PRELIMINARY ESTIMATE OF THE IMMEDIATE EFFECTS OF HURRICANE MARÍA ON THE TREE STRUCTURE AND SPECIES COMPOSITION OF NOVEL FORESTS IN THE MOIST LOWLANDS OF PUERTO RICO

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Abstract

Puerto Rico is regularly affected by the passing of hurricanes, resulting in assemblages of native tree species that are adapted to withstand hurricane effects. Tree species that were introduced for agricultural or ornamental purposes are now abundant in most secondary forests in Puerto Rico, increasing the ecological novelty of island forests and the uncertainty of their response to hurricane events. We report immediate and visible short-term effects of Hurricane María on the tree structure and species composition of four novel-secondary-forests found in the moist lowlands of Puerto Rico. We sampled the density (trees/ha), basal area (m^2/ha), species richness and composition of large (≥ 10 cm diameter at breast height; [DBH]) and small (≥ 2.5 cm to < 10 cm DBH) trees on each site before (between 2005 and 2017) and after (2018) Hurricane María, and used paired T-tests to evaluate the significance of differences observed between sampling dates. Contrary to expectation, we did not find a significant reduction in mean (n = 4) values of tree density, basal area, and species richness on these four sites after the hurricane. In addition, we found no substantial changes in the relative dominance of species and no clear pattern of change in the percentage of introduced species across the four sites. The most extreme hurricane-induced changes in tree structure for pooled size-classes on any one site included 1) a reduction of 38% in density on one site, 2) an increase of 18% in density and a reduction of 26% in basal area on another site, and 3) an increase of 21% in basal area on a third site. Species richness of pooled tree size-classes increased by up to 50% or decreased by up to 30% on each site, and replacement of the dominant tree species was observed only in the small tree size-class and on one site only. Post-hoc Kruskal-Wallis tests revealed no significant differences in the magnitude or direction of changes in tree density, basal area, and species richness between large and small tree size-classes. Although the direction of changes in tree density, basal area, and species richness were highly variable among sites, the mean values of these variables were remarkably similar before and after the hurricane. These results suggest that the immediate effects of Hurricane María were offset by growth and recruitment within a relatively short time span. Our results also indicate that higher sample sizes may reveal patterns in hurricane effects arising from the distance of any given site to the trajectory of Hurricane María. Our findings show that, in the short-term, the tree structure and species composition of novel forests in the moist lowlands of Puerto Rico can be as resilient to immediate hurricane effects as that of the island's original, historic forests.

Keywords Anthropocene, Caribbean coastal and karst forests, introduced species, land-cover change, large infrequent-disturbances, short-term visible hurricane-effects.

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Resumen

Puerto Rico es afectado regularmente por el paso de huracanes, resultando en un arreglo de especies nativas adaptadas a resistir sus efectos. Árboles de especies introducidas, los cuales son abundantes en la mayoría de los bosques secundarios de Puerto Rico, han incrementado la novedad en los bosques insulares y la incertidumbre sobre sus respuestas a tales eventos atmosféricos. Reportamos los efectos visibles del huracán María a corto plazo sobre la estructura y composición de especies de árboles en bosques secundarios noveles encontrados en las tierras bajas húmedas de Puerto Rico. Muestreamos la densidad de árboles (árboles/ha), área basal (m^2/ha), composición y riqueza de especies de arboles grandes (≥ 10 cm diámetro a la altura de pecho; DAP) y pequeños (≥ 2.5 a < 10 cm DAP) en los cuatro sitios antes (entre 2005 y 2017) y después (2018) del huracán María y usamos la prueba T-pareada para evaluar diferencias observadas entre las fechas muestreadas. Contrariamente a lo esperado, no encontramos una reducción significativa en el valor promedio (n = 4) de densidad de árboles, área basal, y riqueza de especies en los sitios después del huracán. Tampoco encontramos un patrón claro de cambio en porcentaje de especies introducidas, en la dominancia de especies, y las curvas de domininacia-diversidad de especies no indicaron cambios sustanciales en la dominancia relativa de especies. Los cambios más extremos en la estructura de los árboles para ambas clases de tamaños agrupadas por sitios incluyeron 1) una reducción de 38% en densidad en un sitio, 2) un aumento de 18% en densidad de árboles y una reducción del 26% en área basal en otro sitio, y 3) un aumento de 21% en área basal en un trecer sitio. A través de los sitios, la riqueza de especies de todos los árboles aumentó hasta por 50% o se redujo hasta por 30%, y el reemplazo de la especie de árbol dominante se observó solo en la clase de tamaño de árboles pequeños y solamente en un sitio. No encontramos diferencias en la magnitud o dirección de los cambios entre las clases de árboles grandes y pequeños. Aunque la dirección de cambios en la densidad, área basal, y riqueza de especies de árboles fueron altamente variables entre los sitios, los valores promedio fueron notablemente similares antes y después del huracán. Esto sugiere que los efectos del huracán fueron compensados por el crecimiento y el reclutamiento de árboles en un período de tiempo relativamente corto. Nuestros resultados indican que un mayor tamaño de muestra puede revelar diferencias en los efectos a corto plazo a raiz de la distancia del sitio a la trayectoria del Huracán María. Nuestros hallazgos muestran que la estructura y la composición de especies de árboles en bosques secundarios noveles puede ser tan resiliente como la de bosques históricos originales a eventos de huracanes, al menos a corto plazo.

Palabras clave Antropoceno, bosques costeros y cársicos del Caribe, especies introducidas, cambio en cobertura de terrenos, disturbios grandes e infrecuentes, efectos visibles de huracanes a corto plazo.

INTRODUCTION

Due to its location in the Caribbean, Puerto Rico is regularly exposed to major hurricane events that cause cyclical and drastic changes to the island's ecosystems (López and Castro 2018). In Puerto Rico, hurricanes make landfall every decade, and their effects on forest ecosystems include immediate and visible physical effects on tree structure and species composition that are observable in the short-term (i.e., up to three years after the event), and non-visible effects on ecosystem function and successional trajectory that are manifested in the long-term (Lugo 2008). The periodicity of hurricane landfalls in Puerto Rico appears to favor native tree species with adaptations to fulfill ecological niches created by such large and infrequent disturbances (Basnet et al. 1993; Dale et al. 1998; Van Bloem et al. 2003). Relative to native tree species, those that were introduced to Puerto Rico prior to colonization by Europeans for agricultural and ornamental purposes may be in ecological disadvantage to adapt to short- and long-term changes in ecological space created in the aftermath of major hurricanes.

Just like hurricanes, humans play an important role in the successional trajectories of Puerto Rican secondary forests. Most of these forests constitute novel ecosystems that emerge as a natural response to high rates of anthropogenic changes and disturbances in the Anthropocene (Lugo 2009; Radeloff et al. 2015). The expansion of agriculture and population growth sped up deforestation rates in Puerto Rico in the 19th century up to the mid 20th century, when forest cover in the island reached a low of 5% that was mostly confined to mountain forest reserves, such as El Yunque in the northeast (March 1899; Álvarez et al. 2013). Today, it is estimated that forests cover 60% of the land area of Puerto Rico as a result of the abandonment of agricultural lands and an economy that is increasingly dependent on fossil fuels and external subsidies (Gould et al. 2017; González and Ma 2017). Centuries of intensive agricultural practices in the lowlands, which were chiefly used for sugar cane plantations, resulted in extensive modification of the land, loss of topsoil, and conditions that can hamper the establishment of native tree species (Silén 1993; Lugo 2004). However, some introduced tree species appear highly adapted to abandoned agricultural lands and in many cases eventually form nearly monodominant forest stands as a consequence of their arrival, colonization, and fast growth in deforested sites (Grau et al. 2003; Lugo 2004). Introduced species are now present throughout Puerto Rico and dominate the island's young secondary forest cover (Lugo and Helmer 2004; Martinuzzi et al. 2013; Marcano-Vega et al. 2015).

In September 2017, hurricanes Irma and María transformed the Puerto Rican landscape and affected the structure and functioning of its social and ecological systems (Cangialosi et al. 2018; Lugo 2018; Pasch et al. 2018). Although both were high-intensity major hurricanes (categories 4–5 in the Saffir-Simpson scale), Hurricane María was the one that made landfall and possibly caused the most significant effects on Puerto Rican forests and landscapes since Hurricane San Felipe's landfall in 1928 (López and Castro 2018). The immediate and visible effects of Hurricane María on forested areas included a reduction of 31% in canopy 'greenness,' estimated from remotely-sensed changes in leaf area, chlorophyll content, canopy cover, and structure at an island-wide scale (Van Beusekom et al. 2018). However, most long-term study plots, in which we base our current knowledge of hurricane effects on Puerto Rican forests, are located in the wet mountains of El Yunque and the dry forests in Guánica. Also, the information available for forests located in the lower elevation moist forest life-zone, which covers most lowlands and happens to be the most extensive on the island, is scant (Ewel and Whitmore 1973; Van Bloem et al. 2005; Brokaw et al. 2012). A notable exception is a study on the effects of Hurricane Georges on the tree structure and species composition in stands of novel forests in the moist lowlands, urban Río Piedras, northern Puerto Rico (e.g., Lugo et al. 2005b).

The moist lowlands of Puerto Rico have historically been subjected to the highest rates of land conversion for agriculture and urbanization, but these lowlands proportionally contain most of the island's novel-forests whose ecological properties, structure, and function are just beginning to be understood (Helmer et al. 2008; Lugo 2009; Martinuzzi et al. 2013). Lowland forests in Puerto Rico exhibit higher levels of ecological novelty due to their relatively young age, previous land use for intensive agriculture (e.g., sugar cane and grazing), high dominance by introduced tree species, and ephemerality due to high land conversion rates when compared to forests found in protected areas (Helmer

Table 1. Site descriptions for the four lowland novel-forest stands sampled in this study. Site elevation is from GPS measurements and topographic maps. Slope landforms are low side-slopes to moderately steep slopes for Guajataca and Río Hondo (Martinuzzi et al. 2007). Area sampled for the large tree size-class is followed by area sampled for the small tree size-class in parenthesis, and all area sampled values are rounded to the nearest 0.01 ha. Four trees per tree size-class were sampled on each point-quarter center method (PQCM) point (Cottam and Curtis 1956). On Pugnado, concentric 250 m^2 and 100 m^2 plots were used to sample large and small tree size-classes, respectively.

Site	Elevation (m)	Slope (°)	Aspect	Substrate and Landform	Year of Sampling		Area Sampled (ha)		PQCM points (plots in Pugnado)	
					Before	After	Before	After	Before	After
Cibuco II	10	0	None	Alluvial Floodplain	2005	2018	0.05 (0.03)	0.03 (0.01)	10	4
Guajataca Left	3–93	13–25	NW	Karst Slope	2017	2018	0.06 (0.02)	0.08 (0.01)	8	7
Pugnado	170	4	None	Karst Depression	2017	2018	0.03 (0.01)	0.03 (0.01)	1	1
Río Hondo	30–40	3–24	SW	Volcanic Slope	2015	2018	0.05 (0.01)	0.04 (0.01)	5	5

et al. 2008; Radeloff et al. 2015; Abelleira 2019). Nevertheless, detailed field-based assessments of short- to long-term hurricane effects on the tree structure and species composition of Puerto Rico's novel forests are scarce. The rarity of these assessments generates a significant gap in our knowledge and understanding of the effects of hurricanes on the island's current forest cover and impairs our capacity to anticipate and manage for extreme hurricane events in the future.

We sampled the tree structure and species composition of four lowland novel-forest sites before (2005, 2015, or 2017; Table 1) and after (2018) the passing of Hurricane María. Our objective was to quantify the short-term changes in tree density, basal area, and species richness that occurred as a result of the immediate and visible effects of Hurricane María on these four novel-forest sites. We expected that the hurricane would set back the process of ecological succession observed in Puerto Rico for secondary forests of this age range (35–60 yrs.), which is typified by an ongoing increase in tree density, basal area, and accumulation of species as forest growth proceeds toward ecological maturity (Aide et al. 2000; Chinea 2002; Flynn et al. 2010). Specifically, we expected that tree density, basal area, and species richness would decrease as a result of the short-term, high-energy effects of Hurricane María, which were manifested by high-velocity winds and copious rainfall that caused extensive breakage of tree branches, tree uprooting, and treefalls. Our results constitute a preliminary estimate of the magnitude and direction of the immediate effects of Hurricane María on the tree structure and species composition of novel forests in the moist lowlands of Puerto Rico. This study contributes to understanding Puerto Rico's current forest cover, which was largely shaped by large and infrequent hurricane disturbances in prehistoric times and is increasingly being shaped by anthropogenic land cover change and species introductions in the Anthropocene.

METHODS

Study Region, Site Selection and Description

The study sites lie in the lowlands located within the subtropical moist forest life-zone of Puerto Rico (Figure 1). In the moist life-zone, mean annual precipitation and air temperature range between 1,000 mm and 2,200 mm, and between 21°C and 25°C, respectively (Ewel and Whitmore 1973). We selected four study sites that are part of on-going studies focused on the ecological structure, function, and management interventions in novel forests dominated by introduced species in Puerto Rico (Abelleira et al. 2010; Túa and Abelleira 2019; Lugo et al. 2020). Two of the sites were dominated by *Spathodea campanulata* (Abelleira et al. 2010), a third site by *Albizia procera*, and a fourth site by *Terminalia catappa* (unpublished data). The location and landform of the study sites are, in order of their location from eastern to western Puerto Rico, the following (Figure 1): (1) Cibuco II, located on riparian alluvial floodplains; (2) Pugnado, located on a karst depression; (3) Guajataca Left, located

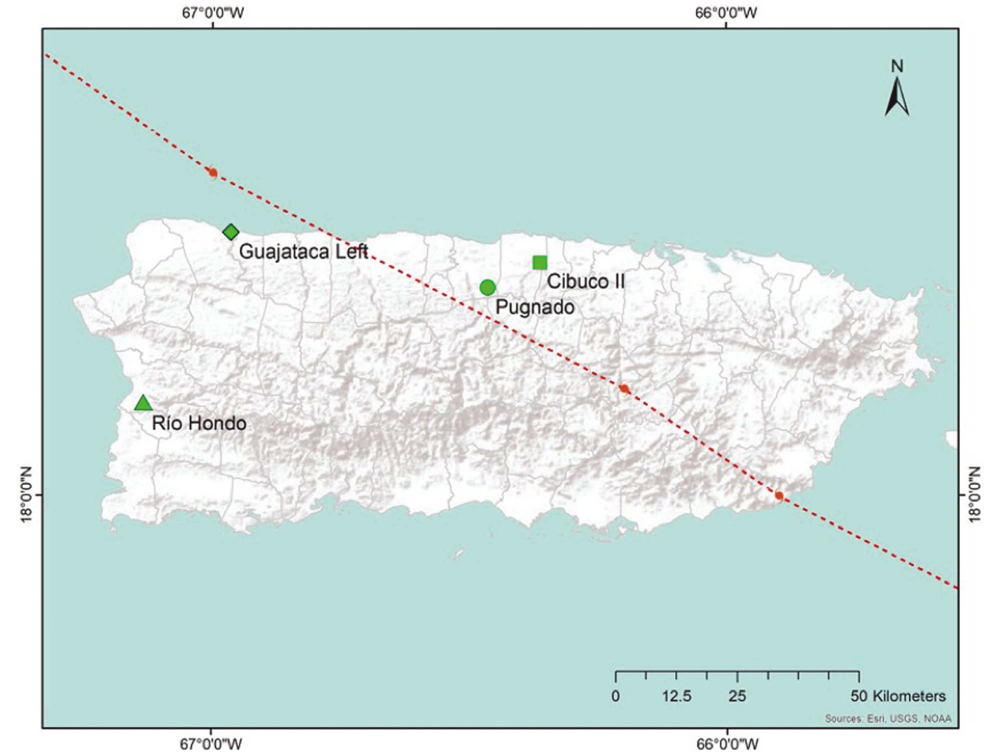

Figure 1. Location of study sites and the trajectory of Hurricane María in Puerto Rico.

in a low karst side slope about 100 m from the coastline; (4) and Río Hondo, located on a low volcanic side-slope (Martinuzzi et al. 2007; Gould et al. 2008). Cibuco II is on flat terrain, and Pugnado is enclosed within a depression that grades from a nearly flat slope at the bottom to a moderate slope on the side-slopes; therefore, these two sites have no aspect. The elevation of the four sites ranged from 10 m to 170 m above sea level (asl), and slope ranged from 0º to 25º (Table 1).

Age since abandonment, estimated from aerial photography coupled with informal interviews with neighbors, ranged from 35 to 60 years among the study sites. Previous land use included sugar cane plantations in Cibuco II and Río Hondo, subsistence farming in Pugnado, and grazing possibly occurring on all sites. The valleys where Cibuco II is located were used for sugar cane plantations since the 16th century, although it is not clear when the crop was first established on the site (Abelleira and Lugo 2008). Likewise, the first sugar cane plantations in the western alluvial valleys near Río Hondo date to the 16th century, yet the crop was possibly established later on gentle, volcanic slopes in the western lowlands where Río Hondo is located (Silén 1993). Previous land use in Pugnado consisted of farming of fruit trees, tubers, and plantains intercalated with occasional grazing (Abelleira et al. 2010). Previous land use of Guajataca Left is less clear, but its close distance (< 50 m) to the coastal railroad tracks suggests the site was likely disturbed by the removal of carbonate rocks for constructing the mound atop which the tracks were placed. The coastal railroad was completed in 1890 and abandoned by the end of the 19th century (Bergad 1978; Muñoz 2017). Given its proximity to alluvial flats currently used for hay cropping, it is possible that Guajataca Left was used for marginal grazing, but the site's topography and substrate would have made any agriculture and grazing difficult.

Hurricanes Irma and María

On 6 September 2017, the eye of the category-5 Hurricane Irma was 92.6 km off the northern coastline of Puerto Rico; it developed a double-eyewall structure, had maximum winds of nearly 287 km/hr, and a large wind-field, but did not make landfall (Cangialosi et al. 2018). In contrast, on 20 September 2017, Hurricane María made landfall in the southeastern coast of Puerto Rico near the municipality of Yabucoa (Figure 1; Pasch et al. 2018). Also, Hurricane María crossed the island diagonally, from the southeast to the northwest, with maximum winds and rainfall accumulations of 150 km/hr and 96.3 mm, respectively, just below the threshold of a category-5 hurricane. On 21 September 2017, the eye of Hurricane María exited between the municipalities of Camuy and Quebradillas, near the northwestern corner of Puerto Rico. Hurricane María is considered one of the most intense hurricanes documented as making landfall in Puerto Rico since Hurricane San Narciso (category-3) in 1867 (López and Castro 2018), along with Hurricanes San Ciriaco (1899), San Felipe II (1928), Hugo (1989), and Georges (1998). In our study, we mainly focus on the immediate effects of Hurricane María because we consider that the effects of Hurricane Irma on our study sites could be negligible for the reasons mentioned above. Nonetheless, we acknowledged that our estimates of changes in tree density, basal area, and species richness and composition could include the combined effects of hurricanes Irma and María, with the latter contributing to most of the changes in vegetation.

Forest Sampling

We sampled the diameter (cm) at breast height (DBH; sampled at 1.4m above the ground) and identified the species of trees alive and standing on each site before and after Hurricane María to estimate changes in tree density, basal area, and species richness. On three of the study sites, we used the Point-Centered Quarter Method (PCQM) (Cottam and Curtis 1956; Ashby 1972) to sample large (≥ 10 cm DBH) and small (≥ 2.5 cm to < 10 cm DBH) trees alive and standing before and after the hurricane (Table 1). On each of these three sites, we placed one PCQM line-transect (approximately 100-m long each), at random on the initial sampling period (i.e., before the hurricane), and set as many PQCM sampling-points as possible on each transect to record vegetation characteristics for large- and small-tree size-classes on each sampling date. On a fourth site, Pugnado, we established one circular concentric plot of 250 m^2 and 100 m^2 to sample trees alive and standing in the large and small tree size-classes, respectively, before and after the hurricane (Table 1). The concentric plot was placed randomly before the hurricane, and the DBH of all trees from each corresponding tree size-class was sampled on the concentric plot before and after the hurricane. Comparisons of PCQM and plot-based methods for the sampling of tree density, basal area, and species richness have shown that estimates from both methods are in very close agreement when applied to novel-forest sites (Abelleira and Colón 2006). Each tree was identified to species following Little and Wadsworth (1964) and Little et al. (1988).

We must clarify that although the PQCM can increase the efficiency of sampling efforts, it may need adaptations when applied to long-term studies (Lessard et al. 2002; Dahdou and Koedam 2006). Therefore, we note that although the location and extent of the transects used for placing PCQM points was the same on each of the three sites where PCQM was used on each sampling date (Table 1), the actual location of the points along each transect was randomized and resampled on each sampling date following the standard application of the PQCM (Cottam and Curtis 1956; Lessard et al. 2002). Since the exact point locations had to be randomized and placed within the initial extent of the lineal transect, the number of points per transect, and the area sampled per tree size-class per site, varied between sampling periods (before and after the hurricane; Table 1). In PQCM, the distances between points and trees are used to estimate tree density and basal area, and therefore a reduction in the number of trees (i.e., in tree density), as indeed happened in most of the sites, inevitably leads to potential overcrowding of PQCM points for any given extent of lineal transect. This is so because contiguous PCQM points on a lineal transect cannot share the same trees in the sample, which would create a condition (i.e., dependence of tree sub-samples between PCQM sample-points) that would invalidate the application of the method.

Data Analysis

We estimated tree density (trees/ha), basal area (m^2/ha), species richness, and species importance values (IV) for each tree size-class on each site before and after Hurricane María. For each variable, we also estimated the mean values, and corresponding

Table 2. Tree density (trees/ha), basal area (m^2/ha), species richness, percentage of introduced species, and dominant species of large (≥ 10 cm diameter at breast height; DBH), small (≥ 2.5 cm to < 10 cm DBH), and pooled size-classes of trees in four, lowland novel-forest sites, before and after Hurricane María. Codes for species: Sc = *Spathodea campanulata*; Tc = *Terminalia catappa*; Ap = *Albizia procera*; Gg = *Guarea guidonia*; Cc = *Calophyllum calaba*; Cs = *Casearia sylvestris*.

Site	Tree Density (trees/ha)		Basal Area (m^2/ha)		Species Richness		Introduced Species (%)		Dominant Species: Importance Value (%)	
	Before	After	Before	After	Before	After	Before	After	Before	After
Large Trees										
Cibuco II	868	607	72.5	87.6	3	2	66.7	50.0	Sc: 84.3	Sc: 83.2
Guajataca Left	517	358	43.4	31.9	9	7	11.1	14.3	Tc: 48.9	Tc: 51.0
Pugnado	840	600	74.6	70.1	4	3	25.0	33.3	Sc: 75.1	Sc: 82.2
Río Hondo	366	552	12.7	14.5	5	7	40.0	42.9	Ap: 36.1	Ap: 38.2
Mean (S.D.)	648 (246.3)	529 (116.8)	50.8 (29.1)	51.0 (33.7)	5 (2.6)	5 (2.6)	35.7 (23.8)	35.1 (15.5)	61.1 (22.4)	63.7 (22.6)
Small Trees										
Cibuco II	1502	1820	2.8	3.5	3	6	66.7	16.7	Sc: 81.1	Gg: 57.3
Guajataca Left	1642	2179	5.5	4.1	12	12	8.3	8.3	Cc: 21.2	Cc: 31.8
Pugnado	1900	1100	3.8	2.1	9	6	25.0	33.3	Sc: 29.3	Sc: 30.3
Río Hondo	1529	1140	4.1	3.7	8	9	14.3	33.3	Cs: 28.4	Cs: 29.9
Mean (S.D.)	1643 (181.6)	1560 (528.8)	4.1 (1.1)	3.4 (0.9)	8 (3.7)	8 (2.9)	28.6 (26.4)	22.9 (12.5)	40.0 (27.6)	37.3 (13.3)
All Trees										
Cibuco II	2370	2427	75.3	91.1	4	6	–	–	–	–
Guajataca Left	2159	2537	48.9	36.0	16	15	–	–	–	–
Pugnado	2740	1700	78.4	72.2	10	7	–	–	–	–
Río Hondo	1895	1692	16.8	18.2	10	10	–	–	–	–
Mean (S.D.)	2291 (356.9)	2089 (456.0)	54.7 (28.6)	54.4 (33.2)	10 (4.9)	10 (4.0)	–	–	–	–

Notes: Species richness totals do not add up due to same species occurring in pooled tree size-classes.

standard deviation, for the four study sites. For each tree size-class, species IV's per site were estimated based on the relative density, basal area, and point frequency for each species in the three sites sampled with PCQM, and on relative density and basal area for each species in Pugnado. Changes (%) in the density, basal area, and species richness of trees on each site were estimated relative to values sampled before the hurricane. We used IV's to develop ranked-species dominance-diversity curves to assess changes in community structure due to the immediate effects of the hurricane.

We used paired-sample T-tests (two-tails) to compare the mean of differences (i.e., changes) in values of tree density, basal area, and species richness sampled before and after Hurricane María on each site for each tree size-class and for pooled (i.e., large and small) tree size-classes (n = 4). Although we initially did not expect any patterns of change in the IV of dominant species and the percentage of introduced species, we also used paired T-tests to compare the means of differences in these values before and after the hurricane to further illustrate short-term patterns of species turnover in the large and small tree size-classes. Normality of data was tested with Shapiro-Wilk tests and homoscedasticity with F-Max tests. We conducted post hoc Kruskal-Wallis tests (non-parametric ANOVA) to compare the mean values of changes (%) in tree density, basal area, and species richness sampled in the large tree size-class (n = 4) to those sampled in the small tree size class (n = 4) to evaluate if immediate hurricane effects were homogeneous among large and small tree size-classes. We used Infostat (Di Rienzo et al. 2014) for all statistical analyses and adopted an alpha value of $p \leq 0.05$ for statistical significance.

RESULTS

Density and Basal Area

The density of large trees ranged from 366 to 868 trees/ha on the four study sites before Hurricane María, and basal area ranged from 12.7 to 74.6 m^2/

ha (Table 2). After the hurricane, the density of large trees ranged from 358 to 607 trees/ha, and basal area ranged from 14.5 to 87.6 m^2/ha. The density of small trees ranged from 1,502 to 1,900 trees/ha before Hurricane María, and basal area ranged from 2.8 to 5.5 m^2/ha (Table 2). After the hurricane, the density of small trees ranged from 1,100 to 2,179 trees/ha, and basal area from 2.1 to 4.1 m^2/ha. We observed a smaller variation around the mean value of the density of large trees after the hurricane relative to the pre-hurricane value (Table 2). On the other hand, we observed the opposite pattern in the small tree size-class, where the variation around mean values of density of small trees was larger after the hurricane relative to pre-hurricane values. In contrast, we observed a somewhat larger variation around the mean value of the basal area of large trees after the hurricane relative to pre-hurricane values when compared with the corresponding pattern of variation observed for small trees before and after the hurricane (Table 2). Despite the wide range of variation in the mean values of density and basal area of large and small trees before and after Hurricane María, we found no significant changes in the mean values of these variables for both tree size-classes, and pooled tree size-classes, attributable to the hurricane (Table 3).

Species Richness and Importance Values

Species richness of large trees ranged from 3 to 9 species per site before Hurricane María, and from 2 to 7 species per site after the hurricane (range of area sampled: 0.03–0.08 ha; Tables 1 and 2). Likewise, species richness of small trees ranged from 3 to 12 species per site before the hurricane, and from 6 to 12 species per site after the hurricane (range of area sampled: 0.01 to 0.03 ha; Tables 1 and 2). However, the mean values and the variation of species richness for the four sites were very similar in the large and small tree size-classes, and for pooled tree size-classes, before and after the hurricane; we found no significant changes in the mean values of

Table 3. Changes in tree density (trees/ha), basal area (m^2/ha), and species richness of four lowland novel-forest sites sampled before and after Hurricane María. Changes are expressed in percentual change from initial pre-hurricane values. Also shown are means and standard deviation in parenthesis, and the T-statistic and corresponding significance (p-value) of paired T-tests conducted on values recorded before and after the hurricane for large, small, and pooled size-classes of trees.

Size-Class and Site	Density (% change)	Basal Area (% change)	Species Richness (% change)
Large Trees			
Cibuco II	-30.1	20.9	-33.3
Guajataca Left	-30.7	-26.5	-22.2
Pugnado	-28.6	-6.0	-25.0
Río Hondo	50.8	14.2	40.0
Mean (S.D.)	-9.7 (40.3)	0.7 (21.4)	-10.1 (33.8)
T-Statistic (p-value)	1.14 (p = 0.3)	-0.04 (p = 1.0)	0.58 (p = 0.6)
Small Trees			
Cibuco II	21.2	24.0	100.0
Guajataca Left	32.7	-25.4	0.0
Pugnado	-42.1	-44.7	-33.3
Río Hondo	-25.4	-10.4	12.5
Mean (S.D.)	-3.4 (36.0)	-14.1 (29.0)	19.8 (56.9)
T-Statistic (p-value)	0.27 (p = 0.8)	1.29 (p = 0.3)	-0.20 (p = 0.9)
All Trees			
Cibuco II	2.4	21.0	50.0
Guajataca Left	17.5	-26.4	-6.3
Pugnado	-38.0	-7.9	-30.0
Río Hondo	-10.7	8.2	0.0
Mean (S.D.)	-7.2 (23.6)	-1.3 (20.5)	3.4 (33.6)
T-Statistic (p-value)	0.67 (p = 0.6)	0.08 (p = 0.9)	0.48 (p = 0.7)

species richness of trees sampled before and after Hurricane María on these four study sites (Table 3).

The mean value of the percentage of introduced species in the large tree size-class remained similar before and after Hurricane María, and decreased slightly, by 6%, in the small tree size-class after the hurricane (Table 2). The percentage of introduced species was highly variable, ranging from 8.3% to 66.7% across sites in the large and small tree size-classes before and after the hurricane, but the variation around mean values was lower after the hurricane. The IV of the dominant species remained similar, and the identity of the dominant species remained the same on each site except for the small tree size-class on Cibuco II (Table 2). On Cibuco II, the IV of the dominant species in the small tree size-class decreased by 23.8% and the dominant species changed from *Spathodea campanulata* to *Guarea guidonia.* Overall, ranked-species curves of IV for

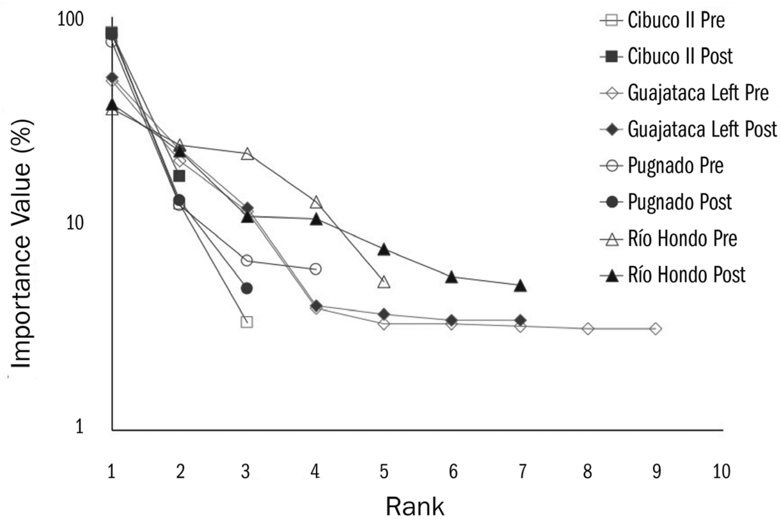

Figure 2. Ranked-species importance-values for large trees before (pre) and after (post) Hurricane María on four novel forests in the moist lowlands of Puerto Rico.

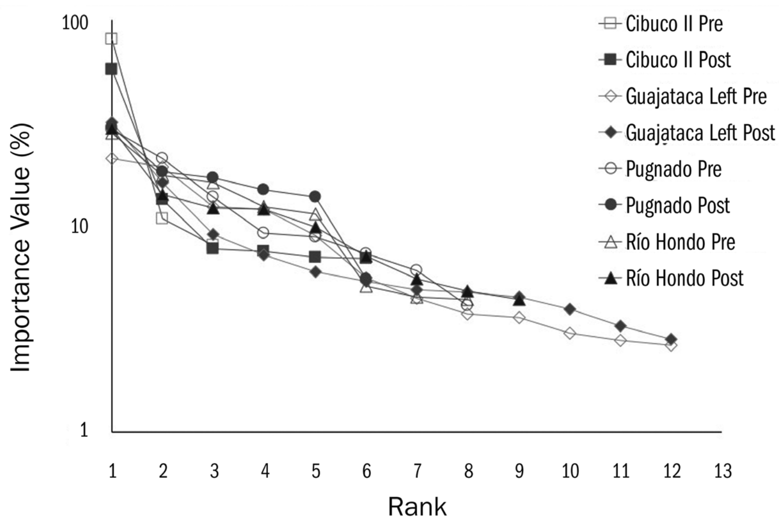

Figure 3. Ranked-species importance-values for small trees before (pre) and after (post) Hurricane María on four novel forests in the moist lowlands of Puerto Rico.

large and small tree size-classes on each site remained unmodified by the immediate effects of Hurricane María, with only the curves for the large tree size-class in Río Hondo exhibiting any perceptible modification (Figures 2 and 3).

Patterns per Site

The density of large trees, basal area, and species richness of large trees tended to increase in all but one site, Río Hondo (Table 2). On the other hand, changes in the density, basal area, and species richness of small trees exhibited a more variable pattern. For example, the density, basal area, and species richness of small trees increased in Cibuco II after the hurricane, but these variables decreased in Pugnado, and increased or decreased on the other two sites (Tables 2 and 3). The largest changes in the density, basal area, and species richness of large trees included a reduction of 33% in species richness in Cibuco II and an increase of 50% in density in Río Hondo. On the other hand, the largest changes in the density, basal area, and species richness of small trees included a reduction of 44% in density in Pugnado and a twofold (100%) increase in species richness in Cibuco II.

Changes in the density, basal area, and species richness of pooled size-classes of trees were also highly variable in direction (i.e., increased and decreased) when compared to changes in the large- and small-tree size-classes separately. However, the range of values was lower, and the means were overall closer to zero percent (i.e., ~no change) for the pooled size-classes of trees (Table 3). Post hoc Kruskal-Wallis tests showed there were no differences in the percentage of change in tree density, basal area, and species richness observed in the large-tree size-class when compared to corresponding changes in the small-tree size-class among the four study sites ($n = 4$, $df = 1$, $H \leq 0.52$, and $p \geq 0.5$ for all tests). Thus, we observed no clear tendency in the direction of changes in the density, basal area, and species richness among large- and small-tree size-classes. We also found no clear patterns or significant changes in the percentage of introduced species and the IV of the dominant species before and after the hurricane in the large- and small-tree size-classes (Table 2; $n = 4$, $T \leq 0.37$, and $p \geq 0.2$ for all paired T-tests).

Table 4. Summary of changes in tree density (trees/ha), basal area (m^2/ha), species richness, and importance values of dominant species on two novel-forests in the short-term (1 yr.) and long-term (5–7 yrs.) aftermath of Hurricane Georges (from Lugo et al. 2005a,b). Trees were sampled on a 0.1 ha plot and classified as large (≥ 4 cm diameter at breast height [DBH]) and small (≥ 2 cm to < 4 cm DBH) in Caguana, a site on volcanic slopes in the moist to wet life-zone in the central mountains in the rural municipality of Utuado, Puerto Rico. Large (≥ 4 cm DBH) trees were sampled on circular 250 m^2 plots (n = 40) distributed across different landforms on moist lowland volcanic slopes and valleys in the New Millennium State Forest in urban Río Piedras, Puerto Rico. IV = Importance Value.

Size-class and site	Short-term changes (%)				Long-term changes (%)			
	Tree Density	Basal Area	Species Richness	Dominant Species IV	Tree Density	Basal Area	Species Richness	Dominant Species IV
Large Trees								
Caguana	27.2	-8.5	6.7	-22.2	56.4	10.4	33.3	-55.6
Río Piedras								
Valley	–	–	–	–	-5.3	0.0	4.4	-13.7
Sloping Valley	–	–	–	–	-2.2	-8.4	-5.1	4.6
Slope	–	–	–	–	-17.6	-19.8	2.8	-50.3
Ridge	–	–	–	–	-12.1	3.9	9.4	-15.8
All Landforms	–	–	–	–	-13.6	-7.1	-5.4	-18.8
Small Trees								
Caguana	-20.9	-22.3	0.0	11.1	23.0	15.1	4.5	22.2

DISCUSSION

Our results stand in contrast to our expectations and to preliminary assessments of the effects of Hurricane María on Puerto Rico's forest cover, which suggested drastic reductions in tree density and basal area due to extensive tree mortality (Feng et al. 2018; Van Beusekom et al. 2018). Our results are comparable to the immediate effects of major (i.e., category-3 and higher) Hurricanes Betsy (1956), Hugo (1989), and Georges (1998) on the tree structure of wet forest stands in El Yunque observed in the short-term (< 3 years after the event), which include high and variable reductions in tree density (e.g., range of 27% to 63%, Brokaw and Walker 1991; Lugo 2008; Brokaw et al. 2012). We found similar reductions in tree density on two sites, but increments of equal magnitude on the other two sites, when data from large- and small-tree size-classes were pooled (Tables 2 and 3). Similar to patterns recorded in El Yunque, changes in basal area were not as large as for tree density and included more positive values (i.e., increments) among large trees, which suggest growth and recruitment into larger-tree size-classes in the short-term aftermath of Hurricane María. Nevertheless, changes in the mean values of density, basal area, and species richness of large and small trees for the four study sites were close to zero (Table 3). This is surprising when considering the wide-spread extent of changes in vegetation-cover and mortality of trees reported throughout Puerto Rico in the immediate aftermath of Hurricane María (Feng et al. 2018; Van Beusekom et al. 2018).

Changes in Forest Structure and Species Richness

Our results are comparable to the immediate effects of Hurricane Georges on a novel forest stand in Caguana, located in the municipality of Utuado in the central mountain range (Lugo et al. 2005a). In Caguana, the density of large trees increased, but the density of small trees and the basal area of both large and small trees decreased in the short-term aftermath of the hurricane (Table 4). In a study that included nine stands of novel forests dominated by *S. campanulata* in the wet mountains of Carite, near the municipality of Cayey in central south-eastern Puerto Rico, Pascarella et al. (2004) found short-term reductions in the density and basal area of large and small tree size-classes following Hurricane Georges. However, reductions in the density of small trees due to hurricane-induced mortality in Carite, although comparably higher than for large trees, were offset by recruitment of juveniles found in the understory into the small tree size-class (Pascarella et al. 2004). In the short-term, the patterns observed in Caguana by Lugo et al. (2005a) are perhaps more similar to those that we observed in Río Hondo, and patterns observed in Carite by Pascarella et al. (2004) are more similar to those that we observed in Guajataca Left.

Similar to the immediate effects of major hurricanes on the tree structure of forest stands in Caguana, Carite, and El Yunque, species richness and the identity of the dominant species remained the same on our study sites in the short-term with the exception of small trees in Cibuco II, where species richness was doubled, and the dominant species was replaced after Hurricane María (Tables 2–4; Lugo 2008; Brokaw et al. 2012). Cibuco II, which is located on an exposed alluvial floodplain valley located near the trajectory of the eye of Hurricane María, stood out as the only site were the changes in the density, basal area, and species richness of small trees were all positive in direction, albeit considerable reductions in density and species richness of large trees (Figure 1; Tables 1–3). Before and after samples, however, were furthest spread apart in Cibuco II, which added uncertainty as to whether species turnover was directly related to the hurricane (Table 1). We elaborate further below on the implications of this and other caveats of sampling. Nevertheless, the high variation around the mean values of changes in the density, basal area, and species richness of large and small trees indicates that the immediate effects of Hurricane María that we were able to sample were highly uneven on the four sites (Tables 2 and 3). This high variation in changes observed due to the immediate effects of Hurricane María may amount to divergent trajectories of ecological succession, including contrasting rates of recruitment, biomass accumulation, species turnover, and dominant species identities, on these lowland novel forest stands in the long-term. Our results also indicate that the distance of forest stands to the trajectory of Hurricane María may have a significant effect on the direction and magnitude of short-term changes in the density and basal area of trees, and possibly on long-term changes in tree species composition as well.

Río Hondo was the site located the furthest from the trajectory of Hurricane María, nearly as far from the hurricane's landfall as Guajataca Left, and its location on a gentle slope facing away from the hurricane eye's trajectory as it crossed the island possibly protected the site from direct winds of the highest velocity and, therefore, energy (Figure 1; Table 1; Lugo 2008; Pasch et al. 2018). Hurricane Irma's trajectory was located further north than Hurricane María's, and therefore Río Hondo, the site located furthest south, was also possibly less affected by the first hurricane relative to the other sites. Perhaps, in consequence, Río Hondo also stood out as the only site where the changes in the density, basal area, and species richness of large trees were all positive in direction (i.e., increased; Table 3). Río Hondo was also the only site where an increase in the density of large trees was observed and, along with Cibuco II, was one of the sites where most of the changes in the density, basal area, and species richness of large and small tree size-classes were positive in direction.

Overall, the positive changes (i.e., increments) observed in the density, basal area, and species richness of large and small trees on Cibuco II and Río Hondo after Hurricane María were offset by changes of similar magnitude, but of opposite direction (i.e., reductions), on Guajataca Left and Pugnado (Tables 2 and 3). Consequently, our statistical tests (i.e., paired-sample T-tests) found no significant changes in the density, basal area, and species richness of large and small trees on these four novel forest sites. Pugando was the site closest to the trajectory of Hurricane María, nearly as close as Cibuco II to the hurricane's landfall, and therefore possibly the site subject to the strongest direct winds of highest velocity and energy (Figure 1; Pasch et al. 2018). This was manifested in notable reductions in the density, basal area, and species richness of both large and small trees in Pugnado (Table 3). Although Pugnado is located within a karst depression protected by surrounding haystack hills (i.e., mogotes), the immediate effects of the hurricane on the tree structure were extensive and included a significant amount of felled, snapped, and uprooted large trees, which in turn caused direct structural changes to small trees.

In the long-term aftermath of Hurricane Georges, which was of lower intensity (category-3), Lugo et al. (2005b) found lower reductions in tree density, basal area, and species richness on novel forest stands located on low protected valleys relative to those located on the exposed hill and mountain slopes in urban Río Piedras (Table 3). This stands in contrast with our findings, in which the site located in a protected valley (i.e., karst depression), Pugnado, was subject to the highest reductions in tree density and basal area (Tables 1 and 3), and suggests that the intensity of Hurricane María was such that it offset any protection provided by landform and topography. In Guajataca Left, the site second closest to Hurricane María's trajectory and located on a coastal karst hill slope facing toward the trajectory of the hurricane's eye, all changes were also negative in direction except for an increase in the density of trees, and no change in species richness, in the small tree size-class (Figure 1; Table 3). It is possible that the traits of the dominant species in the large tree size-class in Guajataca Left, *T. catappa*, conferred some wind resistance to the forest canopy and made it less subject to crown branch breakage and fall to the forest floor. This may have buffered the forest understory from direct winds in Guajataca Left, and resulted in smaller structural changes to the small tree size-class on this site.

Species Composition and Dominance

In spite of a possible tradeoff with flexibility, the higher wood density of *T. catappa* compared to the other two dominant species of large trees on our study sites, *A. procera* and *S. campanulata* (Francis and Lowe 2000), may have contributed to lower crown reductions by branch breakage and snapping in Guajataca Left. In fact, *T. catappa* is a pan-tropical coastal species native to Indo-Pacific islands, which are subjected to intense, large, and infrequent disturbances that include typhoons and tsunamis (Francis and Lowe 2000; Lugo 2008). A lower amount of fallen branches could have protected the cohorts of small and juvenile (≤ 2.5 cm DBH) trees already established in the forest understory in Guajataca Left. Previous observations indicated that the juvenile tree species composition in Guajataca Left was dominated by *Calophyllum calaba* before Hurricane María (unpublished data), and the increase in the IV of this species as dominant in the small tree size-class suggests that an advanced cohort of suppressed juvenile trees was released by the immediate effects of the hurricane (Table 2). Canopy opening from loss of foliage followed by high sunlight and nutrient availability from litter inputs to the forest floor may have favored the growth of *C. calaba* in Guajataca Left after the hurricane.

Although the dominant small-tree species in Guajataca Left remained the same (*C. calaba*), the increase in its dominance after the hurricane is consistent with empirical models (i.e., Vandermeer et al. 1996; Shimizu 2005): the replacement of small trees, which may be disproportionately subject to mortality induced by tree trunk and branch falls, occurred with smaller, juvenile trees that were established in the understory. The increase in the density of small trees observed in Guajataca Left is consistent with predictions of these models if it resulted from recruitment of juveniles into the small-tree size-class (Table 3). Likewise, the replacement of the dominant tree species was observed only in the small tree size-class on any site, but only in Cibuco II. Overall, this is also consistent with predictions of these models given the high abundance of the new dominant small-tree species (*G. guidonia*) in Cibuco II as a juvenile tree in the forest understory before the hurricane (Table 2; Abelleira et al. 2010). In contrast, we did not observe any substantial changes in the identity and IV of the dominant species of small trees on Pugnado and Río Hondo, and of dominant species of large trees on the four sites (Table 2). Also, we did not find any differences in the changes in the tree density and basal area between large- and small-tree size-classes observed because of the hurricane (post -hoc Kruskal-Wallis tests), which suggests that any concomitant, long-term changes in the relative dominance of species due to changes in tree structure will proceed similarly on both tree size-classes.

The short-term effects of hurricanes on the composition and relative dominance of species of trees can be less predictable than changes in forest structure because species vary in ecological strategy, life-history, rates of resource-use and uptake (e.g., light-demanding pioneer species versus shade-tolerant late-successional species), and in adaptations to hurricanes (Lugo and Zimmerman 2002; Lugo 2008). For example, the roots of the late-successional and shade-tolerant canopy tree species *Dacryodes excelsa* graft between individuals in near monodominant stands in ridges in El Yunque, conferring superior stability when subjected to hurricane winds (Basnet et al. 1993). This adaptation can allow the standing and surviving trees of *D. excelsa* to maintain dominance at any given site in the aftermath of a major hurricane event. A shift towards a higher dominance of pioneer, light-demanding species, such as *Cecropia scheberiana*, is not necessarily observed in the short-term aftermath of hurricanes in El Yunque, which is characterized by a massive loss of foliage, downed trees and branches, and extensive canopy gaps that can significantly increase light and nutrient resources (Brokaw and Walker 1991; Scatena et al. 1993; Lugo 2008; Brokaw et al. 2012). Instead, the surviving trees resprout following crown-loss and uprooting, and the relative dominance of species at any one site is usually maintained, with factors such as aspect and topography influencing the magnitude of changes on the existing structure of the forest (i.e., resprouting and persistence-niche; Bond and Midgley 2001). We, therefore, lack previous well-founded reasons to expect any changes in the relative dominance (i.e., IV) and the identity of the dominant species in the large-tree size-class, which is mostly composed of upper-canopy trees that are subjected to the most direct and strongest hurricane winds (Lugo 2008; Brokaw et al. 2012). If anything, our general expectation was a decrease in the dominance of introduced, light-demanding and fast-growing pioneer species, such as *A. procera* and *S. campanulata*, due to their frail and low-density wood (Francis 2000; Francis and Lowe 2000). Contrary to this general expectation, the IV of the dominant species in the large-tree size-class remained the same, and ranked-species IV curves for large- and small-tree size-classes were very similar in length, shape, and steepness before and after the hurricane on each site (Figures 2 and 3). This similarity in the shapes of ranked-species IV curves indicates only subtle short-term changes in tree species-dominance and diversity (Hubbell 2001).

In the short-term, our findings are comparable to those reported by Lugo et al. (2005a) on the immediate effects of Hurricane Georges on the relative dominance of tree species in a novel forest stand in Caguana (Table 4). In Caguana, the native and shade-tolerant treelet species *Miconia prasina* (Little and Wadsworth 1964) was and remained the dominant species in the large- and small-tree size-classes before and after the hurricane; its relative dominance (i.e., IV) also remained largely unchanged in the short-term (Table 4). However, the replacement of *M. prasina* by a native fast-growing and light-demanding pioneer species of tree, *Didimopanax morototoni*, was observed in the large-tree size-class seven years after Hurricane Georges in Caguana, along with considerable changes in the relative dominance of species. On the other hand, the shade-tolerant species *Hymenaea courbaril* and the light-demanding species *Tabebuia heterophylla* (Little and Wadsworth 1964; Francis and Lowe 2000), which are both native species, were the dominant species (along with *S. campanulata*) in the large-tree size-class of stands of novel forests in most landforms sampled by Lugo et al. (2005b) in Río Piedras. The relative dominance of these three species on any given stand remained largely the same when sampled one year and seven years after Hurricane Georges (Table 4). These observations and our findings indicate that there can be a lag-time of at least a decade for the replacement of large tree species that dominate the canopies of lowland novel-forests in Puerto Rico. These examples also show that the replacement of the dominant large-tree species can be accelerated by ecological strategy or life-history traits, such as short stature in the case of *M. prasina*, which may not be favored in the long-term. We observed no consistent pattern of change in the percentage of introduced species in the large- and small-tree size-classes after the hurricane, which suggests that specific life-history traits, rather than biogeographical origin, mediate the influence of hurricanes on the relative dominance of tree species.

Caveats of Sampling and Recommendations

Our study emerged as a necessity to assess the immediate and visible effects of Hurricane María on novel-forest sites where on-going studies were occurring and we, therefore, expand upon some considerations of the sampling design to provide context and ease comparisons with other studies. Since we only sampled trees that were alive, standing, and ≥ 2.5 cm in DBH, our preliminary assessment does not include changes in other attributes of trees and forest stands, for example, crown reduction and loss of main branches. Our assessment also does not quantify tree mortality and cannot be used to determine if the trees that were subject to the most remarkable structural-changes will survive in the long-term. Nonetheless, Lugo et al. (2005b) studied novel-forest stands on various landforms in Río Piedras seven years after Hurricane Georges (Table 4) and found that tree mortality amounted to an overall average of 3.8% per year for standing trees, including those standing trees with significant, visible effects.

Growth and recruitment of trees between sampling dates offset the changes caused by the hurricane, particularly in Cibuco II. In fact, the basal area of trees sampled on Cibuco II after Hurricane María represented an increase to exceptionally-high levels, although within the range found for novel forests dominated by *S. campanulata* on alluvial floodplains in northern Puerto Rico (Abelleira et al. 2010). It is likely that the dozen years that elapsed between 2005, when the site was initially sampled, and the hurricane event in 2017, resulted in an even higher basal area immediately before the hurricane (i.e., right before September 2017) than after the event (i.e., in 2018) in Cibuco II. On the other hand, our implementation of the PCQM, which included randomization of points on both sampling dates, may have added some level of uncertainty to our estimates of immediate effects from the hurricane on three of our study sites, including Cibuco II, because the actual trees sampled before and after the hurricane were not necessarily the same on the three sites where the PCQM was used. Future studies can reduce the magnitude of this uncertainty by resampling the same PQCM points that were initially placed on sampling dates before the hurricane (i.e., no randomization). This would require the development of algorithms to deal with the possibility and problem of sampling the same tree on contiguous PCQM points, which can happen when the points are not randomized and are to be placed on lineal transects that are initially restricted in length. Comparing estimates obtained from both approaches to the method (i.e., with and without randomization of points in post-hurricane sampling) may help clarify the best approach to the method when applied to the long-term sampling of sites that may be subjected to the effects of major hurricanes.

Finally, future studies combining a larger sample-size with continued long-term sampling, can help evaluate if changes in the tree structure and species composition of Puerto Rican forests, at a regional level, are indeed related to the distance from the trajectory of Hurricane María. Establishing whether this relationship holds across numerous sites can be useful to improve upon assessments of the effects of major hurricanes on the structure (e.g., biomass and carbon stocks) and species composition, including flora and fauna, of forests and other ecosystems in Puerto Rico and elsewhere in the Caribbean. Long-term sampling on novel-forest sites can improve our understanding of how novel-forest ecosystems respond to the effects of major hurricane disturbances, and how effects and responses compare with those of other secondary forests, primary forests, and other ecosystem types, such as herbaceous wetlands and prairies, in the Caribbean.

CONCLUSION

We interpret our results to be consistent with high, net growth-rates and recruitment into size-classes of larger trees, which are characteristic of young secondary-forests that have been subject to major hurricane disturbances (Lugo et al. 2005a,b; Pascarella et al. 2004; Flynn et al. 2010). Contrary to our expectations, we found no consistent and general reductions in the density, basal area, and species richness of large and small trees on these four novel-forest sites. Similar to the well-documented case of El Yunque, our findings suggest that little changes in the species richness, composition, and the relative dominance of species in novel-secondary-forests can be expected in the short-term due to the visible and immediate effects of major hurricanes in Puerto Rico. In fact, our results are consistent with studies that report an increase in the variability in tree density, basal area, and species composition, as well as in growth rates and other ecological processes, in short- to long-term aftermaths of hurricanes in novel forests in Puerto Rico (Table 4; Lugo et al. 2005, b). Finally, our results suggest that the distance of any given site from the trajectory of a major hurricane could be a factor to consider in future studies to understand better the effects of hurricanes on the direction and magnitude of changes in the structure and species composition of novel forests and other ecosystems in the Caribbean.

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