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You Can Bend Me but Can't Break Me: Vegetation Regeneration After Hurricane María Passed Over an Urban Coastal Wetland in Northeastern Puerto Rico

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Tropical urban coastal wetland regeneration is complex. Wetland plant biodiversity varies due to past and present land use, nutrient inputs, hydrological conditions, and terrestrial/marine connectivity. The intensity of atmospheric disturbances, such as hurricanes, will determine these systems' level of disturbance and regeneration capacity. On September 20, 2017, category 4 hurricane María passed over Puerto Rico, leaving behind a path of destruction across the entire island, especially in coastal ecosystems, from the combined effects of winds, severe storm surges, and urban runoff. Our question was: to what extent do human-influenced coastal urban wetlands regenerate after such a massive event. This study determines the spatio-temporal regeneration dynamics of plant cover and composition during the first 2 years after hurricane María in a coastal urban wetland, ciénaga Las Cucharillas, located in San Juan Bay. We assessed the distribution of plant functional types using small unmanned aerial vehicles (s-UAV) and monitored climate and environmental data (salinity, phreatic water levels, and precipitation). Wetland vegetation cover had a high recovery rate – 16 months after the hurricane, vegetation cover occupied 87% of the study area. We found a successional pattern of plant regeneration that seemed to be partly explained by the fast-slow continuum. Plants with high specific leaf area (SLA) colonized bare soil spaces first. Plant regeneration also varied according to changes in phreatic water conductivity and waterlogging. Isotopic analyses of plant species signaled high nutrient availability, increasing the system's regeneration speed. After 2 years, the wetland's plant cover and composition of functional plant types proved resilient to the initial hurricane effect and subsequent changes in conductivity and freshwater conditions. Further studies will expand how spatio-temporal conditions will affect long-term plant community dynamics.

Keywords: urban wetlands, hurricanes, plant functional types, SUAV, Puerto Rico, coastal wetlands

INTRODUCTION

Coastal wetlands are transitional areas between terrestrial and marine ecosystems, with variable periods of water saturation (Cowardin et al., 1979). The presence and distribution of coastal wetlands result from eustatic sea-level rise and terrigenous sediment deposition and substrate development (Cohen et al., 2016). Plant species coexist in a dynamic state of change where ecophysiological adaptations to waterlogging and saline conditions predict wetland structure and function (Medina and Francisco, 1997). It is possible to predict regeneration processes by considering these adaptations (Buma, 2015). Determining post-disturbance regeneration in vegetation cover is necessary for coastal urban wetlands which undergo constant stresses yet can establish floral and faunal communities (Perillo et al., 2019). Long-term studies suggest different pathways of succession, where ecosystem recovery can take from a couple years by plant resprouting or decades with shifts in vegetation (Fickert, 2018). Little is known about the factors involved in regeneration in these ecosystems where disturbance effects can be seen even after 30 years (Ferwerda et al., 2007).

The level of vegetation cover loss in wetlands caused by hurricane impacts depends directly on hurricane intensity, duration, forward speed of the storm, and wetland distance over which the storm passes (Morton and Barras, 2011). Indirect effects from hurricanes are prolonged retention of storm-surge seawater, flooding, and adverse physiochemical plant reactions to waterlogging and salinization (Morton and Barras, 2011). On September 20, 2017, at 10:00 am, category 4 hurricane María, with sustained winds of 69 m/s, crossed the island of Puerto Rico diagonally in the SE-NW direction. NOAA simulations estimate maximum flood levels up to 1 meter above mean sea level for the metropolitan area (Pasch et al., 2019). A tide gauge in San Juan reported up to 1.2 meters of swell before going out of service, and a total rainfall of 406 mm was recorded for the metropolitan area (Pasch et al., 2019). In Cucharillas, according to rapid post-hurricane assessment, freshwater flooding, seawater storm surges, and squalls from hurricane María resulted in substantial tree fall, tree decapitation, and extensive defoliation. How has the wetland regenerated after this event? In Branoff et al. (2018), we observed that previous cover and composition of functional plant groups in the wetlands were altered due to initial and subsequent changes in salinity, tidal effects, and light regime in the wetland.

This study determines the spatio-temporal regeneration dynamics of plant cover and composition during the first 2 years after hurricane María by determining current land cover and plant composition and assessing plant regeneration and succession dynamics by means of ecophysiological traits of the vegetation.

MATERIALS AND METHODS

Study Area

The Ciénaga Las Cucharillas natural reserve (18° 26′25.27′′ N, 66° 08′08.39′′ W) is an urban coastal palustrine-estuarine wetland dominated by freshwater herbaceous vegetation transitioning to mangroves. It is located on the western side of the San Juan Bay in the northern metropolitan area of Puerto Rico (Lugo et al., 2011; **Figure 1**). The current extent of Cucharillas covers 500 hectares which is all that remains of the historic wetland area. Studies suggest that as much as 90% of the historic mangrove area may have been lost in the 20th century from filling activity for urban and industrial use of the land (Martinuzzi et al., 2009; Lugo et al., 2011). Our study area covers 2 hectares of the wetland, which have been part of restoration efforts for the last 20 years by the community-based organization Corredor del Yaguazo.

The wetland is part of the Cucharillas drainage basin, located between two large river basins that drain to the bay: the río Bayamón and the río Piedras basins. The present hydrological regime was modified from colonial times to the present, including (a) drainage channels for agricultural use from the 17th century until the mid-20th century (Kennaway and Helmer, 2007); (b) the construction of the Malaria channel in the 1940s, bringing a direct flow of fresh water to the wetland from the upper and middle parts of the basin (Pumarada-O'Neill et al., 1991); and (c) restricted seawater exchange due to the dike effect of an outflow water pump structure at the mouth of the channel (Webb and Gómez-Gómez, 1998). For the metropolitan area of San Juan, the mean annual temperature is 25.7°C, and the average annual precipitation is 1,755 mm (Walter, 1971). Rainfall in the northern Caribbean has a bimodal pattern (Taylor, 2002). Puerto Rico has two wet seasons: a peak in July-December, another in May-June, and a dry season from January to April (Torres-Valcárcel et al., 2014).

Hydrological Conditions

Monthly rainfall measurements were collected from daily values from the National Climate Data Center (NCDC) Toa Baja Station (RQC00669415) and a meteorological station located in the wetland. We gathered water level and conductivity measurements in ten (10) measuring wells installed in the study area in 2015, establishing a spatial gradient from the coast (800 meters from the open water coast) to inland (300 meters from the freshwater Malaria channel) (**Figure 1**). We recorded conductivity (mS) monthly at the water table and at 2.5 m depth with an EcoSense EC300A handheld conductivity meter. Water levels were measured monthly with a measuring tape at each well and deployed water level data loggers (Onset corp.). The results shown here are the monthly averages. We performed ANOVA and Tukey test if significant differences were found between conductivity, water levels, precipitation data, and monitoring wells. Microtopography analysis was done in ArcGIS Pro 2.8 using DEM data sources of elevation surfaces at a 10 m resolution from the USGS National Geospatial Program.

Post-hurricane Image Collection

To capture wet and dry season variability effects on the wetland changes in plant functional forms distribution throughout the 2,000 m^2 study area, we used a Phantom 3 (UAV) electrically powered quadcopter (DJI Company) with a Red-Green-Blue (RGB) camera in April 2018, October 2018, and January 2019. Missions were planned around optimal weather conditions,

FIGURE 1 | Maps showing the study area in panel **(A)** Puerto Rico (red polygon) in the Caribbean Region, within the **(B)** Metropolitan area of San Juan, and **(C)** the study site at ciénaga Las Cucharillas (sample area within red polygon) and monitoring wells (red dots). Maps Data: Google Earth, ©2021 SIO, NOAA, U.S. Navy, NGA, GEBCO Image Landsat/Copernicus, Maxar Technologies.

including no rain and low wind speed (less than 5 m/s). Each mission was flown at an altitude of 50 meters (2.2 cm/pixel resolution) in compliance with FAA regulations, and each flight lasted 18–20 min.

Orthomosaic images were analyzed using the program ArcGIS Pro. The first analysis was to create a vegetation index using only the visible RGB bands. Spectral vegetation indices were used to monitor and analyze spatio-temporal variations in vegetation structure, commonly based on infrared bands. The VARI (Visible Atmospherically Resistant Index) allows the calculation of vegetation indices using the visible bands (Gitelson et al., 2002; Raoufat et al., 2020):

$$VARI = \frac{B_{Green} - B_{Red}}{B_{Green} + B_{red} - B_{blue}}$$

Vegetation cover types were identified manually, creating feature classes, rasterized (converted from vector to a raster image), and adapted to the exact spatial resolution for pixel-by-pixel comparison.

Drone flights in April 2018 produced less usable imagery than the other flight dates because low light and high wind conditions were causing blurry imagery. When these images were stitched together, the output orthomosaic image had empty pixels where the original images were too blurry to analyze. Although this resulted in a loss of 859 m^2 of aerial imagery, this accounts for less than 4 % of the entire study area and results are still significant.

Land cover categories were trees, herbs, shrubs, grasses, water, managed areas, and bare soil. The four vegetation-based categories represented plant growth forms. Using these land cover categories, the description of vegetation types focuses on physiological characteristics in response to environmental factors and ecosystem processes (Chapin et al., 1996). We sampled representative species for three plant types for ecophysiological analyses: (a) trees (*Laguncularia racemosa* and *Avicennia germinans*), (b) shrubs (*Dalbergia ecastaphyllum*), and (c) herbs (*Acrostichum danaeifolium*) (**Table 1**).

Species Composition Assessment

From 2018 to 2019, we conducted a periodic collection of vegetation specimens for classification. Individuals were pressed, dried, identified, and grouped into functional groups based on life forms. We used literature and herbarium specimens from the New York Botanical Garden,[1] University of Puerto Rico, Río Piedras[2] and Mayaguez campus[3] to compare post-hurricane species to the pre-hurricane wetland composition.

Leaf Traits

Fully expanded and exposed adult leaves (at a 2-meter height in trees) of the four plant species representative of plant growth forms present in the wetland (trees, shrubs, and herbs) were sampled and measured throughout the seasons. *L. racemosa* (L.) C.F. Gaertn. and *A. germinans* (L.) L. are both considered salt-tolerant trees (Parida and Jha, 2010). *D. ecastaphyllum*

[1]http://sweetgum.nybg.org/science/vh/
[2]http://herbario.uprrp.edu/bol/
[3]http://herbaria.plants.ox.ac.uk/bol/mapr

TABLE 1 | Land cover categories, definitions for spatial assessment, and species for each plant cover.

Land cover	Species	
Trees – woody vegetation with a trunk, supporting branches, and leaves. More than 2 m in height.	*Annona glabra* *Avicennia germinans* *Amphitecna latifolia* *Terminalia catappa* *Laguncularia racemosa* *Conocarpus erectus* *Stahlia monosperma* *Malachra capitata* *Thespesia populnea* *Rhizophora mangle*	
Herbs – non-woody vegetation, includes ferns and vines.	*Sagittaria intermedia* *Asclepias curassavica* *Lemna aequinoctialis* *Cyanthillium cinereum* *Pluchea odorata* *Eclipta prostrata* *Symphyotrichum expansum* *Gynandropsis gynandra* *Commelina diffusa* *Cyperus difformis* *Cyperus elegans* *Cyperus distans* *Cyperus ligularis* *Eleocharis mutata* *Cuphea strigulosa* *Malachra alceifolia* *Malachra capitata* *Bacopa monnieri* *Polygonum punctatum* *Eichhornia crassipes* *Portulaca oleracea* *Acrostichum aureum*	*Acrostichum danaeifolium* *Ceratopteris thalictroides (L.) Brongn.* *Mitracarpus hirtus* *Spermacoce remota* *Salvinia molesta* *Solanum americanum* *Physalis angulata* *Typha domingensis* *Phyla nodiflora* *Mikania cordifolia (L. f.) Willd.* *Sphagneticola trilobata* *Ipomoea triloba* *Ipomoea tiliacea* *Aniseia martinicensis* *Vigna luteola* *Passiflora foetida* *Paullinia pinnata* *Cissus verticillata*
Shrubs- woody vegetation that does not exceed 2 meters in height.	*Dalbergia ecastaphyllum* *Senna alata*	
Grasses – hollow stems and narrow alternate leaves.	*Gynerium sagittatum* *Steinchisma laxum (Sw.) Zuloaga* *Echinochloa polystachya (Kunth) Hitchc.*	
Water – no vegetation or soil seen.		
Managed areas – infrastructure, recreation, and educative areas.		
Bare soil – no vegetation seen, includes educative and work trails.		

(L.) Taub. is a climbing decumbent shrub, reaching 1–5 m in length and grows in non-forested areas forming monospecific stands (Acevedo-Rodríguez, 2005). *A. danaeifolium* Langsd. & Fisch. Is an herbaceous, rhizomatous fern common in brackish swamps, tolerant to soil saline conditions up to 45–50 mS/cm but requires freshwater for establishment (Medina et al., 1990a). We sampled during 2018-2019 in the wet (May to October) and dry (November – April) periods. We assessed leaf area and dry mass at least once each dry and wet period for the three plant types representative of the plant growth form (**Table 1**). At the end of the study, we measured $\delta^{13}C$ and $\delta^{15}N$ isotopes in the leaf tissue for assessing long-term water use efficiency (WUE).

The leaves were stored in a cooler to prevent water loss until analysis. Leaf area was measured with an LI-3100C Area Meter and later dried in a forced-air circulation oven at 60°C for dry mass determination. Specific leaf area (SLA; the area of a fresh leaf divided by its oven-dry mass) was calculated as an index of the construction cost of leaves. SLA tends to relate positively to relative growth among species (Pérez-Harguindeguy et al., 2016). In the leaf economics spectrum, SLA indicates habitat preferences and plant productivity in environments under stress (Medina et al., 1990b). The SLA is also related to light conditions, where high values indicate shaded leaves and low values suggest high light or open canopies.

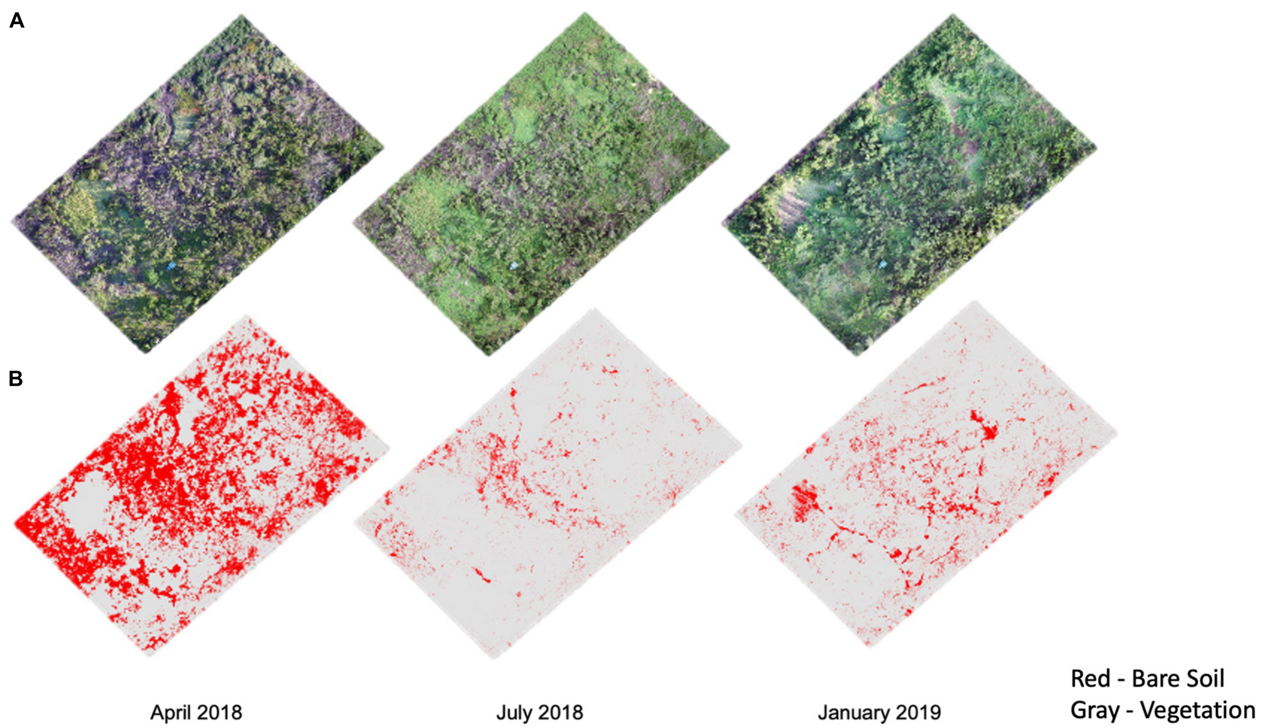

FIGURE 2 | Aerial imagery of the study area. **(A)** Red-Green-Blue (RGB) drone images taken in April 2018, July 2018, and January 2019 are the raw images collected to determine **(B)** area of standing vegetation and bare soil within the study site in April 2018, July 2018, and January 2019; red color indicates bare soil and gray color indicates alive vegetation.

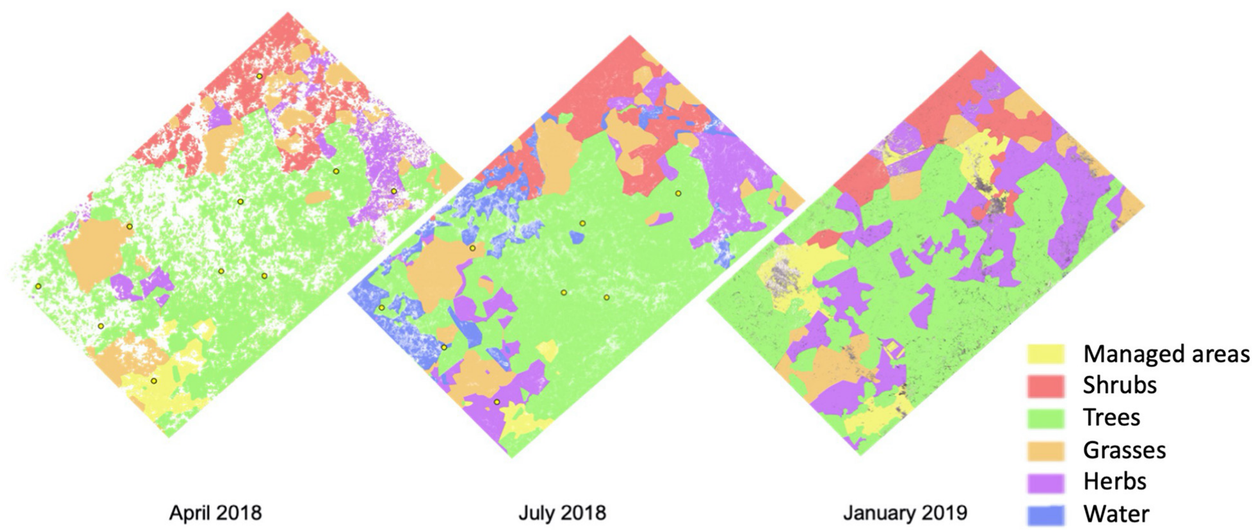

FIGURE 3 | Spatial classification of land cover of each vegetation type in April 2018, July 2018, and January 2019. Yellow dots denote monitoring wells where phreatic water measurements were taken.

Carbon isotope analyses ($\delta^{13}C$) were performed in leaf samples to reveal plant long-term WUE which has been associated with salt tolerance (Ball and Passioura, 1995). Intracellular CO_2 and plant WUE was calculated based on the Farquhar et al. (1989) equation: $\delta^{13}C_{leaf} = \delta^{13}C_{air} - a - (b\text{-}a)\ C_i / C_a$, where $\delta^{13}C_{air}$ is the carbon isotope ratio of the CO_2 in the air (around 8.2 ‰); a is the fractionation by slower diffusion of $\delta\ ^{13}C$ to $\delta\ ^{12}C$ (4.4 ‰); b is the fractionation by ribulose biphosphate carboxylase against ^{13}C (27 ‰); and C_a is the atmospheric CO_2 concentration which averaged 413 μmol/mol at the time of the

TABLE 2 | Land cover area in m^2.

	Apr 2018	July 2018	January 2019
Trees	8,221 (37.9)	10,929 (48.5)	10,435 (46.3)
Managed areas	778 (3.6)	312 (1.4)	1,677 (7.4)
Grass	2,532 (11.7)	2,955 (13.1)	1,767 (7.8)
Herbs	1,368 (6.3)	2,763 (12.3)	5,363 (23.8)
Shrubs	1,545 (7.1)	2,077 (9.2)	2,084 (9.2)
Surface water	0	2,489 (11.0)	0
Bare soil	7,217 (33.3)	995 (4.4)	1,208 (5.4)
Total	21,661	22,520	22,534

Values in parentheses are percent (%) area cover of the total study area for each date.

study. Intrinsic WUE was derived from the Lambers et al. (2008) equation, where intrinsic WUE = (A_n/g_s).

Shapiro Wilk test was used to test normality in distribution. Analysis of variance (ANOVA) was used when data fits normality; if not, a nonparametric Wilcoxon/Kruskal Wallis test was used with the statistical program JMP Pro version 13.

RESULTS

Land Cover

Around 33% of the study area was devoid of standing vegetation (**Figure 2**), which decreased considerably in July 2018 and January 2019. In April, trees were the predominant cover with 8,221 m^2, followed by grasses, 2,532 m^2, shrubs, 1,545 m^2, herbaceous vegetation, 1,368 m^2, and managed areas with 778 m^2 of the study area (**Figure 3**; **Table 2**).

In July 2018, trees continued as the dominant cover with 10,929 m^2, followed by grasses, 2,955 m^2, herbaceous cover 2,763 m^2, shrubs 2,077, and managed spaces with 312 m^2. In January 2019, trees occupied 10,345 m^2, a decrease related to the removal of trees due to rehabilitation efforts, herbaceous cover 5,363 m^2, shrubs 2,084 m^2, grasses 1,767 m^2, and managed areas 1,677 m^2 within the study area.

Hydrological Conditions

Precipitation data exhibited the bimodal pattern for the island, June (316 mm) and August (281 mm) being the wettest months. The driest month was March (60.9 mm; **Figure 4**). At the phreatic level, we found higher conductivity values closer to the coastline with a sharp drop around 1 km inland, with conductivity values ranging spatially from 10 to 35 mS. We found marine intrusion at a depth of 2.5 meters in most of the wells (**Figure 5**). This trend prevailed through the wet period (September to November) and to the beginning of the dry period (January 2019; **Figure 4**). An elevation profile of the microtopography shows that most of the wetland is below sea level – 0.4 meters below sea level at its lowest point and only 0.14 meters above sea level at its highest elevation (**Figure 6**).

Species Composition Assessment

From May 2018 to March 2019, we collected a total of 58 species which we categorized into 32 families. The predominant plant growth form was herbs with 34 species, followed by 10 species of trees, 10 vines, and 2 species of shrubs and 3 grasses. We found a proportion of 0.17 of woody species to non-woody (10 woody vs. 48 non-woody species), and 47 native species and 11 nonnatives (4.3 ratio). There were 42 dicotyledons and 12 monocotyledons. Of the collected species, 46 were perennial species, and 12 were annual (**Table 3**).

Leaf Traits

Trees had a lower leaf area than herbaceous and shrub species, where *Avicennia* and *Laguncularia* leaves were smaller than *Acrostichum* and *Dalbergia* (**Table 4**). The heaviest leaves were from *Dalbergia*; *Laguncularia* and *Avicennia* trees had similar foliar weights to each other. Leaves for all species followed the same weight area relationship, indicating a uniform sampling of adult leaves, allowing for comparison within dates (**Figure 7**). SLA for species varied significantly between dates, showing decreasing patterns post-hurricane in *Avicennia*, and increasing SLA values in *Dalbergia*. *Laguncularia* remained constant, except for June 2019 which SLA values decreased significantly from the rest of the dates (average 47.2 g/cm^2). The pattern of SLA was *Acrostichum* > *Dalbergia* ≥ *Avicennia* > *Laguncularia*.

Leaf carbon (C) concentration varied from 36 to 58%, with a mean of 45 ± 7 % in all species. *Dalbergia* had the highest C concentration with 53 ± 3 %, and *Laguncularia* had the least with 37 ± 0.8 %. Tukey-Kramer comparison showed significant differences between species, except between *Acrostichum* and *Laguncularia*. Leaf nitrogen (N) concentration ranged from 0.91 to 3.95 %, with a mean of 2.4 ± 0.8 %. *Dalbergia* had the highest N concentration with 3 ± 3.1%, and *Laguncularia* had the least with 1.1 ± 0.1 %.

Leaf C isotope ratios spanned a range of over 6 ‰ with a mean of −28.7 ± 2.1 ‰. *Avicennia* showed a large range of values from −32.2 to −28.2 ‰, (average −29.8 ± 1.9 ‰) while the rest of the species had smaller ranges (standard deviations <0.8 ‰). *Acrostichum* and *Dalbergia* C stable isotopes were similar and differed significantly from *Laguncularia* and *Avicennia*. N isotope ratios spanned a range of over 8 ‰ with a mean of 3.79 ± 2.7 ‰. *Avicennia* had the highest values with 6.6 ± 1.2 ‰ and *Dalbergia* the lowest with 0.3 ± 0.7 ‰. Plant WUE varied significantly among plant life-forms where trees had lower values than herbaceous species.

DISCUSSION

This study evaluated plant successional dynamics in coastal urban wetlands after a hurricane. The fast-slow continuum can explain these dynamics, where fast-growing but short-lived leaves are on one side of the spectrum, and slow-growth long-lived leaves are on the other, as leaf traits results suggest. Changes in hydrological conditions to more freshwater conditions will favor the establishment of herbaceous, non-halophyte species; however, as conditions stabilize to more saline, woody vegetation

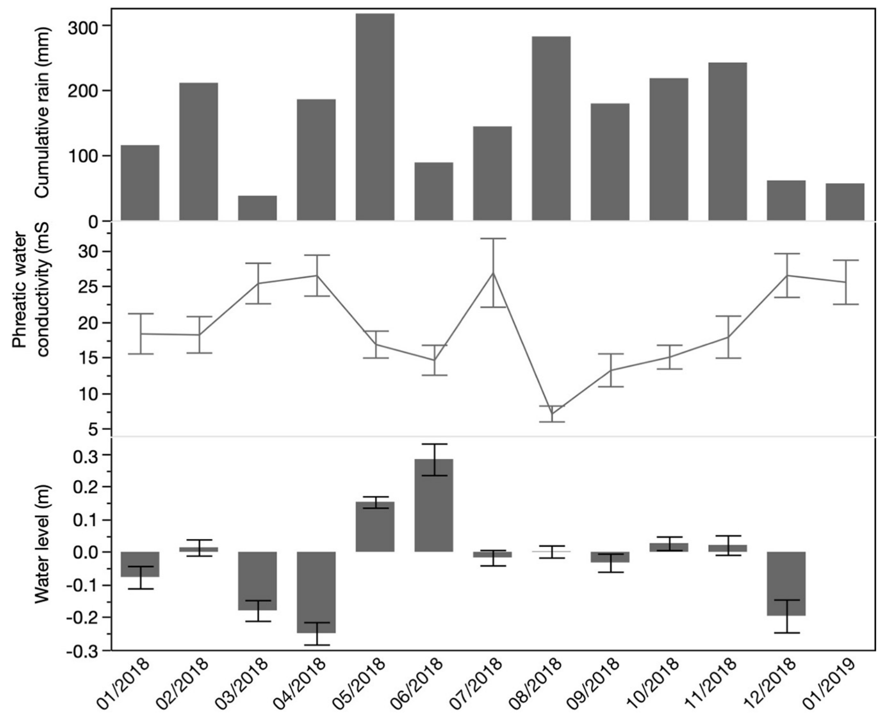

FIGURE 4 | Total monthly rainfall accumulation (mm) and average monthly phreatic water conductivity (mS/cm) and water levels (negative values indicate below soil level, positive values are above soil level) in ciénaga Las Cucharillas. Error bars represent ± standard error.

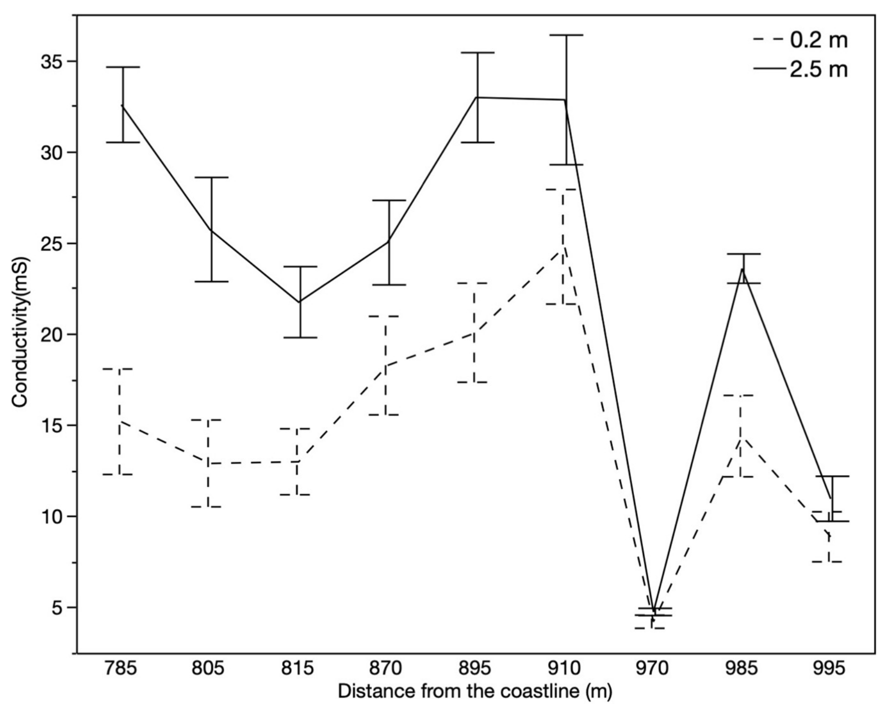

FIGURE 5 | Average monthly water conductivity at the phreatic level (0.2 m) and 2.5-meter depth at specific distances from the coastline (n = 12). Error bars represent ± standard error.

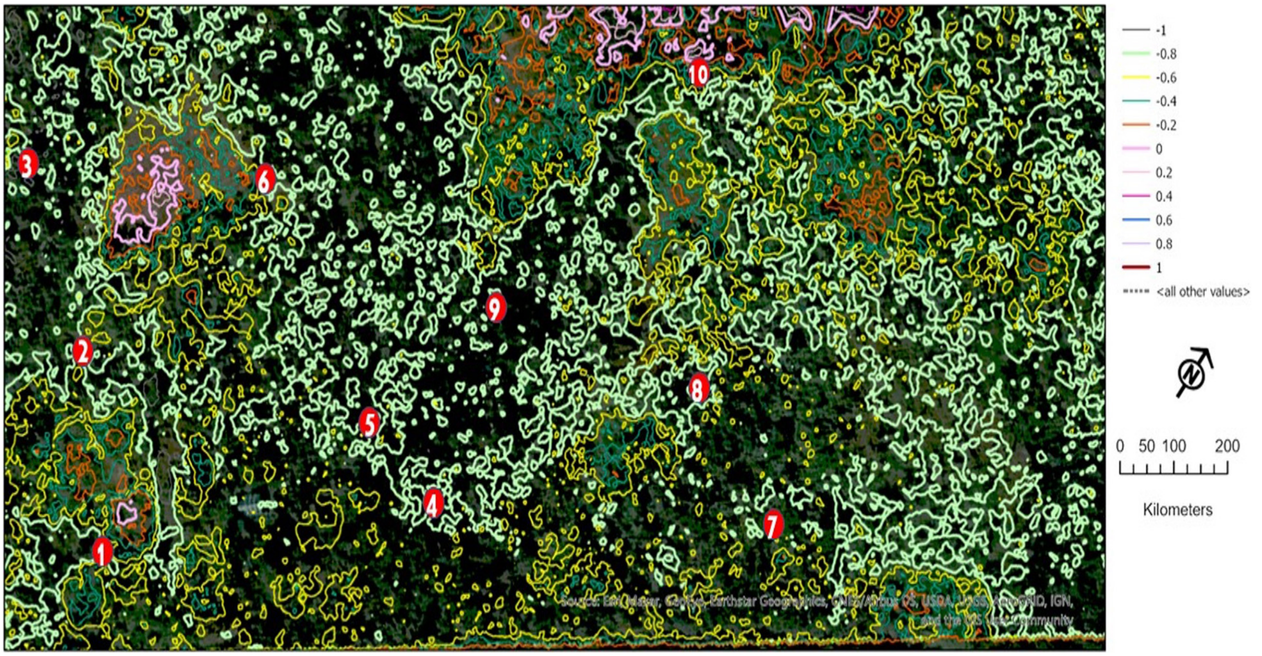

FIGURE 6 | Soil profile elevation for the study area in ciénaga Las Cucharillas. Red dots denote monitoring wells. Contour lines are in meters.

TABLE 3 | Previous and post hurricane plant composition parameters comparison.

Parameters	Pre-hurricane (based on Axelrod 2003)	Post-hurricane (present study)
Species richness: total number of species found	28 spp	58 spp
Species diversity	19 families	32 families
Dominant plant life-form	Herb (65%)	Herb (53%)
Proportion of woody species to non-woody	0.16 (4 woody/25 non-woody)	0.17 (10 woody/ 48 non woody)
Proportion native- not native species	8.7 (26 native/ 3 nonnative)	4.3 (47 native/ 11 nonnative)
Proportions dicotyledons – monocotyledons	n/a	3.1 (42 dicot/ 12 monocot) 4 ferns
Perennial/annual	2.6 (21 perennial/8 annual)	3.8 (46 perennial/12 annual)

will replace these species. High ^{15}N values suggest that hurricanes possibly bring nutrient inputs to the ecosystem, increasing the speed of the ecosystem's recovery. Hurricanes in coastal urban wetlands might initially affect plant cover but do not affect plant composition in the long term. Climate change, expressed as precipitation extremes, sea-level rise, and increased evapotranspiration due to increased temperatures resulting in an increase in dry days (PRCCC, 2014), establishes the stressor baseline for coastal wetland ecosystems dynamics.

Wetland vegetation cover had a high recovery rate – 16 months after the hurricane, vegetation cover occupied 87 % of the study area, a 20 % increase in a year and a half post-hurricane. Regeneration dynamics were seen 7 months after the hurricane as barren substrate was occupied by polyhaline tolerant plants characterized by high SLA, fast growth, and short-lived leaves (Poorter and Remkes, 1990). Non-flooded conditions facilitated recolonization.

Leaf economics spectrums correlate with the plant fast-slow continuum, where plants that live longer invest more resources in leaf construction, whereas short-lived plants usually have fast growth leaves but are shorter-lived (Salguero-Gómez, 2016). We found that to be the case in this study, as the plant cover succession is related to the leaf investment of dominant plant species. Herbaceous cover doubled during the first 10 months, in contrast to tree cover, which had a moderate increase. Of the dominant species we assessed, *Acrostichum* (herbs) had a significantly higher SLA than *Laguncularia* and *Avicennia*.

As the wet season started, changes favored herbaceous species such as *A. danaeifolium,* tolerant to waterlogging, which doubled their plant cover. Sharpe (2009) reported increases in biomass rates and fertile leaf production of *A. danaeifolium* 8 months after a hurricane and a five-time increase in biomass rates after 2 years. This shift in vegetation could be due to changes in hydrological conditions, as has been previously reported in other coastal wetlands, where changes from saltwater conditions to freshwater inputs will favor the establishment of herbaceous wetland instead of woody vegetation (Ball, 1980; Clark and Csiro, 1988). Changes in soil microtopography is another factor that can play a role in the establishment of vegetation in wetlands (Moser et al., 2009). Microtopographical changes at our site likely

TABLE 4 | Plant functional traits, carbon and nitrogen contents, isotopic signatures, intracellular CO_2 concentrations (*ci*), and intrinsic water use efficiency (*WUE*) for the plant functional types.

	Acrostichum	*Avicennia*	*Dalbergia*	*Laguncularia*
Leaf area (cm^2)	68 ± 22*a*	20.3 ± 8*c*	47 ± 14*b*	22 ± 12*c*
Leaf dry weight (g)	0.63 ± 0.2*a*	0.37 ± 0.4*b*	0.55 ± 0.2*a*	0.37 ± 0.3*b*
SLA (g/cm^2)	110 ± 12*a*	84 ± 34*b*	87 ± 14*b*	69 ± 22*c*
C %	41 ± 1*c*	46 ± 4*b*	53 ± 3*a*	37 ± 0.9*c*
N %	2.5 ± 0.1*b*	2.7 ± 0.3*ab*	3.1 ± 0.5*a*	1.1 ± 0.1*c*
^{13}C ‰	−26.7 ± 0.6*a*	−29.8 ± 1.8*b*	−27.3 ± 0.8*a*	−31.2 ± 0.8*b*
^{15}N ‰	5.4 ± 1*a*	6.6 ± 1.2*a*	0.30 ± 0.7*c*	3 ± 0.2*b*
ci (μ mol/mol)	252.2 ± 9*b*	309.3 ± 33*a*	259.4 ± 12*b*	334.5 ± 14*a*
intrinsic WUE (mmol/mol)	0.100 ± 0.005*a*	0.064 ± 0.02*b*	0.096 ± 0.007*a*	0.049 ± 0.008*b*

Means (± SD) with different letters in each row denotes significant differences among groups.

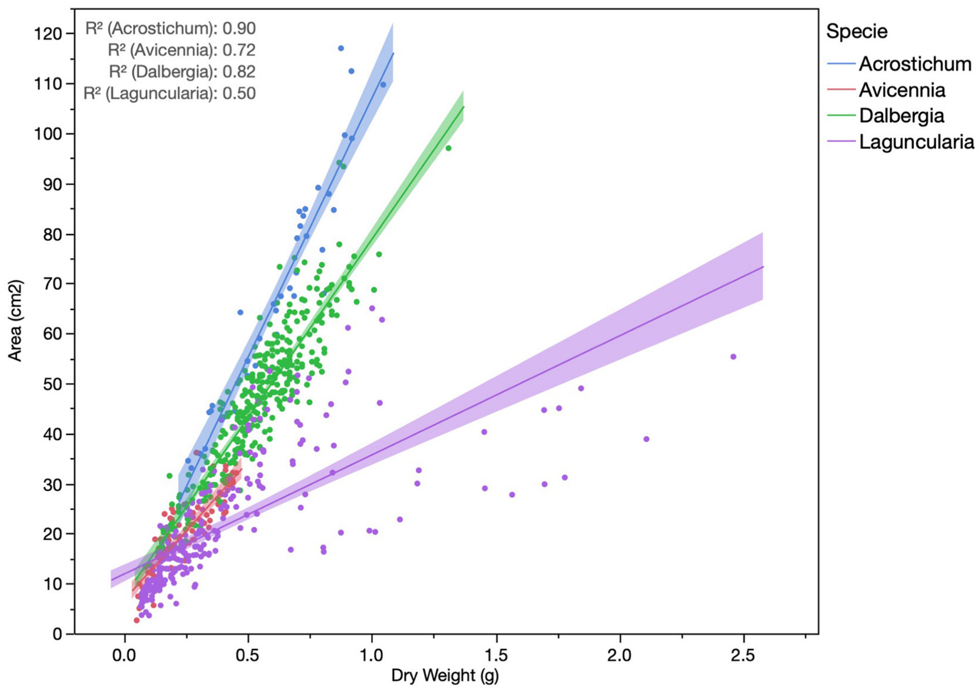

FIGURE 7 | Area – weight relationship of the four species sampled.

effected species composition and cover since we observed that the sites above sea level had no tree cover. The 20 % increase in tree cover observed in July 2018 can be explained as branching and canopy development of surviving trees. McKee et al. (2007) found positive interactions between herbaceous vegetation and mangroves, proposing the former as facilitators of mangrove recolonization in disturbed areas by trapping propagules and increasing survival and growth by possible enhancement of edaphic physiochemical factors. This proposed facilitation was not part of our study. Seedling distribution and survival should be included in future studies.

Hartman (1988) found that after disturbances in tidal saline wetlands, regeneration is controlled by vegetative propagation due to the scarcity of a seed bank. Based on field observations and image visual interpretation, the moderate increase in *D. ecastaphyllum* shrub cover in a saline area was due to vegetative propagation (Francis, 2004). Our results suggest the importance of vegetative propagation under constant salinity stress.

After 16 months, a shift in vegetation cover was observed where species with long-lived, slow growth and low N content leaves (as in *Laguncularia*) had larger plant cover. WUE analysis seems to support these observations as species with higher WUE have higher chances of surviving and regrowing despite waterlogging or dry periods that intensify after hurricanes. High ^{15}N values in the sampled species point toward a eutrophic system where high nutrient availability increases the system's regeneration speed. *Dalbergia* is an exception because of the symbiotic relationship with nitrogen-fixing bacteria (Saur et al., 2000). Another aspect to consider in urban coastal wetlands after disturbances is the arrival of non-indigenous species. Bhattarai and Cronin (2014) argued that hurricanes bring non-indigenous species to the ecosystem. We did not find this in our study area reserve, as native species present outnumbers non-indigenous species. This can be credited to several factors, such as biotic resistance or environmental factors in urban wetlands (Ehrenfeld, 2008; Ackerman et al., 2016).

Hurricanes are a stress test to ecosystems where vegetation response will vary according to their severity (Lugo, 2000). The dynamic nature of coastal wetlands allows for resilience to stressors of different intensities. Hurricane María, an acute catastrophic stressor, severely affected the coastal wetland. Our results show that although the wetland was observably greatly affected initially, it was resilient in the continuous recovery of the vegetation cover despite the severity of the disturbance. How chronically stressed wetlands respond to catastrophic stressors will test the resiliency of these systems.

CONCLUSION AND RECOMMENDATIONS

- Plant functional types proved to be resilient to the initial hurricane effect and subsequent changes in conductivity and freshwater conditions. Fast-slow continuum traits could help explain plant regeneration dynamics after a hurricane.
- High ^{15}N values in the sampled species point toward a eutrophic system where high nutrient availability increases the system's regeneration speed.
- Wetland vegetation cover had a high recovery rate without rehabilitation intervention. The succession dynamics and the hydrological conditions described in this study can help wetland managers prioritize rehabilitation (if necessary) efforts after disturbances.
- Future studies will expand how spatio-temporal conditions in the wetlands, sea-level rise, and extremes of precipitations and the degree and intensity of further atmospheric disturbances will affect long-term community dynamics.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

EC and EH conceived and designed the study, analyzed the data, and wrote the manuscript. EH, SP-P, and GO-R field sampling and analysis. All authors contributed to the article and approved the submitted version.

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