Hurricane driven changes in vegetation structure and ecosystem services in tropical urban yards: a study case in San Juan, Puerto Rico

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Abstract
Urban forests are valuable spaces for species conservation, protection of local biodiversity and provision of ecosystem services. However, they are also vulnerable to the impact of extreme climate events like hurricanes. Understanding how urban forests are responding to hurricane disturbances is crucial to improve their design, management, and resilience. Here we analyzed pre-and post-hurricane vegetation surveys in 52 residential yards in San Juan to assess urban forest responses after Hurricanes Irma and María impacted Puerto Rico in 2017. We used these surveys to compare vegetation structure and composition (including species-specific mortality and damage rates) and to quantify changes in the ecosystem services provided by these yards. We found that hurricane disturbances significantly altered the structure but not the composition of yard vegetation. We detected a 27% reduction and 31% mortality of standing stems, and a significant reduction in plants health. Yard species composition was dominated by non-native species and this trend did not change with hurricane disturbance. Changes in vegetation structure translated into substantial reductions in ecosystem services. Food provision, an important service provided by a large proportion of yards before the hurricane, reported the highest reduction (41.9%) while carbon storage was the service that changed the least (9%). Our combined results emphasize the key role played by residential yards providing ecosystem services in tropical cities and call for further efforts to manage private and public urban forests in ways that may ensure their resilience to mitigate extreme climate events, provide multiple ecosystem services, and promote long-term urban sustainability.

Keywords Caribbean · i-Tree · Non-native trees · Tree mortality · Urban forestry · Wind damage

Introduction
Globally, urban forests provide many essential ecosystem services such as carbon sequestration, reduction of air and noise pollution, mitigation of urban heat island effect and flood risk and they are also important recreational areas (Kleerekoper et al. 2012; Roy et al. 2012; Berland et al. 2017; Escobedo et al. 2019). Private green spaces (e.g., residential yards and gardens) are increasingly in the spotlight as important contributors of some of these ecosystem services because they often contain most of the urban forest resources and may provide functional connectivity across green infrastructure in cities (Gaston et al. 2005; Cook et al. 2012; Nowak and Greenfield 2018). However, studies have shown that in cities, both public and private green spaces are vulnerable to the impacts of climate change (Burley et al. 2008; Foran et al. 2015; Ordóñez-Barona and Duinker 2014; Yan and Yang 2018). Climate change models predict increases in extreme climate events worldwide, (i.e., hurricanes, tornadoes, snowstorms, heat waves, and flooding), which could disproportionately impact cities (Méndez-Lázaro et al. 2016; Yin et al. 2018; Steenberg et al. 2019). Evidence shows that urban areas are often more vulnerable to these events compared to natural areas due to the high concentration of people, infrastructure, and services (Dickson et al. 2012; McPhillips et al. 2018; Elmqvist et al. 2019). Additionally, urban forests that provide multiple ecosystem services to city residents and often mitigate problems associated to the urban
condition and climate change are also expected to experience extreme weather events (Gill et al. 2007; Matthews et al. 2015; Laforteza et al. 2017; Zölch et al. 2016; Khan and Conway 2020; Bonilla-Duarte et al. 2021). Therefore, it is critical to understand the responses of urban forests to extreme climate events for their successful planning and management in ways that ensure their resilience and sustainability in the face of climate change.

Tropical cyclones, also known as hurricanes and ty phoons, are large-scale natural disturbances with the potential to affect the structure, composition, and function of forested ecosystems in many parts of the world (Tanner et al. 2014; Xi 2015). Across the Caribbean region, hurricanes are common events, but their intensity is expected to increase in the future due to climate change (Gould et al. 2015; Kossin et al. 2020). For this region, there is a vast number of studies showing that hurricane disturbances and recovery responses can play a key role in influencing tree community composition (Lugo 2000; Ostertag et al. 2005; Canham et al. 2010; Brokaw et al. 2012). Additionally, hurricane disturbances may generate heterogeneous environments, increase resources, reduce competition, and generate growing spaces for plant recruitment (Webster et al. 2005). However, most of this information is circumscribed to natural forests limiting our understanding on how urban forests are responding to hurricane disturbances.

In 2017, Puerto Rico was impacted by two intense hurricanes. Hurricane Irma (category 5) passed 90 km north of Puerto Rico on September 7, 2017, leaving perceivable impacts on the island’s green and grey infrastructure (Uriarte et al. 2019). Two weeks later, hurricane María (category 4) struck Puerto Rico with sustained winds of 155 mph and the highest rainfall intensity ever recorded on the island (Ramos-Scharrón and Arima 2019). The combined impact of these two hurricanes caused the destruction of electric infrastructure, major disruptions in telecommunications, significant damage to highways and roads, and resulted in limited access to potable water and food for several weeks (Rodriguez-Díaz 2018). Additionally, these hurricanes severely affected urban and natural forests across Puerto Rico, with an estimated immediate loss of greenness ranging from 31%-51% (Van Beusekom et al. 2018) and between 20–40 million trees killed or severely damaged (Feng et al. 2018; Uriarte et al. 2019).

The passage of hurricanes Irma and María presented an extraordinary opportunity to evaluate the extent of damage on green urban spaces and to assess how these green spaces are responding to hurricane disturbances. Here, we took advantage of an ongoing study monitoring residential yards in San Juan that was interrupted by the impacts of these two major hurricanes. Rapid post-hurricane vegetation assessments were conducted in yards previously surveyed. We used these yards to perform a direct comparison of pre- and post-hurricane conditions. The specific goals of this study were to: (1) determine the impact of hurricanes Irma and María on vegetation structure and composition of San Juan residential yards by comparing pre- and post-hurricanes vegetation surveys, (2) evaluate and quantify hurricane-driven changes in the ecosystem services provided by these yards, and (3) assess if there were species-specific differences in terms of mortality and response to hurricane damage. The results of this study provide insight into the vulnerability and recovery potential of urban vegetation after a major hurricane. Understanding the changes in vegetation condition and ecosystem services following a major hurricane may lead to improved urban green infrastructure and management strategies.

**Methods**

**Study site**

The San Juan Metropolitan Area (SJMA) is the largest urban area on the island of Puerto Rico with an estimated population of 318,441 people (U.S. Census Bureau 2019). The yards surveyed in this study were single-family housing units from three neighborhoods (Puerto Nuevo, Avenida Central and La Sierra) located along the urban cover gradient of the Río Piedras Watershed (RPWS), the main watershed in the SJMA covering an area of 49 km² (Fig. 1). These yards were selected using a stratified random sampling design and they are part of a larger project setup established by the San Juan ULTRA Network across the RPWS (Meléndez-Ackerman et al. 2014, 2016; Vila-Ruiz et al. 2014; Torres-Camacho et al. 2017; Olivero-Lora et al. 2020). The RPWS is characterized by a land cover gradient that ranges from highly urbanized areas near the coast to highly forested areas around the headwater and has a mean annual temperature of 25.7 °C and a mean annual precipitation that ranges from 1,509 mm in the coast to 1,755 mm in the upland (Lugo et al. 2011). Previous studies have shown that green spaces in residential areas within the RPWS support a biodiversity-rich flora but dominated by non-native plant species (Vila-Ruiz et al. 2014; Meléndez-Ackerman and Rojas-Sandoval 2021). Originally, the yards included in this study were intended to be part of a larger vegetation monitoring project that was disrupted by the hurricanes before the inventory was completed.

**Hurricanes Irma and María**

On September 6, 2017, Hurricane Irma, a category 5 storm, passed 90 km off the northeast coast of Puerto Rico bringing more than 300 mm of precipitation to some parts of the island (Hall et al. 2020). Two weeks later, on September 20,
2017, Hurricane María, a category 4 storm, struck Puerto Rico with sustained winds of 250 km/hr and 500 mm of precipitation fell over 24 h, the highest rainfall intensity ever recorded on the island (Ramos-Scharrón and Arima 2019). These two hurricanes generated massive destruction, causing an estimate of $90 billion in damages (Caraballo-Cueto 2021) and directly impacted and transformed both urban and natural forests across the island (Uriarte et al. 2019). Hurricane María is the strongest hurricane to make direct landfall in Puerto Rico since Hurricane San Felipe in 1928.

Pre- and post-hurricane yard surveys

The pre-hurricane surveys included a total of 89 backyards (hereafter “yards”) that were visited between June 2016 and May 2017 and inventoried following the i-Tree Eco protocol (Nowak et al. 2018). Within each yard, all woody species (trees and shrubs) as well as palms and large herbs (e.g., plantains and bananas) with diameter at breast height (DBH) ≥ 2.5 cm were surveyed and used to gather the following variables: species, DBH, height, crown length, percent crown missing, percent dieback, and crown light exposure. Each species was classified as native or non-native in Puerto Rico following Axelrod (2011) and the presence (or not) of food provision value and ornamental value was evaluated following USDA-ARS-GRIN (2019). Finally, information on wood density for each species was also collected from the literature (Brown 1997; Chave et al. 2009; Carsan et al. 2012) and used to evaluate a potential association between wood density and the likelihood of surviving hurricane damage.

In October 2017, one month after hurricane María, when yards were revisited to perform post-hurricane surveys, we were granted access to only 69 out of the original 89 yards due to different reasons mainly related to the hurricane emergency. To assess the tree’s “health condition” and the “damage” caused by the hurricanes, the variable crown condition (defined as 1-% dieback) was recorded for each individual plant. The frequency of broken or uprooted trees as well as information about any indication of “recovery” (e.g., presence of new leaves and branches resprouting from trunks or stumps) were also documented for each individual plant. Out of the 69 revisited yards, 17 did not have plants fulfilling the DBH sampling requirement (DBH ≥ 2.5 cm) and therefore they were not included in post-hurricane surveys lowering the sample size to 52 yards. For all the surveyed yards, we estimated the total area (m²) from using Google Earth Pro v.7.3. The 52 yards with pre- and post-hurricane surveys covered an area of 7,129 m². All the variables recorded for pre- and post-hurricane surveys, their definitions and sources are provided in Table 1.
The i-Tree Eco v.6 modeling tool (https://www.itreetools.org/) was used to generate pre- and post-hurricane estimates for all yards pooled and for each yard separately for the following ecosystem services: (1) Carbon storage (kg); (2) Gross carbon sequestration (kg/yr); (3) Avoided runoff (m²/yr); (4) Oxygen produced (kg/yr); (5) Pollution removed (g/yr); and (6) Cooling energy savings (Kwh/yr). The i-Tree Eco protocol has been extensively used to assess the structure and related ecosystem services and disservices of urban forests. To estimate ecosystem services provided for the surveyed yards, air quality data [carbon monoxide CO (ppm/hr), nitrogen dioxide NO₂ (ppm/hr), ozone O₃ (ppm/hr), sulfur dioxide SO₂ (ppm/hr), breathable suspended particulate matter PM10 (μg/m³), and fine particulate matter PM2.5 (μg/m³)], as well as temperature (°C), rainfall (cm/hr) and wind velocity (m/s) were obtained from the National Weather Service Station located in Luis Muñoz Marín International Airport (LMMA-USAF:785263). Values for electricity were modified to 20 cents (US$) per kilowatt-hour based on estimates for Puerto Rico in 2017 (U.S. Energy Information Administration 2018) and heating costs to zero due to the lack of frost days on the island. Default values were used for the price of carbon (US$188/metric ton) and avoided runoff (US$2.36/m³).

### Data analysis

Descriptive statistics, contingency analyses, and sign tests were used to evaluate changes in vegetation structure and composition between pre- and post-hurricane surveys. We used χ² tests to compare the pre- and post-hurricane distribution frequency of individuals across the five DBH classes and to evaluate differences in the distribution frequency considering two condition categories: “dead” or “alive”. For these analyses, the expected frequencies were the frequencies collected in the pre-hurricane surveys and standardized residuals (z-scores) were considered for post-hoc analyses of cell comparisons (Field 2013; Agresti 2019). A Wilcoxon signed-rank test was used to determine hurricane-driven changes in crown condition. This analysis was performed using the ordinal position assigned to each of the seven categories evaluated for the “crown condition” variable (Table 1). To evaluate potential changes in the ecosystem services provided by yards, we used the pre- and post-hurricane surveys to estimate the percent loss of each ecosystem service for each yard and pooled yards as:

\[
\% \text{ loss} = -100 \times \frac{(\text{post} - \text{pre})}{\text{pre}}
\]

### Species-specific difference in hurricane damage and contribution to ecosystem services

To evaluate species-specific differences in terms of mortality and response to hurricane damage, we first evaluated the relative contribution of each species to the total amount of each ecosystem service (species ES contribution / total ES contribution × 100). Then, for each species we created an ecosystem service index (ESI) by adding its relative contribution to each of the eight ecosystem services evaluated. For food and ornamental services, values were calculated as the relative

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Table 1 Description of the variables evaluated in pre- and post-hurricane surveys performed in San Juan residential yards

| Variable            | Description                                                                                                                                                                                                 |
|---------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Origin              | Native or non-native to Puerto Rico. Native distribution range according to Axelrod (2011)                                                                                                                  |
| Life-form           | Tree, shrub, palm, large herb (including plantains and bananas). According to USDA-NRCS Plant Database (2019)                                                                                               |
| DBH                 | Diameter at the breast height (cm). Five categories: 1 = 2.5–7.6 cm, 2 = 7.7–15.2 cm, 3 = 15.3–30.5 cm, 4 = 30.6–45.7 cm, 5 > 45.7 cm                                                                                  |
| Plant height        | Distance in meters (m) between the highest point of the main stem and the ground level                                                                                                                      |
| Canopy cover        | Area in m² covered by the vertical projection of the tree crowns                                                                                                                                         |
| Leaf area           | Area in m² = leaf length × leaf width                                                                                                                                                                       |
| Leaf area index     | LAI = leaf area (m²)/ground area (m²). Defined as the one-sided green leaf area per unit ground surface area                                                                                            |
| Leaf biomass        | Product in kilograms (kg) of leaf dry matter content and leaf area index                                                                                                                                     |
| Crown condition     | Health condition of tree crowns that describes the amount of dieback within a tree’s canopy. Estimated here as 1-% dieback. Seven categories: 1 = dead, 2 = dying, 3 = critical, 4 = poor, 5 = fair, 6 = good, 7 = excellent |
| Mortality           | Binary (yes/no). 1 = dead, 0 = alive                                                                                                                                                                         |
| Bole damage         | Damage caused by hurricane winds in stems and trunks. Three categories: 0 = no damage, 1 = snapped trunks, 2 = uprooted stems                                                                                |
| Recovery            | Binary (yes/no). Evidence of new leaves production and/or new branches resprouting from stumps                                                                                                               |
| Food provision value| Binary (yes/no). Species grown in gardens for food production According to USDA-ARS-GRIN (2019)                                                                                                           |
| Ornamental value    | Binary (yes/no). Species grown in gardens for its esthetic value. According to USDA-ARS-GRIN (2019)                                                                                                          |
frequency of stems with those services out of the total number of stems of all species combined. For all other ecosystem services, values were extracted from i-Tree estimates. For each species, the ESI index then reflects its relative contribution to multiple ecosystem services. To estimate hurricane-driven changes on ecosystems service at the species level, we calculated the percent loss of these services for each species using the same method that was previously used to estimate losses at the yard level but using values for each species.

For each species, we also estimated the mortality rate as the ratio between the number of dead individuals in post-hurricane surveys and number of individuals alive in the pre-hurricane surveys (Tables S1 and S2). Generalized Linear Mixed-Models (GLMM) with binomial error distribution and log link function were used to evaluate if the probability of dying (mortality) for each species could be influenced by specific structural variables, tree density in each yard and pre-hurricane crown condition. For these analyses, DBH, plant height, tree density, and pre-hurricane crown condition were included as predictor variables (fixed factors), while yard location was included as a random effect to account for spatial autocorrelation. Only species with 10 or more individuals/surveys were used to fit the GLMMs. Due to low frequencies in cross-tabulation, the original seven categories evaluated for crown condition were reduced to just three categories: bad (≥ 26% dieback), fair (11% to 25% dieback) or good (≤ 10% dieback). The function `glmer` from the package `lme4` in R (version 4.1.2) was used to fit the GLMMs (Bates et al. 2015).

**Results**

**Hurricane-driven changes in vegetation structure and composition**

Pre-hurricane surveys accounted for a total of 491 individuals distributed across 95 species (16 natives and 79 non-natives). A clear dominance of non-native species was detected at the individual level (91.6% non-native species and 8.4% native species). Pre-hurricane surveys also showed that yards were dominated (82.3% of all vegetation) by small-stem plants with DBH ≤ 15.2 cm and the species *Musa paradisiaca*, *Hibiscus rosa-sinensis*, *Ptychosperma macarthurii* *Ficus benjamina*, and *Musa acuminata* were at the top of the most abundant (Fig. 2; Table S1). The total canopy cover estimated was 4,760 m² (66.8% of the total area surveyed).

The post-hurricane surveys showed that yards lost 152 individuals (27.7%) and 9 species (9.5%) representing an overall mortality of 31%. The proportion of native and non-native species in post-hurricane surveys changed very little (89.3% non-native species and 10.7% native species). However, when we analyzed the life-form of the surviving species, we found a significant reduction in the number of individuals classified as large herbs, decreasing from 115 individuals (23.4%) in the pre-hurricane survey to just 45 individuals (12.7%) after the hurricane. This reduction was mostly due to high mortality rates detected for two herb species, *Musa paradisiaca* (mortality = 65.9%) and *Musa paradisiaca*.
**acuminata** (mortality = 55.6%), the species with the highest mortality rates in our yards (Table S1). Nevertheless, after the hurricane, the species *Musa paradisiaca* was still at the top of the most abundant followed by *Hibiscus rosa-sinensis, Ficus benjamina, Ptychosperma macarthurii,* and *Dypsis lutescens* (Fig. 2; Table S1). At the yard level, we also detected a significant reduction in the median value for most of the variables associated with vegetation structure (Table 2). Some of the structural variables that registered significant losses were total canopy cover (20.5% loss), leaf area (19.6% loss), and leaf biomass (22.2% loss). No significant differences were observed for DBH, plant height, and basal area (Table 2). Wood density values between species ranged from 0.36 to 0.70 g/cm$^3$, but no association was detected between wood density and tree survival ($p > 0.05$).

When we compared the distribution frequency of individuals across the DBH size-classes for pre- and post-hurricane surveys, no significant differences were detected ($\chi^2 = 5.95$, df = 4, $p = 0.203$). However, significant differences were observed for the frequency distribution of trees that were “dead” or “alive” ($\chi^2 = 21.86$, df = 4, $p < 0.001$, Fig. 3). We found that the proportion of “dead” individuals was significantly higher in the two smallest DBH size-classes ($< 15.2$ cm; $z = -2.7$, $p < 0.01$) relative to larger ones (DBH $> 15.3$ cm; $z = 3.5$, $p < 0.001$; Fig. 3). The crown condition of surveyed plants displayed a dramatic decline following the hurricanes ($\chi^2 = 7028.6$, df = 6, $p < 0.001$; Fig. 4). The number of individuals in excellent, good, and fair condition decreased by 92%, 75%, and 70% respectively, while the number of individuals in poor and critical condition increased by a factor of three and 10 respectively (Wilcoxon signed-ranked test $Z = -17.3$, $p < 0.001$; Fig. 4). One month after the hurricane, 88.7% of the remaining standing plants within the yards were showing some form of recovery including the production of new leaves and new branches resprouting from stems and trunks.

**Table 2** Range values (lowest and highest), median values, and paired Sign test evaluating changes in vegetation structure and composition for 52 residential yards in San Juan

| Variables                  | Pre-hurricane | Post-hurricane | Statistics          |
|----------------------------|---------------|----------------|---------------------|
| Number of individuals      | 1–42          | 0–33           | -5.66 p < 0.001*    |
| Number of species          | 1–21          | 0–19           | -4.36 p < 0.001*    |
| Number of native species   | 0–11          | 0–9            | -1.16 p = 0.250     |
| DBH (cm)                   | 5.2–80.7      | 0–80.7         | 1.20 p = 0.230      |
| Plant height (m)           | 1.8–19.00     | 0–19.00        | 0.70 p = 0.486      |
| Canopy cover (m$^2$)       | 1.3–546.9     | 0–430.6        | -5.75 p < 0.001*    |
| Leaf area (m$^2$)          | 4.6–1,713.6   | 0–1,441.9      | -5.75 p < 0.001*    |
| Leaf biomass (kg)          | 0.3–140.0     | 0–136.1        | -5.75 p < 0.001*    |
| Leaf area index            | 1.2–6.9       | 0–5.9          | 2.87 p = 0.134      |
| Basal area (m$^2$)         | 0–2.9         | 0–2.5          | -1.79 p = 0.062     |

Asterisks (*) indicate significant differences ($p < 0.05$) between pre- and post-hurricane surveys.

**Fig. 3** Frequency of dead and alive individual plants in each of the five DBH size-classes comparing pre- and post-hurricane surveys.

**Fig. 4** Crown condition for individual plants comparing pre- and post-hurricane surveys.
Hurricane-driven changes in ecosystem services

When we analyzed pre- and post-hurricanes surveys pooling data from all yards, we found reductions for all the ecosystem services evaluated but these reductions were not necessarily homogeneous across services. The percent loss ranged from 9.2% to 41.9% with the largest and smallest losses observed for food production and carbon storage respectively (Table 3). A similar trend was detected when individual yard data were considered (Fig. 5). For those services evaluated with i-Tree-Eco, the largest losses were detected in avoided runoff and pollution removal in both the pooled (Table 3) and the individual yard data analyses (Fig. 5).

Species-specific differences in hurricane damage and contribution to ecosystem services

Before the hurricane, the species with the highest ESI index and therefore with the highest contribution to different ecosystem services was Mangifera indica, followed by Musa paradisiaca, Psychosperma macarthurii and Caesalpinia ferrea (Fig. 6a). Eleven species included in the ESI top-20 were species often planted as “food species” (Musa spp., Citrus spp., Psidium guajava, Mangifera indica, Annona muricata, Persea americana, Artocarpus altilis, and Cocos nucifera). We also found that seven species in this top-20 ESI list (Caesalpinia ferrea, Artocarpus altilis, Cocos nucifera, Pterocarpus indicus, Schefflera arboricola, Malpighia emarginata, and Roystonea regia) are species that beside their contribution to the different ecosystem services, were found in low frequency (< 5 individuals) across the yards (Fig. 6; Tables S1 and S2). The GLMMs testing species mortality as a function of structural variables, tree density and previous crown condition showed that the probability of dying depends significantly on two factors: DBH and plant height (Table 4). Our models suggest that for plants growing in yards the likelihood of dying decreases 0.9 times with each increase in DBH units while it increases 1.5 times with each increase in plant height units.

At the species level, important losses for all ecosystem services evaluated were observed, with some species experiencing ESI value reductions of more than 50% (Fig. 6b). For example, Musa acuminata and M. paradisiaca, two of the species with the highest ESI indexes and among the most common across yards in pre-hurricane surveys, were the species registering the largest losses (Fig. 6b). The tree Pterocarpus indicus and the palm Roystonea regia were the species showing the largest losses in ornamental value. On the other hand, Mangifera indica, the species with the highest ESI index and highest contribution to different ecosystem services before the hurricane, experienced a

| Ecosystem service                  | Pre-hurricane | Post-hurricane | Net loss | % loss |
|-----------------------------------|---------------|----------------|----------|--------|
| Food production (# plants)        | 227           | 132            | 95       | 41.9   |
| Avoided runoff (m³/yr)            | 154.9         | 124.1          | 30.8     | 19.9   |
| Pollution removed (g/yr)          | 25,082.6      | 20,154.1       | 4,928.5  | 19.6   |
| Ornamental value (# plants)       | 262           | 221            | 41       | 15.6   |
| Cooling effects (Kwh/yr)          | 6,081.1       | 5,285.6        | 795.5    | 13.1   |
| Oxygen produced (kg/yr)           | 4,902.0       | 4,348.1        | 553.9    | 11.3   |
| Carbon sequestration (kg/yr)      | 1,836.2       | 1,630.1        | 206.1    | 11.2   |
| Carbon storage (kg)               | 29,914.8      | 27,165.1       | 2,749.7  | 9.2    |

Services are arranged from higher to lower percent loss.

Fig. 5 Mean percent of losses in ecosystem services provided by 52 yards in San Juan.
Fig. 6  Distribution of ecosystem services by species. 

a) Comparison of the top 20 species with the highest relative contribution to multiple ecosystem services (ESI = ecosystem service index) before the hurricane events. 

b) Percent of losses of ecosystem services for the top contributors. Species are ranked according to the cumulative % of losses. Only species with losses were included in this figure.

Table 4  Generalized linear mixed effects models (GLMMs) evaluating mortality as a function of pre-hurricane values for vegetation structural variables and crown condition

| Variable                  | Estimates | SE  | z-value | P     | Odds ratio | 95% CI lower | 95% CI upper |
|---------------------------|-----------|-----|---------|-------|------------|--------------|--------------|
| Intercept                 | -2.74     | 1.31| -2.09   | 0.04  | 0.14       |               |              |
| Tree density              | 0.03      | 0.02| 1.40    | 0.16  | 1.02       | 0.99          | 1.05         |
| DBH (cm)*                 | -0.16     | 0.08| -2.02   | 0.02  | 0.88       | 0.77          | 0.96         |
| Tree height*              | 0.42      | 0.20| 2.09    | 0.03  | 1.48       | 1.16          | 1.92         |
| Crown condition           | -0.02     | 0.42| -0.05   | 0.96  | 0.81       | 0.43          | 1.52         |

Significant predictor variables with $P < 0.05$ are indicated in bold letters.

The plant species with $n > 10$ included in the analyses were: *Annona muricata*, *Citrus aurantifolia*, *Codiaeum variegatum, Duranta spp.*, *Dypsis lutescens*, *Ficus benjamina*, *Hibiscus rosa-sinensis*, *Mangifera indica, Psidium guajava* and *Ptychosperma macarthurii*.
25% reduction on the food production’s ESI value but just minimal losses (< 5%) for the other ecosystem services (Fig. 6a and b).

Discussion

Hurricane-driven changes in vegetation structure and composition

This study evaluated hurricane-driven changes in vegetation structure, composition, and ecosystem services in residential yards in San Juan, an urban area where private yards occupy a significant fraction of the total green infrastructure available (Lugo et al. 2011; Ramos-González 2014). Our results showed that Hurricanes Irma and María produced high overall mortality (~ 31%) in these residential yards, with mortality values twice as high as the average reported for forested areas on the island after the same hurricanes (average = 15.40%; Uriarte et al. 2019). One potential explanation for this elevated overall mortality in our yards could be related to the inclusion of large herbs in our vegetation surveys, specifically the inclusion of Musa spp. These species registered the highest mortality rates (> 55%) in post-hurricane surveys, and due to their life-form, they are highly susceptible to wind damage (Paull and Duerte 2011). Nevertheless, when we recalculated the overall mortality excluding Musa spp., the resulting rates remained considerably high (~21%). Another potential explanation could be related to the dominance of non-native species (> 90%) registered in these yards. Our findings agree with previous studies showing that San Juan residential yards are composed of more non-native species and fewer native species (Meléndez-Ackerman et al. 2014; Vila-Ruiz et al. 2014; Meléndez-Ackerman and Rojas-Sandoval 2021). Additionally, it has been suggested that native species cope better with hurricane disturbances and have higher survival rates than non-native species (Brokaw et al. 2012; Duryea et al. 2007; Duryea and Kampf 2014). These differences in the responses of native and non-native species to hurricane damage could explain (at least in part) the high mortality rates observed in our yards that are dominated by non-natives and the relative lower mortality rates reported for natural forests, which are areas often dominated by native species or with lower proportion of non-native species than our yards (Ackerman et al. 2017; Zimmerman et al. 2021). However, more studies evaluating hurricane responses of native and non-native species in urban and natural forests are needed to understand the extent of these results.

Based on previous studies, we expected to find relationships between plant structural variables and tree damage/mortality related to hurricane disturbance. For example, previous studies evaluating hurricane damage have suggested a positive relationship between plant height and mortality, and lower mortality rates have been detected for species with higher wood densities (Zimmerman et al. 1994; Francis 2000; Uriarte et al. 2019). Similarly, crown condition has been used as a good predictor of tree mortality in urban forests (Koeser et al. 2013; Steenberg et al. 2019) and as an indicator of vulnerability to hurricane damage in natural forests (Ostertag et al. 2005; Tanner et al. 2014). Our results are partially in agreement with these previous studies. As expected, we detected a positive relationship between plant height and mortality, but our results also show a negative correlation between DBH and mortality (see below) and no correlation between mortality and crown condition. This discrepancy in our results and the lack of association with crown condition could be explained by the small sample size (only 52 yards with pre- and post-hurricane surveys) and/or to the low number of individuals registered for most species in the surveyed yards (> 88% species have less than 10 individuals in the pre-hurricane survey). Another possible explanation could be related to differences in the methods used to collect the data. For example, there are clear differences between studies in the classification used to evaluate canopy health and crown condition as well as the time intervals after the hurricane when data were collected (varying from days, weeks, and months; Ostertag et al. 2005; Tanner et al. 2014; McLaren et al. 2019). In this regard, evidence indicates that hurricane damage can result in “delayed” mortality that can occur several months or even years after the hurricane event (Lugo 2008; Uriarte et al. 2019), including an additional variation factor that should be considered when comparing studies. Our mortality estimates took place immediately after the hurricane and may not reflect long-term mortality. Our results also showed that tree-condition based on dieback evaluations worsen for most trees following the hurricanes. Therefore, long-term tree mortality in residential yards is still possible which may present further losses in the ecosystem services provided.

We found that for plants growing within yards in San Juan, the probability of dying decreased with increases in stem size (DBH). This result appears somewhat contradictory when compared to findings from a previous study suggesting that for some species mortality increases with stem size (Zimmerman et al. 1994). However, it is consistent with results obtained from urban forests where high mortality rates were observed in small-stem classes (Steenberg et al. 2017, 2019). This apparent incongruency could be explained by the forest type evaluated: urban vs. natural. Evidence has shown that natural and urban forests often differ in their structural variables, composition, and management regimes (Zhao et al. 2010; Timilsina et al. 2014). Therefore, two plausible alternatives could be that hurricanes are having different impacts in urban and natural forests, or that in urban spaces, plant species may be responding differently.
to hurricane damage compared to plants in natural forests. Nevertheless, as we mentioned before, more studies assessing how plant species are responding to hurricane disturbances in urban and natural forests are needed to evaluate these hypotheses.

**Hurricane-driven changes in ecosystem services**

When we analyzed the impact of hurricane disturbances on ecosystem services, we found that the damage caused in leaves, branches, and canopy structure (i.e., changes in canopy cover, leaf area and leaf biomass) translated into considerable reductions in the supply of ecosystem services. Among all the ecosystem services evaluated, food production was the most affected, losing up to 40% of its pre-hurricane capacity. This value is critical, even more when we consider that Puerto Rico currently imports over 80% of its food supply (Gould et al. 2015). This dependency on food imports makes Puerto Rican food security vulnerable to fluctuations in global food prices, transportation fuel prices, and the effects of climate change all of which may influence and interrupt supply chains (Gould et al. 2017; Benach et al. 2019; National Academies of Sciences, Engineering, and Medicine 2020). The other two ecosystem services vastly affected by hurricanes were avoided runoff (also known as rainfall infiltration) and pollution removal. Decreases in air quality and rainfall infiltration are also problematic in San Juan, since a large part of the city is in a nonattainment area for sulfur dioxide SO₂ with high air pollution concentrations due to local emissions from power plants and generators and high vehicle and ship traffic (Subramanian et al. 2018). Additionally, some of the largest residential areas in San Juan (e.g., the RPWS) are in flood hazard areas and are highly vulnerable to extreme heat events (Muñoz-Erickson et al. 2014; Méndez-Lázaro et al. 2018). Overall, this indicates that San Juan is already a vulnerable urban system and by losing ecosystem services this city is becoming even more vulnerable to hurricane disturbances. These results also warn about the need to improve the resilience capacity of this fragile urban system. Previous studies have suggested that urban forests in Puerto Rico are very dynamic and that high humidity and warm conditions prevailing all year long facilitate rapid growth and recovery of urban vegetation after disturbances (Lugo et al. 2011; Tucker Lima et al. 2013; Muñoz-Erickson 2014). However, residential yards are privately owned and subject to human selective pressures and management that may hinder the recovery of ecosystem services. A prior study shows that yard owners in San Juan have prioritized food production, air purification, ornamental value, and temperature reduction above other services (Olivero-Lora et al. 2020). Therefore, decision makers and managers should use these preferences as a guide to develop management plans for these areas. Sustainable and resilient yards providing multiple ecosystem services should be a priority in this city even more in the face of ongoing climate change.

**Species-specific difference in hurricane damage and contribution to ecosystem services**

Our results showed that plant species growing in San Juan yards differed in their contribution but also in their losses to ecosystem services. For example, *Musa* species led the contribution to food production service and are important food plants cultivated across the yards, but they are highly vulnerable to hurricane damage and among the species contributing the most to the loss of ecosystem services. On the other hand, *Mangifera indica* was the species with the highest individual contribution to different ecosystem services before the hurricanes and just minimal losses in its contribution to most ecosystem services were detected after the hurricanes. These species-specific differences call for further examination in the selection and management of plant species promoted for ecosystem services including additional evaluation of their susceptibility/resilience to climate change and hurricanes.

One interesting result of this study is that many species that are popular and preferred by yard owners for their fruits (e.g., *Annona muricata*, *Artocarpus altilis*, *Psidium guajava*) and as ornamentals (e.g., *Psychosperma macarthurii*, *Hibiscus rosa-sinensis*, *Pterocarpus indicus*), in addition to had been among those contributing significantly to the loss of ecosystem services, are non-native species that have been listed as invasive and/or potentially invasive in Puerto Rico and other Caribbean islands (Rojas-Sandoval and Acevedo-Rodríguez 2015; Rojas-Sandoval et al. 2017; Meléndez-Ackerman and Rojas-Sandoval 2021). Because it has been shown that cultivation for ornamental and food purposes are among the main pathways for the introduction of invasive plants on Caribbean islands (Rojas-Sandoval and Ackerman 2021), the continued cultivation of these non-native species entails the risk of becoming an environmental problem if they escaped cultivation. Therefore, additional studies looking for native options to replace these popular non-native ornamentals and food plants that at the same time can provide effective ecosystem services in urban areas are urgent and should be encouraged. One suitable example of a native species that could be promoted is the endemic palm *Roystoe nea borinquena*. This is a native palm, with great ornamental potential, that can also provide an important food source to native birds and bees and our results for this species showed very low damage and high survival rates after hurricanes Irma and María (Francis and Lowe 2000; this study). At the same time, we recognize that applying ecosystem services approaches to support biodiversity may bring challenges when social and ecological trade-offs and other complexities
are considered (Ingram et al. 2012; Birkhofer et al. 2015; Austin et al. 2016).

A potential methodological limitation of the study is that approximately 4 months had passed between the initial yard surveys and the post-hurricane yard inventories. While it could be argued that some of the tree losses and structural changes could have occurred from management decisions before the hurricane events, we consider that yard changes due to tree management are minimal in this case for a number of reasons. First, it has been suggested that forest cover has been increasing in the San Juan Metropolitan Area (Ramos-González 2014; Martinuzzi et al. 2021). Second, time and monetary investment by San Juan residents in yard management has been reported to be somewhat minimal for those who have a propensity for yard plantings (Meléndez-Ackerman et al. 2016). Therefore, tree losses due to yard management are expected to be minimal under this scenario. Last, post-hurricane surveys were carried out quickly and started less than a month following Hurricane María event when hurricane-induced tree damage and structural changes were easy to tease out from those that could be attributed to management.

Conclusion

Our data for the surveyed yards in San Juan showed that hurricane disturbances significantly altered vegetation structure and those changes translated into substantial reductions in the ecosystem services provided by these yards, highlighting the vulnerability of this urban system to major storms. Overall, our results emphasize the key role that residential yards can play providing ecosystem services in tropical cities and call for further efforts to evaluate more extensively private areas that may contribute to support green infrastructure, mitigate extreme climate events, provide multiple ecosystem services, and promote long-term urban sustainability. From our perspective, this could be achieved through regulation, education, experimental plantings with native plant species, and the promotion of best management practices, with the goals of improving ecosystem services, increasing connectivity, conservation of native species, educational value, and open space for the community. Further studies using interdisciplinary approaches (planning, landscape design, forestry) to evaluate the long-term dynamics of ecosystem services provided by public and private green spaces in this city are recommended. For cities like San Juan, located in hurricane-prone areas, increasing our understanding of how gray and green infrastructures are responding to extreme climate events such as tropical storms and hurricanes can help inform future management decisions and improve restoration efforts following disaster and it is very relevant within the context of the ongoing climate change.

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Authors’ contributions S.O-L and E.M-A conceived and designed the study, S.O-L and J.O performed the fieldwork and compiled the dataset. S.O-L and J.R-S analyzed the data. S.O-L and J.R-S led the manuscript writing with major inputs from E.M-A. All authors provided final approval for publication and agreed to be accountable for all aspects of the work.

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Availability of data and material All the data used in this study are available upon request in the San Juan ULTRA Project website http://sanjuanultra.org/.

Code availability Not applicable.

Declarations

Compliance with ethical standards This work did not involve research with human subjects. Required information related to Ethics Approval, Consent to participate and Consent for Publication is therefore “Not Applicable”.

Conflicts of interest/Competing interests There are no conflicts of interest and/or competing interests.

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