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Litterfall Production Prior to and during Hurricanes Irma and Maria in Four Puerto Rican Forests

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Abstract: Hurricanes Irma and Maria struck Puerto Rico on the 6th and 20th of September 2017, respectively. These two powerful Cat 5 hurricanes severely defoliated forest canopy and deposited massive amounts of litterfall in the forests across the island. We established a 1-ha research plot in each of four forests (Guánica State Forest, Río Abajo State Forest, Guayama Research Area and Luquillo Experiment Forest) before September 2016, and had collected one full year data of litterfall production prior to the arrival of Hurricanes Irma and Maria. Hurricane-induced litterfall was collected within one week after Hurricane Irma, and within two weeks after Hurricane Maria. Each litterfall sample was sorted into leaves, wood (branches and barks), reproductive organs (flowers, fruits and seeds) and miscellaneous materials (mostly dead animal bodies or feces) after oven-drying to constant weight. Annual litterfall production prior to the arrival of Hurricanes Irma and Maria varied from 4.68 to 25.41 Mg/ha/year among the four forests, and annual litterfall consisted of 50–81% leaffall, 16–44% woodfall and 3–6% fallen reproductive organs. Hurricane Irma severely defoliated the Luquillo Experimental Forest, but had little effect on the other three forests, whereas Hurricane Maria defoliated all four forests. Total hurricane-induced litterfall from Hurricanes Irma and Maria amounted to 95–171% of the annual litterfall production, with leaffall and woodfall from hurricanes amounting to 63–88% and 122–763% of their corresponding annual leaffall and woodfall, respectively. Hurricane-induced litterfall consisted of 30–45% leaves and 55–70% wood. Our data showed that Hurricanes Irma and Maria deposited a pulse of litter deposition equivalent to or more than the total annual litterfall input with at least a doubled fraction of woody materials. This pulse of hurricane-induced debris and elevated proportion of woody component may trigger changes in biogeochemical processes and soil communities in these Puerto Rican forests.

Keywords: annual litterfall; Hurricane Irma; Hurricane Maria; Puerto Rico; subtropical forest; the Guayama Research Area; the Guánica State Forest; the Luquillo Experimental Forest; the Río Abajo State Forest; wood debris

1. Introduction

Litterfall regulates nutrient cycling [1], changes diversity and biomass of soil and litter invertebrates [2,3], boosts the transfer of soil CO_2 to the atmosphere [4], may cause seedling mortality [5], is a major source of soil organic carbon [6], and reflects the complex interaction between

environmental and physiological factors [7,8] in forest ecosystems. The instant input of massive litterfall amounts after a hurricane can trigger changes in physical and chemical environments within forests at both small and large temporal and spatial scales, resulting in the alteration of forest successional stage and development [9,10]. Hurricane-induced leaffall can return nutrients to soil within a few months, while woodfall alters soil nutrients and changes the microenvironment over a decadal time scale [9,11,12]. In addition, a thick litterfall accumulation on the forest floor offers abundant food and shelter for soil organisms [12] and fuel for wildfires [13,14].

Forest productivity is the primary factor controlling litterfall production [15,16]. Annual litterfall production of the world's tropical forests have been reported to range from 15.3 Mg/ha/year in Zambezian woodlands [17] to 5.2 Mg/ha/year in Hawaiian montane rain forests [1]. It was reported that the net primary productivity in Puerto Rican Tabonuco forest, Palo Colorado forest and Elfin forest was 10.5, 7.6 and 3.7 Mg/ha/year, respectively, and the annual litterfalls were 8.6, 6.8 and 3.1 Mg/ha/year, respectively [18].

The most apparent impact of hurricanes on forests is the instantaneous defoliation in the forest canopy and the sudden massive amounts of litterfall on the forest floor [9,19,20]. Hurricane Hugo occurred in September 1989 and defoliated approximating 56% trees in study plots at El Verde in the Luquillo Experimental Forest [21]. Hurricane Iniki occurred in September 1992 and caused a decrease in the leaf area index of 3% to 59%, and deposited litterfall 1.4 times greater than annual litterfall in the Na Pali-Kona Forest Reserve in Kokee State Park, island of Kauai, Hawaii [20].

Hurricane Irma struck the northeastern part of Puerto Rico on 6 September 2017, reaching Cat 5 as it passed north of Puerto Rico [22], with the highest wind speed of 179 km/h measured on Culebra (https://www.nhc.noaa.gov/archive/2017/al11/al112017.update.09062000.shtml). Hurricane Maria passed through the island two weeks later, on 20 September, from the southeast corner to the northwest corner of Puerto Rico. The highest wind speed was 287 km/h (155 mph), making it a Cat 5 hurricane [22]. This study focused on the quantity and composition of litterfall prior to the arrival of and from Hurricanes Irma and Maria. Our objectives were to: (1) compare annual litter deposition and composition among four Puerto Rican forests prior to the arrival of Hurricanes Irma and Maria; and (2) evaluate litter deposition and composition resulting from Hurricanes Irma and Maria in the four Puerto Rican forests.

2. Materials and Methods

2.1. Study Sites

This study was conducted in four Puerto Rican forests: The Guánica State Forest, the Río Abajo State Forest, the Guayama Research Area and the Luquillo Experimental Forest (also known as El Yunque National Forest) from August 2016 to December 2017. In the Río Abajo State Forest and the Guayama Research Area, we established a 1-ha (100 m × 100 m) forest research plot before August 2016. The Guánica State Forest has a permanent 1.44-ha (120 m × 120 m) research plot [23], in which we selected a 1-ha (100 m × 100 m) area in the center as our research plot. The Luquillo Experimental Forest has an approximately 13-ha (was divided into 88 grid points, on the scale of 40 m × 40 m for each grid point) permanent research plot in the Bisley Experimental Watersheds [24] in Sabana, where we selected 1-ha (100 m × 100 m) area in the eastern site of the research plot. According to the Holdridge Life Zone [25] and based on their locations in Puerto Rico, these four forests were named in this study as: Guánica dry forest, Río Abajo wet forest, Guayama moist forest and Bisley wet forest (Table 1).

Table 1. Plot information for the Guánica dry forest, the Río Abajo wet forest, the Guayama moist forest and the Bisley wet forest of Puerto Rico.

Forest	Location	Holdridge Life Zone	Coordinates	Elevation (m a.s.l.)	MAP (mm/year)	MAT (°C)	Relative Humidity (%)	Dominant Tree Species
Guánica dry forest	Guánica State Forest	Subtropical dry forest	17°58′17.47″ N 66°52′27.95″ W	162	860 [26]	25.8–26.5	65–72	*Gymnanthes lucida* Sw. *Exostema caribaeum* (Jacq.) Roem. & Schult. *Pisonia albida* (Heimerl) Britton
Río Abajo wet forest	Río Abajo State Forest	Subtropical wet forest	18°19′45.07″ N 66°42′38.10″ W	355	2050 [27]	22.9–23.6	92–96	*Hibiscus elatus* Sw. *Pinus caribaea* Morelet *Casearia sylvestris* Sw.
Guayama moist forest	Guayama Research Area	Subtropical moist forest	18°02′18.31″ N 66°10′08.27″ W	311	1420 [27]	23.7–24.2	74–80	*Bucida buceras* L. *Licaria parvifolia* (Lam.) Kosterm *Andira inermis* (W. Wright) H. B. K.
Bisley wet forest	Luquillo Experimental Forest	Subtropical wet forest	18°18′57.08″ N 65°44′40.22″ W	319	3000–4000 [28]	22.1–23.0	93–97	*Dacryodes excelsa* Vahl *Prestoea montana* (R. Grah.) Nichols *Manilkara bidentata* (A. DC.) Chev.

Note: MAP means Mean Annual Precipitation; MAT means Mean Annual Temperature.

The Guánica dry forest is located in southwestern Puerto Rico and is managed by the Department of Natural and Environmental Resource of Puerto Rico (DRNA) (Figures 1 and 2a). The 1.44-ha permanent forest research plot in this forest was established in 1981, with mostly mature trees. Stem density was 10,400 per hectare (≥2.5 cm diameter at breast height (dbh)), and the number of tree species was 37 [23,26]. Average tree height was 5.2–7.8 m. The dominant tree species included *Gymnanthes lucida* Sw., *Exostema caribaeum* (Jacq.) Roem. & Schult., *Pisonia albida* (Heimerl) Britton, *Pictetia aculeate* (Vahl) Urban, and *Thouinia portoricensis* Radlk. [23]. The Río Abajo wet forest is located in northwestern Puerto Rico and is managed by the DRNA (Figures 1 and 2b). We established a new 1-ha (100 m × 100 m) forest research plot in August 2016 and finished the census of tree species and individuals (stem ≥ 1.0 cm dbh) in November 2017. Stem density was 4200 per hectare, and the number of tree species was 70. Average tree height was 23.9–37.8 m. Dominant tree species included *Hibiscus elatus* Sw., *Casearia sylvestris* Sw., *Guarea Guidonia* (L.) Sleumer, *Calophyllum calaba* Jacq. and *Pinus caribaea* Morelet (unpublished data collected by Xianbin Liu and Xiucheng Zeng). The Guayama moist forest is located in southeastern Puerto Rico and is administered by the USDA Forest Service International Institute of Tropical Forestry (IITF) (Figures 1 and 2c). A new 1-ha (100 m × 100 m) forest research plot was established and census of tree species and individuals (stem ≥ 1.0 cm dbh) were completed before July 2015. Stem density was 4000 per hectare, and the number of tree species was 76. Average tree height was 15.7–24.6 m. The dominant tree species included *Bucida buceras* L., *Casearia guianensis* (Aubl.) Urban, *Pictetia aculeate* (Vahl) Urban, *Andira inermis* (W. Wright) H. B. K., and *Licaria parvifolia* (Lam.) Kosterm (unpublished data collected by Xiucheng Zeng and J. Aaron Hogan). The Bisley wet forest is located in northeastern Puerto Rico and is administered by the IITF (Figures 1 and 2d). Total area of the original research plot in the Bisley Experimental Watersheds was approximately 13-ha [24]. We selected a 1-ha area (100 m × 100 m) in the eastern corner as our research plot. Stem density was 3200 per hectare (≥1.0 cm dbh), and the number of tree species was 36. Average tree height was 22.5–31.6 m. This forest was dominated by *Dacryodes excelsa* Vahl, *Prestoea montana* (R. Grah.) Nichols, *Inga vera* Wild., *Manilkara bidentata* (A. DC.) Chev. and *Alchornea latifolia* Sw. [24].

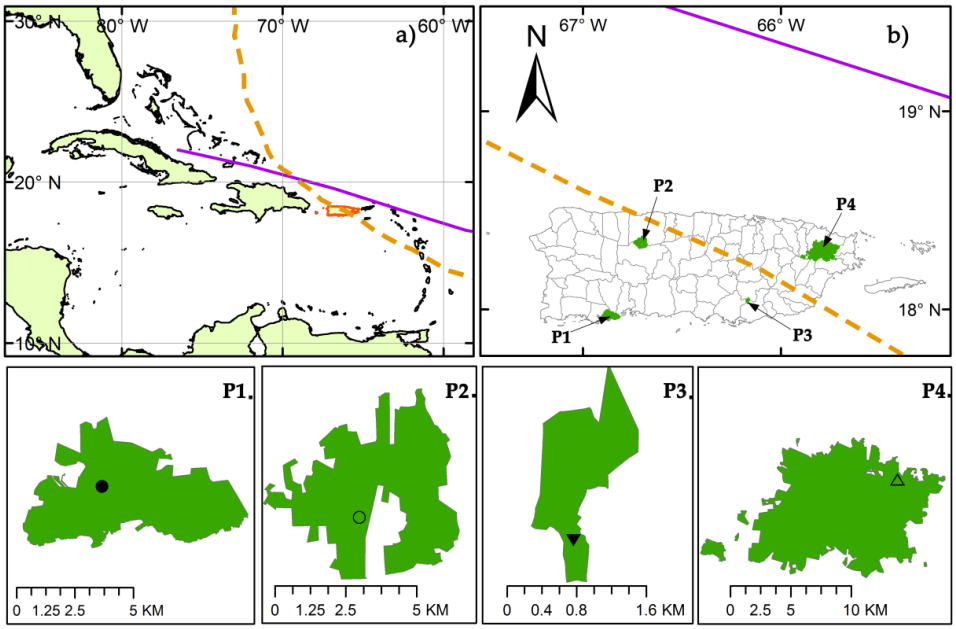

Figure 1. (**a**) Tracks of Hurricanes Irma (purple solid line) and Maria (brown dotted line) across the Caribbean basin (the island with red boundary is Puerto Rico); (**b**) Location of the four research forests in Puerto Rico (P1: the Guánica dry forest; P2: the Río Abajo wet forest; P3: the Guayama moist forest; and P4: the Bisley wet forest). Note: Marks (●, ○, ▼ and △) represent, respectively, the location of 1-ha research plot in each forest.

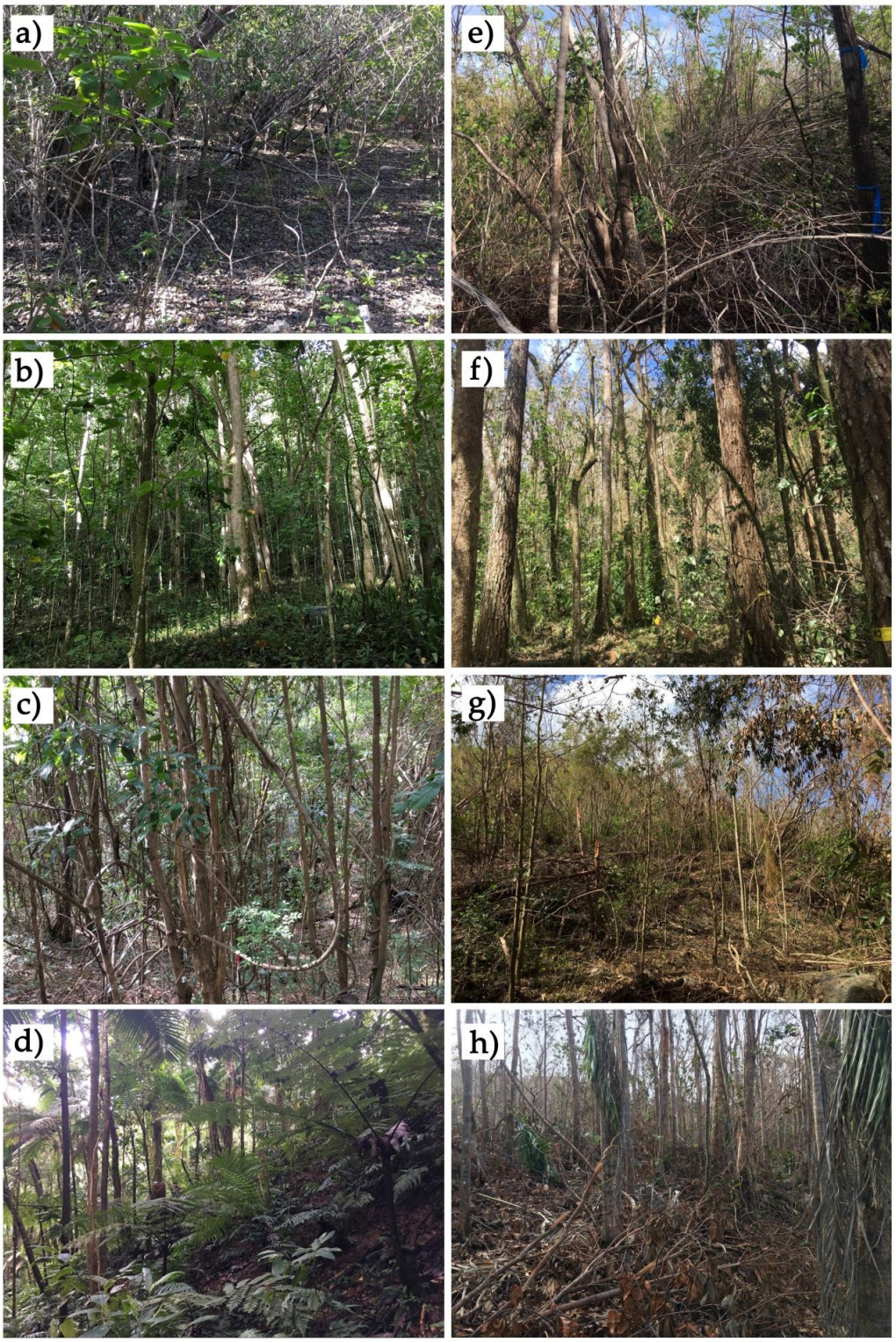

Figure 2. Photos of the four Puerto Rican forests before and after Hurricanes Irma and Maria: (**a**) the Guánica dry forest before Hurricane Irma; (**b**) the Río Abajo wet forest before Hurricane Irma; (**c**) the Guayama moist forest before Hurricane Irma; (**d**) the Bisley wet forest before Hurricane Irma; (**e**) the Guánica dry forest after Hurricane Maria; (**f**) the Río Abajo wet forest after Hurricane Maria; (**g**) the Guayama moist forest after Hurricane Maria; and (**h**) the Bisley wet forest after Hurricane Maria. The photos (**a**–**d**) were taken by Xianbin Liu in August 2016; the photos (**e**–**h**) were taken by Xianbin Liu in October 2017, within two weeks after Hurricane Maria.

2.2. Litterfall Sampling and Processing

We randomly placed 30 litterfall traps (0.5 m × 0.5 m) with 1 mm × 1 mm fiberglass mesh nettings at the end of August 2016 in the Río Abajo wet forest, the Guayama moist forest and the Sabana wet forest. The same work was also done in the Guánica dry forest, except that the litterfall traps were 0.7 m × 0.5 m in size [23]. All litterfall traps were supported by PVC pipes at the height of 0.5 m above ground.

We collected litterfall at monthly intervals starting in September 2016. The last litterfall collection before the arrival of Hurricane Irma was dated on the 4th and 5th of September 2017. On 6 September, Hurricane Irma stroked Puerto Rico with a peak wind speed of 179 km/h. Litterfall from Hurricane Irma was collected on 10 and 11 September 2017. After Hurricane Maria passed Puerto Rico on 20 September, litterfall was collected again within two weeks, on 2 and 3 October 2017. All the collected litterfall samples were transported to the lab in the University of Puerto Rico-Río Piedras campus on the same day, weighed wet weight, oven-dried for 10 days at 65–70 °C to constant weight, then divided into leaves, wood (branches and barks), reproductive organs (flowers, fruits and seeds), and miscellaneous materials (mostly dead animal bodies or animal feces).

2.3. Data Collection

We determined coordinates and elevation at the center of each forest research plot by Garmin GPS 72H (Garmin, Olathe, KS, USA). Mean temperature and relative humidity were determined four times during the year (September and December 2016, March and June in 2017) between 10 a.m. and 3 p.m. on a sunny day, by Extech Digital Hygro-thermometer 445717 (Extech Instrument Inc., 445703, Waltham, MA, USA).

2.4. Data Analysis

The data of monthly, annual, and hurricane-induced litterfall, leaffall, woodfall, fallen reproductive organs and miscellaneous materials were calculated using the corresponding data from the 30 litterfall traps in the same forest.

We pooled two collections of litterfall samples from the same litterfall traps to form a hurricane-induced composite sample, one from Hurricane Irma and one from Hurricane Maria.

The ratio of leaffall, woodfall and fallen reproductive organs to total litterfall (annual litterfall, hurricane-induced litterfall) was calculated from the same litterfall traps. The standard error of ratios was performed among the data from the 30 litterfall traps. The ratio of hurricane-induced litterfall to annual litterfall from the same trap was performed, and the standard error of ratios was calculated among the data from the 30 litterfall traps.

We compared the statistical difference of annual and hurricane-induced litterfall, leaffall, woodfall, fallen reproductive organs and miscellaneous materials among the four forests by one-way ANOVA using the software Statistical Package for the Social Sciences 20 (SPSS 20). The independent variables were the four forests, and the dependent variables were annual and hurricane-induced litterfall, leaffall, woodfall, fallen reproductive organs and miscellaneous materials. Differences among the four forests were also tested for the ratios of annual and hurricane-induced leaffall, woodfall, fallen reproductive organs to total annual and hurricane-induced litterfall, and for ratios of annual and hurricane-induced leaffall, woodfall, fallen reproductive organs to total annual and hurricane-induced litterfall with the four forests as independent variable. A total of 1680 litterfall samples were calculated for this study. All data were log-transformed prior to analyses in order to meet the homogeneity (Levene's test [29]) and normality (Kolmogorov-Smirnov test [30]) requirements. The significance level was set at $\alpha < 0.05$.

3. Results

3.1. Annual Litterfall Prior to Hurricanes

Prior to the arrival of the Hurricanes Irma and Maria, annual litterfall varied greatly among the four forests. The highest litterfall production was found in the Río Abajo wet forest with 25,409 kg/ha/year that differed significantly from the Guánica dry forest and the Guayama moist forest, but not from the Bisley wet forest (Table 2). Annual leaffall in the Bisley wet forest was highest with 15,581 kg/ha, significantly higher than the other three forests. Annual fallen wood and reproductive organs in the Río Abajo wet forest were significantly higher than the other three forests. Miscellaneous materials in the Guayama moist forest (mostly bird feces) was highest with 59 kg/ha/year that differed significantly from the Guánica dry forest (mostly bird feces) and the Bisley wet forest (mostly *Pleurodonte caracolla*), but did not differ from the Río Abajo wet forest (mostly *Eleutherodactylus coquí* and *Pleurodonte caracolla*). Among these four forests, the Guánica dry forest had the least total litterfall, leaffall, woodfall, fallen reproductive organs and miscellaneous materials during the year prior to the Hurricanes Irma and Maria.

The monthly variation of litterfall prior to Hurricanes Irma and Maria differed drastically among the four forests (Figure 3). There was a pronounced high litterfall peak between August and September in the Río Abajo wet forest, attributed to high woodfall (Figure 3c). In comparison, the other three forests had relatively less pronounced seasonality in litterfall and woodfall. In the Guánica dry forest, high leaffall occurred in the dry season of February and March and again in the early summer of May and June, and high production of fallen reproductive organs occurred from November through March. In the Guayama moist forest, high leaffall occurred in the dry season of March and again in the late summer of August and September, and high production of fallen reproductive organs occurred between May (mostly flowers) and July (mostly fruit). In the Bisley wet forest, high leaffall occurred from October through February and again in July, and high production of fallen reproductive organs occurred in March (mostly flowers) and in June and July (mostly fruit). The Guayama moist forest differed from all the other three forests by having a very weak seasonality of leaffall yet still maintaining a strong seasonality of reproductive organ production. In the Río Abajo wet forest, leaffall peaked four times for every period of three months with similar values, but high production of reproductive organs occurred during the period from December through March and was near zero in September.

Table 2. Mean (±SE) annual leaffall, woodfall, fallen reproductive organs and miscellaneous materials prior to Hurricanes Irma and Maria from September 2016 to August 2017 and litterfall from Hurricanes Irma and Maria in the four forest research plots of the Guánica dry forest, the Río Abajo wet forest, the Guayama moist forest and the Bisley wet forest in Puerto Rico. Same superscripts (a, b and c) indicate no significant difference among forests at $\alpha = 0.05$.

Forest	Leaffall (±SE)	Woodfall (±SE)	Fallen Reproductive Organs (±SE)	Miscellaneous Components (±SE)	Total Litterfall (±SE)
Annual litterfall (kg/ha/year)					
Guánica dry forest	3779.69 ^{c} (44.41)	738.23 ^{c} (5.71)	259.90 ^{c} (5.48)	0.40 ^{b} (0.32)	4681.50 ^{c} (45.70)
Río Abajo wet forest	12,762.76 ^{a} (69.06)	11,094.36 ^{a} (497.37)	1533.41 ^{a} (25.22)	33.88 ^{a} (15.81)	25,409.43 ^{a} (467.89)
Guayama moist forest	9559.94 ^{b} (90.59)	4635.88 ^{b} (73.88)	813.85 ^{b} (19.10)	58.64 ^{a} (35.49)	14,837.76 ^{b} (112.50)
Bisley wet forest	15,580.75 ^{a} (115.40)	3692.83 ^{b} (69.35)	654.16 ^{b} (13.02)	0.73 ^{b} (0.73)	20,064.55 ^{a} (136.53)
Litter deposition resulting from hurricane Irma (kg/ha)					
Guánica dry forest	137.31 ^{c} (55.86)	60.16 ^{c} (14.52)	0 ^{b}	0	197.48 ^{d} (57.65)
Río Abajo wet forest	323.01 ^{b} (36.02)	330.28 ^{bc} (119.77)	60.21 ^{a} (60.21)	0	713.51 ^{c} (134.32)
Guayama moist forest	479.53 ^{b} (76.04)	852.73 ^{b} (227.58)	0 ^{b}	0	1332.27 ^{b} (246.00)
Bisley wet forest	10,563.45 ^{a} (4889.76)	21,269.27 ^{a} (5691.80)	0 ^{b}	0	31,832.72 ^{a} (5787.55)
Litter deposition resulting from hurricane Maria (kg/ha)					
Guánica dry forest	2231.26 ^{b} (182.03)	5575.20 ^{b} (1422.12)	0 ^{b}	0	7802.30 ^{b} (1460.36)
Río Abajo wet forest	9192.44 ^{a} (1012.30)	13,192.36 ^{a} (3527.36)	1171.37 ^{a} (356.33)	0	23,489.17 ^{a} (3875.63)
Guayama moist forest	7951.37 ^{a} (1285.42)	9529.53 ^{ab} (1717.91)	0 ^{b}	0	17,260.00 $^{a\,b}$ (2869.89)
Bisley wet forest	351.00 ^{c} (33.72)	48.03 ^{c} (9.98)	0 ^{b}	0	392.35 ^{c} (31.50)
Litter deposition combined hurricanes Irma and Maria (kg/ha)					
Guánica dry forest	2368.57 ^{b} (183.07)	5635.36 ^{c} (1420.02)	0 ^{b}	0	7999.78 ^{c} (1460.19)
Río Abajo wet forest	9515.45 ^{a} (1010.12)	13,522.64 ^{b} (3502.94)	1231.59 ^{a} (391.44)	0	24,202.68 ^{ab} (3844.99)
Guayama moist forest	8430.91 ^{ab} (1285.39)	10,382.27 ^{bc} (1697.42)	0 ^{b}	0	18,592.27 ^{b} (2845.43)
Bisley wet forest	10,914.45 ^{a} (1904.87)	21,317.29 ^{a} (5692.11)	0 ^{b}	0	32,225.07 ^{a} (5788.18)

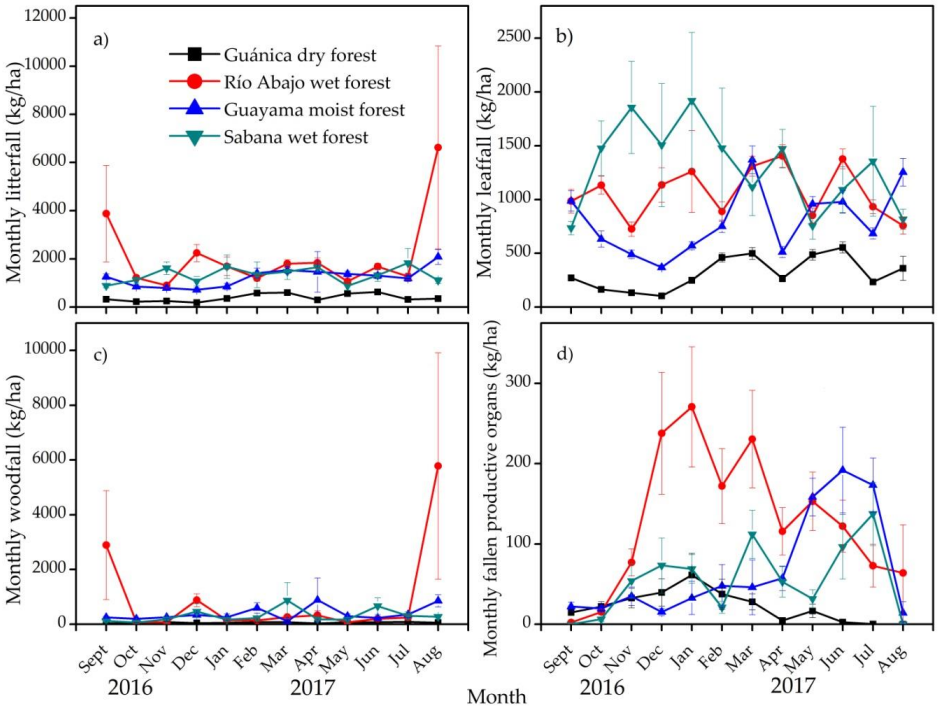

Figure 3. Monthly litterfall (±SE) (**a**), leaffall (**b**), woodfall (**c**) and fallen reproductive organs (**d**) from September 2016 to August 2017 in the four forest research plots of the Guánica dry forest, the Río Abajo wet forest, the Guayama moist forest and the Bisley wet forest in Puerto Rico.

3.2. Hurricane Damages

All trees in these four forest research plots suffered severe hurricane damage varying from near-complete defoliation to tree snapping or uprooting. In the Guánica dry forest, only a few tree stems were snapped by Hurricanes Irma and Maria, but almost all tree individuals were totally defoliated except a few species, such as *Gymnanthes lucida* Sw. and *Reynosia uncinata* Urb., which suffered only partial defoliation (Figure 2e). Of the 30 litterfall traps, two traps were blown over by hurricane winds and all the other 28 traps survived Hurricanes Irma and Maria. In the Río Abajo wet forest, all canopy tree species were totally defoliated, and most understory plant species were partially defoliated (Figure 2f). Almost all the crown branches of the forest canopy in the research plot were broken. There were few uprooted individuals in the plot. Among the 30 litterfall traps, three were brought down by fallen trees. In the Guayama moist forest, all plant species were totally defoliated including both canopy tree species and understory shrubs, except for a few understory shrubs and vines with partial defoliation (Figure 2g). The crown of most canopy tree species was severely broken. Few canopy tree individuals on slope areas were uprooted, and most individuals growing on alluvial soils along streams were uprooted by floods following Hurricanes Irma and Maria in the valley. Among the 30 litterfall traps, two were broken by fallen trees and two were washed away by the flood. In the Bisley wet forest, all plant species were totally defoliated including canopy tree species and understory shrubs, except for a few understory shrub and vine individuals with only partial defoliation (Figure 2h). The crown of most canopy tree species was severely broken. Compared to the other three forests, the Bisley wet forest had the most uprooted trees. Of the 30 litterfall traps, five were broken by fallen trees.

3.3. Litterfall from Hurricanes Irma and Maria

Hurricane Irma produced the highest amount of litterfall in the Bisley wet forest, with 31,833 kg/ha of total litterfall, 10,563 kg/ha of leaffall and 21,269 kg/ha of woodfall (Table 2). The Guánica dry forest

was least affected by Hurricane Irma with only 197 kg/ha litterfall production. Both the Río Abajo wet forest and the Guayama moist forest experienced partial defoliation. However, a significant amount of fallen reproductive organs (60 kg/ha, mostly pinecones and seeds of *Pinus caribaea* Morelet) were blown off the tree canopy in the Río Abajo wet forest by Hurricane Irma, and there were no fallen reproductive organs found in litterfall traps in the other three forests from Hurricane Irma (Table 2).

In contrast, Hurricane Maria produced the least amount of total litterfall in the Bisley wet forest, with only 392 kg/ha (Table 2). The Río Abajo wet forest had the highest total litterfall, leaffall and woodfall, with 23,489 kg/ha of total litterfall that was significantly greater than the other three forests. Again, the Río Abajo wet forest was the only one among the four forests with fallen reproductive organs (mostly pinecones and seeds of *Pinus caribaea* Morelet) amounting to 1171 kg/ha from Hurricane Maria.

Jointly, Hurricanes Irma and Maria produced the highest amount of total litterfall and leaffall in the Bisley wet forest, amounting to 32,225 kg/ha and 10,914 kg/ha, respectively, that were significantly greater than those in the Guánica dry forest and the Guayama moist forest, but did not differ from the Río Abajo wet forest (Table 2). Hurricanes Irma and Maria produced the highest amount of woodfall in the Bisley wet forest, and the least amount of woodfall in the Guánica dry forest and the Guayama moist forest. The Guánica dry forest had the least amount of total litterfall (8000 kg/ha) and leaffall (2369 kg/ha) produced by these two hurricanes. The Río Abajo wet forest was the only site with fallen reproductive organs (mostly pinecones and seeds of *Pinus caribaea* Morelet) from Hurricanes Irma and Maria.

3.4. Composition of Annual Litterfall and Hurricane-Induced Litterfall

For the annual litterfall prior to Hurricanes Irma and Maria, the Guánica dry forest had the highest ratio of leaffall to total litterfall (0.81), and the lowest ratio of woodfall to total litterfall (0.16) (Table 3). The Río Abajo wet forest had the lowest ratio of leaffall to total litterfall (0.50) and the highest ratio of woodfall to total litterfall (0.44). The Guayama moist forest had a lower ratio of leaffall to total litterfall and higher ratio of woodfall to total litterfall than the Bisley wet forest. Ratios of woodfall to total litterfall were all less than ratios of leaffall to total litterfall prior to Hurricanes Irma and Maria.

Following Hurricane Irma, the Guánica dry forest had the highest ratio of leaffall to total litterfall (0.70) and the lowest ratio of woodfall to total litterfall (0.30). The Bisley wet forest had the lowest ratio of leaffall to total litterfall (0.33) and the highest ratio of woodfall to total litterfall (0.67).

After Hurricane Maria, the Guánica dry forest had the lowest ratio of leaffall to total litterfall (0.29) and the highest ratio of woodfall to total litterfall (0.71). While the Bisley wet forest had the highest ratio of leaffall to total litterfall (0.89), and the lowest ratio of woodfall to total litterfall (0.11). In the Río Abajo wet forest and the Guayama moist forest, the ratio of leaffall to total litterfall was lower than the ratio of woodfall to total litterfall.

After Hurricanes Irma and Maria, the Guánica dry forest and the Bisley wet forest had the lowest ratio of leaffall to total litterfall (0.30), and the highest ratio of woodfall to total litterfall (0.70), whereas the Guayama moist forest had the highest ratio of leaffall to total litterfall (0.45) and the lowest ratio of woodfall to total litterfall (0.55). Ratios of woodfall to total litterfall were all greater than ratios of leaffall to total litterfall from Hurricanes Irma and Maria.

Table 3. Ratios of leaffall (L), woodfall (W) and reproductive organs (R) to total litterfall (T) prior to and from Hurricane Irma and Hurricane Maria in the Guánica dry forest, the Río Abajo wet forest, the Guayama moist forest and the Bisley wet forest in Puerto Rico.

Forest	Annual Litterfall			Litterfall from Hurricane Irma			Litterfall from Hurricane Maria			Litterfall from Irma + Maria		
	L/T	W/T	R/T	L/T	W/T	R/T	L/T	W/T	R/T	L/T	W/T	R/T
Guánica dry forest	0.81 ^{a}	0.16 ^{c}	0.06 ^{a}	0.70 ^{a}	0.30 ^{c}	0 ^{b}	0.29 ^{c}	0.71 ^{a}	0 ^{b}	0.30 ^{c}	0.70 ^{a}	0 ^{b}
Río Abajo wet forest	0.50 ^{c}	0.44 ^{a}	0.06 ^{a}	0.45 ^{b}	0.46 ^{b}	0.08 ^{a}	0.39 ^{bc}	0.56 ^{b}	0.05 ^{a}	0.39 ^{b}	0.56 ^{b}	0.05 ^{a}
Guayama moist forest	0.64 ^{b}	0.31 ^{b}	0.05 ^{a}	0.36 ^{c}	0.64 ^{a}	0 ^{b}	0.45 ^{b}	0.55 ^{b}	0 ^{b}	0.45 ^{a}	0.55 ^{b}	0 ^{b}
Bisley wet forest	0.78 ^{a}	0.18 ^{c}	0.03 ^{b}	0.33 ^{c}	0.67 ^{a}	0 ^{b}	0.89 ^{a}	0.11 ^{c}	0 ^{b}	0.34 ^{c}	0.66 ^{a}	0 ^{b}

Same superscripts (a, b and c) indicate no significant difference among forests at $\alpha = 0.05$.

3.5. Fractions of Hurricane Litterfall to Annual Litterfall

The four forests varied greatly in the ratios of hurricane-induced to annual total litterfall. The Guánica dry forest had the highest ratio of total hurricane-induced to annual litterfall (1.71), the lowest ratio of hurricane-induced to annual leaffall (0.63), and the highest ratio of hurricane-induced to annual woodfall (7.63; Table 4). The Río Abajo wet forest had the lowest ratio of hurricane-induced to annual total litterfall (0.95), and the lowest ratio of hurricane-induced to annual woodfall (1.22). The Guayama moist forest had the highest ratio of hurricane-induced to annual leaffall (0.88). In the Bisley wet forest, the ratio of hurricane-induced to annual total litterfall was 1.61, which was significant higher than the ratios in the Río Abajo wet forest and the Guayama moist forest but did not differ from those in the Guánica dry forest; the ratio of hurricane-induced to annual leaffall was 0.70, that was significant lower than the Guayama moist forest but did not differ from those in the other two forests; the ratio of hurricane-induced to annual woodfall was 5.77, which was intermediate among these four forests. Additionally, the Río Abajo wet forest deposited abundant hurricane-induced reproductive organs, with the ratio of hurricane-induced to annual fallen reproductive organs at 0.80.

Table 4. Ratios of total hurricane-induced litterfall (Th) to annual litterfall (Ta), hurricane-induced leaffall (Lh) to annual leaffall (La), hurricane-induced woodfall (Wh) to annual woodfall (Wa), and hurricane-induced fallen reproductive organs (Rh) to annual fallen reproductive organs (Ra) in the Guánica dry forest, the Río Abajo wet forest, the Guayama moist forest and the Bisley wet forest in Puerto Rico.

Forest	Th/Ta	Lh/La	Wh/Wa	Rh/Ra
Guánica dry forest	1.71 ^{a}	0.63 ^{c}	7.63 ^{a}	0 ^{b}
Río Abajo wet forest	0.95 ^{c}	0.75 ^{b}	1.22 ^{c}	0.80 ^{a}
Guayama moist forest	1.25 ^{b}	0.88 ^{a}	2.24 ^{c}	0 ^{b}
Bisley wet forest	1.61 ^{a}	0.70 ^{bc}	5.77 ^{b}	0 ^{b}

Same superscripts (a, b and c) indicate no significant difference among forests at $\alpha = 0.05$.

4. Discussion

4.1. Wind Strength of Hurricanes Irma and Maria

Hurricane Irma passed through Puerto Rico about 95 km from the northeast corner of the island. Wind gust speeds were recorded as 72.2, 68.5, 87.0, and 92.5 km/h in Guánica, Río Abajo, Guayama, and Fajardo near the Bisley wet forest, respectively (https://www.weather.gov/sju/irma2017). All of our study sites were under the impact of tropical storm strength wind.

Hurricane Maria passed through central Puerto Rico entering from Yabucoa near Guayama moist forest and leaving the island at Arecibo near the Río Abajo wet forest. Wind speed gusts of 145, 180, 190, and 161 km/h were recorded in Guánica, Río Abajo, Guayama, and Fajardo near the Bisley wet forest, respectively (https://www.weather.gov/sju/maria2017).

4.2. Pulse Input of Hurricane-Induced Litterfall

With a hurricane's passage, powerful wind energy at the forest canopy interface results in devastating defoliation and severe structural damage [9,31]. For example, Hurricane Gilbert completely defoliated all trees in the northeastern Yucatan Peninsula in September 1988, and deposited more hurricane litterfall than the amount of annual litterfall collected in 1984 [13]. Hurricane Iniki generated an instantaneous fine litterfall pulse equivalent to 1.4 times of annual litterfall input, and decreased leaf area index by 3% to 59% in the Na Pali-Kona Forest Reserve of Hawaii in September 1992 [20]. During the period from August 1992 to November 2000, sixteen typhoons passed through the Fushan Experimental Forest of northern Taiwan, and deposited hurricane-induced and annual litterfall varying from 10,800 kg/ha in 1994 to 3020 kg/ha in 1995 [19].

Among the four forest research plots in our study, all canopy trees and most understory shrubs were almost-completely defoliated by Hurricanes Irma and Maria (Figure 2e–h). This was especially evident in the Bisley wet forest, where the canopy trees and understory shrubs were completely defoliated, resulting in the highest hurricane-induced litterfall and the highest ratio of hurricane-induced litterfall to annual litterfall. Composite litterfall from Hurricanes Irma and Maria averaged 1.38 times annual litterfall production in the four research forests, with the highest in the Guánica dry forest and the Bisley wet forest (1.70) and the lowest in the Río Abajo wet forest (0.95). In the Guánica dry forest, average litterfall generated by Hurricanes Irma and Maria was 7999.78 kg/ha, similar to litterfall from hurricane Georges in 1998 [26]. Composite litterfall from Hurricanes Irma and Maria was 2.97 times the litterfall from Hurricane Hugo in September 1989, which meant Hurricanes Irma and Maria produced greater defoliation than Hurricane Hugo in the Bisley wet forest [32].

4.3. Variation among Puerto Rican Forests

The four Puerto Rican forests not only differ in the quantity of hurricane-induced litterfall from Hurricanes Irma and Maria, but also differ in the components of leaffall, woodfall, fallen reproductive organs and miscellaneous materials. The most pronounced differences occurred in the Río Abajo wet forest where hurricane fruitfall was the highest and woodfall was the lowest among the four forests. Prior to Hurricanes Irma and Maria, the Río Abajo wet forest had the highest fruitfall and woodfall. In fact, fruitfall remained high for 10 months during the year except for September and October. This might be the reason why the Río Abajo wet forest became the major refuge for the Puerto Rican parrot *Amazona vittata* [33–35]. Trees in the Río Abajo wet forest shed their branches regularly during the year without hurricane disturbances, and thus had less wood to shed during hurricanes.

The Guánica dry forest differed from the other three forests in our study by having shorter stature trees and often with multiple-stem clumps. Most plant species in the Guánica dry forest belonged to small trees or shrubs with multiple-stems and clumped-growth form that have strong root systems, resulting in less uprooting. Woodfall was low during the year without hurricane disturbance. Hurricanes Irma and Maria produced the highest ratio of hurricane-induced to annual woodfall in the Guánica dry forest, with insignificant difference from the Bisley wet forest.

The Guayama moist forest suffered the most severe flooding damage among the four forests. Precipitation in the Guayama moist forest was normally low and floods rarely occur during non-hurricane years. The Guayama moist forest is prone to damage by flooding because of thick loose alluvial soils along streams in the valleys. Most trees growing on alluvial soils in the valleys were uprooted by flooding during the hurricanes. In addition, the Guayama moist forest hosted the most plant species, the least number of multiple-stem clumps, and had the fewest old fallen-tree trunks. In addition, the Guayama moist forest had the highest ratio of fallen leaves from Hurricanes Irma and Maria to annual fallen leaves without hurricane disturbance.

The Bisley wet forest was almost completely defoliated including canopy trees and understory shrubs after the passage of Hurricanes Irma and Maria, with the highest total litterfall, leaffall and woodfall among the four forests. This forest suffered the most damage from Hurricane Irma compared with the other three forests. To our surprise, we found much less fruitfall in the Bisley wet forest, another refuge for the Puerto Rican parrot, during the year prior to hurricanes Irma and Maria than in the Río Abajo wet forest. This might be the reason why the Río Abajo wet forest bred more bird species than the Luquillo Mountains [35–37].

Because of the extremely powerful wind and the massive production of hurricane-induced litterfall, litterfall traps may underestimate hurricane litterfall production. Especially, woodfall from Hurricanes Irma and Maria was likely underestimated because our data did not represent trunk wood and large branches since tree trunks and large branches destroyed our litterfall traps (3 from Río Abajo wet forest, 2 from Guayama moist forest, and 5 from Bisley wet forest), and these data were excluded from our analyses. In addition, branches longer than the litterfall traps (0.50–0.71 m) were

more likely bounced out than into the litterfall traps. However, this underestimation of woodfall prior to Hurricanes Irma and Maria was likely less pronounced because few tree trunk and large branch fell.

We noticed that our data (20,064.55 kg/ha/year) of annual litterfall were apparently higher than the data (approximately 9100 kg/ha/year) of previous study conducted during the period of 1999–2000 in the same forest [38]. The causes for this variation can be either the systematic error embedded in the sampling methods where the earlier study set up litterfall traps along a trail that over-represents the ridges [28] and our litterfall traps were placed randomly across the entire 1-ha plot, or the forest was still in the process of recovery after Hurricane Georges and released less litterfall than pre-hurricane forest [39]. In our study, total annual litterfall in the Guánica dry forest was 4681.50 kg/ha, almost double that determined from August 1998 to August 2000, but with a similar ratio of fallen leaves and reproductive organs to total litterfall of approximately 85% [26]. This might be because of the varying forest successional states.

Nutrient concentrations of annual leaffall, such as N, P, K, Ca and Mg, were significantly lower than those in the hurricane-induced green leaffall in a tropical dry forest in the northeastern Yucatan Peninsula after Hurricane Gilbert and in the subtropical wet and lower montane rain forests of Puerto Rico after Hurricane Hugo [13,32]. In addition, litter and soil invertebrate community were altered by canopy loss and litterfall accumulation on the ground surface [3,40]. The complete loss of tree canopy and thick deposition of floor mass in these four forests after Hurricanes Irma and Maria will release abundant nutrients to the soil and greatly alter litter and soil communities. In the long-term, sudden litter deposition can significantly increase surface- and subsoil carbon and nutrient storage [11,32,41], and the decaying wood in the forest can affect physical, chemical, and biotic properties on the underlying soil [12,42,43].

5. Conclusions

In summary, Hurricanes Irma and Maria caused significant defoliation to Puerto Rican forests, resulting in massive amounts of hurricane-induced litterfall equivalents to 95–171% of the annual litterfall production in dry, moist and wet forests. Furthermore, hurricane-induced litterfall differs from annual litterfall by consisting of a high fraction of woodfall and a low fraction of reproductive organs.

Hurricane Irma severely defoliated the Bisley wet forest but had little effect on the other three forests. In contrast, Hurricane Maria severely struck all four forests. The Bisley wet forest deposited the most hurricane-induced litterfall, and the Guánica dry forest produced the least hurricane-induced litterfall. The Guánica dry forest had the highest ratio of hurricane-induced to annual litterfalls, the lowest ratio of leaffall from hurricanes to annual leaffall and the highest ratio of woodfall from hurricanes to annual woodfall. The Bisley wet forest had the second highest ratio of hurricane-induced to annual woodfall. The Río Abajo wet forest deposited abundant hurricane-induced reproductive organs. The pulse and components of hurricane-induced litterfall vary among these forests.

Author Contributions: X.L., X.Z. (Xiaoming Zou) and G.G. designed this study; X.L. placed the litterfall traps in the four forest fields; X.L., X.Z. (Xiucheng Zeng), and C.W. collected litterfall from forest fields; X.L. processed the litterfall samples at lab; X.L., X.Z. (Xiaoming Zou) and X.Z. (Xiucheng Zeng) analyzed the data; X.L. took the photos of the four forests before and after hurricanes Irma and Maria; X.L. and C.W. made the tables and figures; X.L. wrote the manuscript; X.Z. (Xiaoming Zou) and G.G. revised the manuscript; S.Y. participated in partial field work.

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