutrient Release in Peatlands." In *Carbon Cycling in Northern Peatlands* (*Geophysical Monograph Series*), Vol 184, edited by A. J. Baird, R. Li, X. Belyea, A. Comas, S. Reeve, and L. D. Slater, 99–110. Washington, DC: American Geophysical Union.
- Brown, S., A. E. Lugo, S. Silander, and L. Liegel. 1983. Research History and Opportunities in the Luquillo Experimental Forest. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station.
- Cantrell, S. A., D. J. Lodge, I. I. Moreno, M. F. Barberena-Arias, and G. González. 2021. "Nutrient Mineralization from Green Leaves in Litterbags of Three Mesh Sizes in the LUQ-LTER Canopy Trimming 2 Experiment Ver 2." Environmental Data Initiative. https://doi.org/10.6073/pasta/f27efaa8fa45f1f2c55e4 96c53d800ff.
- Cantrell, S. A., M. Molina, D. J. Lodge, F. J. Rivera-Figueroa, M. L. Ortíz-Hernández, A. A. Marchetti, M. J. Cyterski, and J. R. Pérez-Jiménez. 2014. "Effects of Simulated Hurricane Disturbance on Forest Floor Microbial Communities." *Forest Ecology* and Management 332: 22–31.
- Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, J. Ni, and E. A. Holland. 2001. "Net Primary Production in Tropical Forests: An Evaluation and Synthesis of Existing Field Data." *Ecological Applications* 11: 371–84.
- Cleveland, C. C., S. C. Reed, and A. R. Townsend. 2006. "Nutrient Regulation of Organic Matter Decomposition in a Tropical Rain Forest." *Ecology* 87: 492–503.
- Climate Prediction Center. 2014. "Cold and Warm Episodes by Season." https://origin.cpc.ncep.noaa.gov/products/analysis\_ monitoring/ensostuff/ONI\_v5.php.
- Coleman, D. C., D. A. Crossley, and P. F. Hendrix. 2004. *Fundamentals of Soil Ecology*, 2nd ed. Cambridge, MA: Academic Press.
- Dalling, J. W., K. Heineman, G. González, and R. Ostertag. 2016. "Geographic, Environmental, and Biotic Sources of Variation in the Nutrient Relations of Tropical Montane Forests." *Journal of Tropical Ecology* 32: 368–83.
- David, J. F. 2014. "The Role of Litter-Feeding Macroarthropods in Decomposition Processes: A Reappraisal of Common Views." Soil Biology and Biochemistry 76: 109–18.

- Delettre, Y. R. 2000. "Larvae of Terrestrial Chironomidae (Diptera) Colonize the Vegetation Layer during the Rainy Season." *Pedobiologia* 44: 622–6.
- Denslow, J. S., A. M. Ellison, and R. E. Sanford. 1998. "Treefall Gap Size Effects on above- and below-ground Processes in a Tropical Wet Forest." *Journal of Ecology* 86: 597–609.
- Djukic, I., S. Kepfer-Rojas, I. K. Schmidt, K. S. Larsen, C. Beier, B. Berg, K. Verheyen, et al. 2018. "Early Stage Litter Decomposition across Biomes." *Science of the Total Environment* 628–629: 1369–94.
- García-Martinó, A. R., G. S. Warner, F. N. Scatena, and D. L. Civco. 1996. "Rainfall, Runoff and Elevation Relationships in the Luquillo Mountains of Puerto Rico." *Caribbean Journal of Science* 32: 413–24.
- González, G. 2002. "Soil Organisms and Litter Decomposition." In Modern Trends in Applied Terrestrial Ecology, edited by R. S. Ambasht and N. K. Ambasht, 315–29. New York: Kluwer Academic/Plenum Publishers.
- González, G., R. E. Ley, S. K. Schmidt, X. Zou, and T. R. Seastedt. 2001. "Soil Ecological Interactions: Comparisons between Tropical and Subalpine Forests." *Oecologia* 128: 549–56.
- González, G., D. J. Lodge, B. A. Richardson, and M. J. Richardson. 2014. "A Canopy Trimming Experiment in Puerto Rico: The Response of Litter Decomposition and Nutrient Release to Canopy Opening and Detritus Deposition in a Subtropical Wet Forest." Forest Ecology and Management 332: 32–46.
- González, G., and T. R. Seastedt. 2001. "Soil Fauna and Plant Litter Decomposition in Tropical and Subalpine Forests." *Ecology* 82: 955–64.
- González, G., and D. J. Lodge. 2017. "Soil Biology Research across Latitude, Elevation and Disturbance Gradients: A Review of Forest Studies from Puerto Rico during the Past 25 Years." Forests 8(6): 178.
- Gould, W. A., A. Alarcon, B. Fevold, M. E. Jimenez, S. Martinuzzi, G. Potts, M. Quinones, M. Soórzano, and E. Ventosa. 2008. *The Puerto Rico Gap Analysis Project, Volume 1: Land Cover, Vertebrate Species Distributions and Land Stewardship.* IITF GTR-39. Rio Piedras, Puerto Rico: USDA Forest Service, International Institute of Tropical Forestry.
- Hangs, R. D., J. J. Schoenau, K. C. J. Van Rees, N. Bélanger, and T. Volk. 2014. "Leaf Litter Decomposition and Nutrient-Release Characteristics of Several Willow Varieties within Short-Rotation Coppice Plantations in Saskatchewan, Canada." *Bioenergy Research* 7: 1074–90.
- Harris, N. L., and E. Medina. 2013. "Changes in Leaf Properties across an Elevation Gradient in the Luquillo Mountains, Puerto Rico." *Ecological Bulletins* 54: 169–79.
- Jenny, H., S. Gessel, and F. T. Bingham. 1949. "Comparative Study of Decomposition Rates of Organic Matter in Temperate and Tropical Regions." Soil Science 68: 419–32.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. "Organisms as Ecosystem Engineers." *Oikos* 69: 373–86.
- Knutson, T. R., J. J. Sirutis, M. Zhao, R. E. Tuleya, M. Bender, G. A. Vecchi, G. Villarini, and D. Chavas. 2015. "Global Projections of Intense Tropical Cyclone Activity for the Late Twenty-First Century from Dynamical Downscaling of CMIP5/RCP4. 5 Scenarios." *Journal of Climate* 28: 7203–24.
- Lavelle, P., E. Blanchart, A. Martin, S. Martin, and A. Spain. 1993. "A Hierarchical Model for Decomposition in Terrestrial

Ecosystems: Applications to Soils of the Humid Tropics." *Biotropica* 25: 130–50.

- Lawrence, W. T. 1996. "Plants: The Food Base." In *The Food Web of* a *Tropical Rain Forest*, edited by D. P. Reagan and R. B. Waide, 17–51. Chicago, IL: University of Chicago Press.
- Lodge, D. J., S. A. Cantrell, and G. González. 2014. "Effects of Canopy Opening and Detritus Deposition on Fungal Connectivity, Phosphorus Movement between Litter Cohorts and Mass Loss." Forest Ecology and Management 332: 11–21.
- Lodge, D. J., and W. H. McDowell. 1991. "Summary of Ecosystem-Level Effects of Caribbean Hurricanes." *Biotropica* 23: 373–8.
- Lodge, D. J., W. H. McDowell, and C. P. McSwiney. 1994. "The Importance of Nutrient Pulses in Tropical Forests." *Trends in Ecology & Evolution* 9: 384–7.
- Lodge, D. J., F. N. Scatena, C. E. Asbury, and M. J. Sanchez. 1991. "Fine Litterfall and Related Nutrient Inputs Resulting from Hurricane Hugo in Subtropical Wet and Lower Montane Rain Forests of Puerto Rico." *Biotropica* 23: 364–72.
- Lodge, D. J., W. H. McDowell, J. Macy, S. K. Ward, R. Leisso, K. Claudio Campos, and K. Kuhnert. 2008. "Distribution and Role of Mat-Forming Saprobic Basidiomycetes in a Tropical Forest." In *Ecology of Saprobic Basidiomycetes*, edited by L. Boddy and J. C. Frankland, 195–208. Amsterdam: Elsevier.
- Lodge, D. J., et al. 2022. "Xxx." *Ecosphere* xxx: xxx-x.
- Lodge, D. J., A. E. Van Beusekom, G. González, M. Sánchez, and S. Stankavich. 2022. "Disturbance Reduces Fungal White-Rot Litter Mat Cover in a Wet Subtropical Forest." *Ecosphere* 13 (2): 373.
- McCune, B., and J. B. Grace. 2002. *Analysis of Ecological Communities*. Gleneden Beach, OR: MjM Software Design.
- McDowell, W. H., and D. A. Liptzin. 2014. "Linking Soils and Streams: Response of Soil Solution Chemistry to Simulated Hurricane Disturbance Mirrors Stream Chemistry Following a Severe Hurricane." Forest Ecology and Management 332: 56–63.
- McDowell, W. H., C. P. McSwiney, and W. B. Bowden. 1996. "Effects of Hurricane Disturbance on Groundwater Chemistry and Riparian Function in a Tropical Rain Forest." *Biotropica* 28: 577–84.
- McDowell, W. H. Forthcoming. "Context Dependence in a Tropical Forest: Repeated Disturbance Reduces Soil Nitrate Response but Increases Phosphate Concentration." *Ecosphere*. in press.
- Moreno, I.I., M.F. Barberena-Arias, G. González, S.A. Cantrell, and J.D. Lodge. 2022. "Canopy Opening Increased Leaf Shredding Arthropods and Nutrient Mineralization but Not Mass Loss in a Wet Tropical Forest Version 1." Dataset. Environmental Data Initiative. https://doi.org/10.6073/pasta/facc2b533a70e205c5af112482bc437f.
- Moreno, I., M. F. Barberena-Arias, S. A. Cantrell, G. González, and D. J. Lodge. 2019. "Arthropod and Fungi Interact during Green Litter Decomposition in a Simulated Hurricane Experiment." https://www.researchgate.net/publication/331644636
- Olson, J. S. 1963. "Energy Storage and the Balance of Producers and Decomposers in Ecological Systems." *Ecology* 44(2): 322–31.
- Ostertag, R., C. Restrepo, J. W. Dalling, P. H. Martin, I. Abiem, S. Aiba, E. Alvarez-Dávila, et al. 2022. "Litter Decomposition Rates across Tropical Montane and Lowland Forests Are Controlled Foremost by Climate." *Biotropica* 54(2): 309–26. https://doi.org/10.1111/btp.13044.

- Ostertag, R., F. N. Scatena, and W. L. Silver. 2003. "Forest Floor Decomposition Following Hurricane Litter Inputs in Several Puerto Rican Forests." *Ecosystems* 6: 261–73. https://doi.org/ 10.1007/s10021-002-0203-8.
- Qian, P., and J. J. Schoenau. 2002. "Practical Applications of Ion Exchange Resins in Agricultural and Environmental Soil Research." *Canadian Journal of Soil Science* 82(1): 9–21.
- Quiñones, M., I. K. Parés-Ramos, W. A. Gould, G. Gonzalez, K. McGinley, and P. Ríos. 2018. *El Yunque National Forest Atlas. IITF GTR-47.* San Juan, Puerto Rico: USDA Forest Service, International Institute of Tropical Forestry.
- Raich, J. W., and A. Tufekciogul. 2000. "Vegetation and Soil Respiration: Correlations and Controls." *Biogeochemistry* 48: 71–90.
- Ramírez, A. 2021. "Meteorological Data from El Verde Field Station: NADP Tower Ver 1676169." Environmental Data Initiative. https://doi.org/10.6073/pasta/

60138713ab3466e00b5bc3f7045144b7.

- Richardson, B., M. Richardson, G. González, A. Shiels, and D. Srivastava. 2010. "A Canopy Trimming Experiment in Puerto Rico: The Response of Litter Invertebrate Communities to Canopy Loss and Detritus Deposition in a Tropical Forest Subject to Hurricanes." *Ecosystems* 11: 286–301.
- Richardson, B. A., M. J. Richardson, and F. N. Soto-Adames. 2005. "Separating the Effects of Forest Type and Elevation on the Diversity of Litter Invertebrate Communities in a Humid Tropical Forest in Puerto Rico." *Journal of Animal Ecology* 74(5): 926–36.
- Rivera, F. 2008. "The Effect of a Natural Disturbance in the Microbial Community's Fatty Acid Profiles in the Luquillo Experimental Forest." MS Thesis, Universidad Ana G. Méndez, Gurabo, Puerto Rico.
- Sanaullah, M., C. Rumpel, X. Charrier, and A. Chabbi. 2012. "How Does Drought Stress Influence the Decomposition of Plant Litter with Contrasting Quality in a Grassland Ecosystem?" *Plant and Soil* 352: 277–88.
- Sandler, R., L. Falco, C. Di Ciocco, R. De Luca, and C. Coviella. 2010. "Eficiencia del embudo Berlese-Tullgren para extracción de artrópodos edáficos en suelos argiudoles típicos de la provincia de Buenos Aires." *Ciencia Del Suelo* 28: 1–7.
- Sayer, E. J., L. M. Sutcliffe, R. I. Ross, and E. V. Tanner. 2010. "Arthropod Abundance and Diversity in a Lowland Tropical Forest Floor in Panama: The Role of Habitat Space vs. Nutrient Concentrations." *Biotropica* 42(2): 194–200.
- Schreeg, L. A., M. C. Mack, and B. L. Turner. 2013. "Nutrient-Specific Solubility Patterns of Leaf Litter across 41 Lowland Tropical Woody Species." *Ecology* 94: 94–105.
- Shiels, A. B., and G. González. 2014. "Understanding the Key Mechanisms of Tropical Forest Responses to Canopy Loss and Biomass Deposition from Experimental Hurricane Effects." *Forest Ecology and Management* 332: 1–10.
- Shiels, A. B., G. González, D. J. Lodge, M. R. Willig, and J. K. Zimmerman. 2015. "Cascading Effects of Canopy Opening and Detritus Deposition from a Large-Scale Hurricane Experiment in a Tropical Rain Forest." *Bioscience* 65: 871–81.
- Shiels, A., J. Zimmerman, D. García-Montie, I. Jonckheere, J. Holm, D. Horton, and N. Brokaw. 2010. "Plant Responses to

Simulated Hurricane Impacts in a Subtropical Wet Forest, Puerto Rico." *Journal of Ecology* 98: 659–67.

- Silver, W. L., S. J. Hall, and G. González. 2014. "Differential Effects of Canopy Trimming and Litter Deposition on Litterfall and Nutrient Dynamics in a Wet Subtropical Forest." *Forest Ecol*ogy and Management 332: 47–55.
- Steudler, P. A., J. M. Melillo, R. D. Bowden, M. S. Castro, and A. E. Lugo. 1991. "The Effects of Natural and Human Disturbances on Soil Nitrogen Dynamics and Trace Gas Fluxes in a Puerto Rican Wet Forest." *Biotropica* 23: 356–63.
- Sun, J., X. Wei, Y. Zhou, C. Chan, and J. Diao. 2022. "Hurricanes Substantially Reduce the Nutrients in Tropical Forested Watersheds in Puerto Rico." *Forests* 2022(13): 71. https://doi. org/10.3390/f13010071.
- Swift, M. J., O. W. Heal, J. M. Anderson, and J. M. Anderson. 1979. Decomposition in Terrestrial Ecosystems. Berkeley, CA: University of California Press.
- Tanner, E. V. J., P. M. Vitousek, and E. Cuevas. 1998. "Experimental Investigations of Nutrient Limitation of Forest Growth on Tropical Mountains." *Ecology* 79: 10–22.
- Torres, J. A. 1992. "Lepidoptera Outbreaks in Response to Successional Changes after the Passage of Hurricane Hugo in Puerto Rico." *Journal of Tropical Ecology* 8: 285–98.
- Triplehorn, C. A., and N. F. Johnson. 2005. Borror and DeLong's Introduction to the Study of Insects. Belmont, CA: Thompson Brooks.
- Turner, B. L., T. Brenes-Arguedas, and R. Condit. 2018. "Pervasive Phosphorus Limitation of Tree Species but Not Communities in Tropical Forests." *Nature* 555(7696): 367–70.
- U.S. Drought Monitor. 2018. "Caribbean." https://droughtmonitor. unl.edu/CurrentMap/StateDroughtMonitor.aspx?Caribbean.
- Van Beusekom, A. E., G. González, S. Stankavich, J. K. Zimmerman, and A. Ramírez. 2020. "Understanding Tropical Forest Abiotic Response to Hurricanes Using Experimental Manipulations, Field Observations, and Satellite Data." *Biogeosciences* 17: 3149–63. https://doi.org/10.5194/bg-17-3149-2020.
- Vincent, A. G., B. L. Turner, and E. V. J. Tanner. 2010. "Soil Organic Phosphorus Dynamics Following Perturbation of Tropical Moist Forest." *European Journal of Soil Science* 61: 48–57.
- Vitousek, P. M., and R. L. Sanford, Jr. 1986. "Nutrient Cycling in Moist Tropical Forest." *Annual Review of Ecology and Systematics* 17: 137–67.
- Walker, L. R., W. L. Silver, M. R. Willig, and J. K. Zimmerman. 1996. "Long-Term Responses of Caribbean Ecosystems to Disturbance." *Biotropica* 28: 414–614.
- Wall, D. H., M. A. Bradford, M. G. St, J. A. John, V. Trofymow, D. E. Behan-Pelletier, and X. Z. Bignell. 2008. "Global Decomposition Experiment Shows Soil Animal Impacts on Decomposition Are Climate-Dependent." *Global Change Biology* 14(11): 2661–77. https://doi.org/10.1111/j.1365-2486.2008.01672.x.
- Walter, D. E. 1987. "Below-Ground Arthropods of Semiarid Grasslands." In Integrated Pest Management on Rangeland: A Shortgrass Prairie Perspective, edited by J. L. Capinera, 271–90. Boulder, CO: Westview Press.
- Wardle, D. A. 1999. "How Soil Food Webs Make Plants Grow." Trends in Ecology & Evolution 14: 418–20.
- Wardle, D. A., and P. Lavelle. 1997. "Linkages between Soil Biota, Plant Litter Quality and Decomposition." In Proceedings of an International Symposium, Driven by Nature, edited by G.

Cadisch and K. E. Giller, 107–24, September 17–20, 1995, London. Wallingford: CAB International.

- Wardle, D. A. 2013. Communities and Ecosystems: Linking the Aboveground and Belowground Components (MPB-34). Princeton, NJ: Princeton University Press.
- Willig, M. R., D. L. Moorehead, S. B. Cox, and J. C. Zak. 1996. "Functional Diversity of Soil Bacterial Communities in the Tabonuco Forest: The Interaction of Anthropogenic and Natural Disturbance." *Biotropica* 28: 471–48.
- Zalamea, M., and G. González. 2008. "Leaffall Phenology in a Sub-Tropical Wet Forest in Puerto Rico: From Species to Community Patterns." *Biotropica* 40: 295–304.
- Zhang, X., Q. Zhang, A. Li, W. Zhu, J. Z. Liang, and Y. Steinberger. 2012. "Effects of Tillage and Residue Management on Soil Nematode Communities in North China." *Ecological Indicators* 13: 75–81. https://doi.org/10.1016/j.ecolind.2011.05.009.
- Zhao, M., and I. M. Held. 2012. "TC-Permitting GCM Simulations of Hurricane Frequency Response to Sea Surface Temperature Anomalies Projected for the Late-Twenty-First Century." *Journal of Climate* 25: 2995–3009.
- Zimmerman, J. K., J. A. Hogan, A. B. Shiels, J. E. Bithorn, S. M. Carmona, and N. Brokaw. 2014. "Seven-Year Responses of Trees to Experimental Hurricane Effects in a Tropical

Rainforest, Puerto Rico." *Forest Ecology and Management* 332: 64–74.

- Zimmerman, J. K., W. M. Pulliam, D. J. Lodge, V. Quiñones-Orfila, N. Fetcher, S. Guzman-Grajales, J. A. Parrotta, C. E. Asbury, L. R. Walker, and R. B. Waide. 1995. "Nitrogen Immobilization by Decomposing Woody Detritus and the Recovery of Tropical Wet Forest from Hurricane Damage." *Oikos* 72: 314–22.
- Zou, X., C. P. Zucca, R. B. Waide, and W. H. McDowell. 1995. "Long-Term Influence of Deforestation on Tree Species Composition and Litter Dynamics of a Tropical Rain Forest in Puerto Rico." *Forest Ecology and Management* 78: 147–57.

How to cite this article: Moreno, Ivia I., Maria F. Barberena-Arias, Grizelle González, D. Jean Lodge, and Sharon A. Cantrell. 2022. "Canopy Opening Increases Leaf-Shredding Arthropods and Nutrient Mineralization but Not Mass Loss in Wet Tropical Forest." *Ecosphere* 13(6): e4084. <u>https://doi.org/10.1002/ecs2.4084</u>