The short-term impacts of Hurricane Maria on the forest birds of Dominica

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Photo: Jack Baddams

Birds Caribbean

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Abstract Island ecosystems are particularly vulnerable to the predicted increases in the intensity and frequency of tropical storms resulting from climate change. In this study, we assess the short-term effects of Hurricane Maria (September 2017) on forest bird communities on the Caribbean island of Dominica. We compared community composition, functional composition, biometrics, and forest structure changes pre- and two years post-hurricane. We caught a total of 408 birds of 18 species across the three years using mist nets. Post-hurricane catch rates were lower than pre-hurricane, and we observed changes in abundance between years across all functional groups, with decreases in the relative abundance of all groups except for omnivores. Hummingbirds showed the greatest reduction in both abundance and richness. Non-metric multidimensional scaling and analysis of dissimilarity indicate a significant shift in community composition for 2018, with 2019 overlapping both 2017 and 2018. The observed changes in richness, abundance, and community composition show that Dominica's forest birds varied in response to Hurricane Maria, and that these changes are still observed two years following the storm. Severe storms like Hurricane Maria disproportionately impact some functional groups, while other species may be able to capitalize on the changes in habitat.

Keywords bird conservation, Caribbean, climate change, island, tropical storm

Resumen Los impactos a corto plazo del huracán Maria en las aves de boque de Dominica. • Los ecosistemas insulares son particularmente vulnerables a los aumentos previstos en la intensidad y frecuencia de tormentas tropicales como consecuencia del cambio climático. En este estudio, evaluamos los efectos a corto plazo del huracán María (septiembre de 2017) en las comunidades de aves de bosque de la isla caribeña de Dominica. Comparamos la composición de la comunidad, la composición funcional, la biometría y los cambios en la estructura del bosque antes y dos años después del huracán. Capturamos un total de 408 individuos de 18 especies de aves durante los tres años con redes de niebla. Las tasas de captura posteriores al huracán fueron más bajas que antes del huracán, y observamos cambios en la abundancia entre años en todos los grupos funcionales, con disminuciones en la abundancia relativa de todos los grupos, excepto los omnívoros. Los colibríes mostraron la mayor reducción, tanto en abundancia como en riqueza. El escalado multidimensional no métrico y el análisis de similitud indican un cambio significativo en la composición de la comunidad para 2018, y una superposición de 2019 con 2017 y 2018. Los cambios observados en la riqueza, abundancia y composición de la comunidad de aves de bosque de Dominica muestran una variedad de respuestas al huracán María, y que estos cambios aún se observan dos años después de la tormenta. Las tormentas severas, como María, impactan de manera desproporcionada en algunos grupos funcionales, mientras que otras especies pueden ser capaces de beneficiarse con los cambios sufridos en el hábitat.

Palabras clave cambio climático, Caribe, conservación de aves, isla, tormenta tropical

Résumé Les effets à court terme de l'ouragan Maria sur les oiseaux forestiers de la Dominique • Les écosystèmes insulaires sont particulièrement vulnérables aux augmentations prévues de l'intensité et de la fréquence des tempêtes tropicales résultant du changement climatique. Dans cette étude, les effets à court terme de l'ouragan Maria (septembre 2017) sur les communautés d'oiseaux forestiers de l'île caribéenne de la Dominique ont été analysés. La composition de la communauté, la composition fonctionnelle, la biométrie ainsi que la structure forestière avant l'ouragan et deux ans après ont été comparées. Au total, 408 oiseaux de 18 espèces ont été capturés à l'aide de filets japonais au cours de ces trois années. Les taux de capture après l'ouragan étaient inférieurs à ceux enregistrés avant l'ouragan, et des variations de l'abondance ont été observés entre les deux périodes pour tous les groupes fonctionnels, avec une baisse de leur abondance relative pour tous à l'exception des omnivores. Les colibris ont présenté la plus grande réduction en matière d'abondance et de richesse. L'échelle multidimensionnelle non métrique et l'analyse de similarité indiquent un changement important dans la composition de la commu-

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nauté pour 2018, 2019 chevauchant à la fois 2017 et 2018. Les changements observés de la richesse, de l'abondance et de la composition de la communauté d'oiseaux forestiers de la Dominique démontrent qu'ils ont eu lieu en réponse à l'ouragan Maria, et qu'ils perdurent deux ans après la tempête. Les fortes tempêtes telles que Maria ont un effet disproportionné sur certains groupes fonctionnels, tandis que certaines espèces peuvent réussir à bénéficier des changements de leurs habitats.

Mots clés Caraïbes, changement climatique, comportement en cas de tempête tropicale, île, préservation des oiseaux

Global climate change is predicted to increase the frequency, intensity, and breadth of disturbances to forest ecosystems, including fires to droughts, invasive species, and tropical storms (Dale *et al.* 2001). Tropical island ecosystems are particularly at risk to climate change-induced disturbance through the predicted increase in the intensity and frequency of tropical storms (Emanuel 2005, Walsh *et al.* 2016). Tropical storm intensity is projected to increase 2–11% by the end of the 21st century (Knutson *et al.* 2010), and the frequency of high-intensity, Category 4 and 5 storms is predicted to increase by as much as 25% (Sobel *et al.* 2016, Walsh *et al.* 2016). Meteorological data, beginning in the 1970s, show an increase in the frequency of Category 4 and 5 storms in the North Atlantic (Sobel *et al.* 2016). The Caribbean is a global hotspot for biodiversity and endemism and an already highly disturbed region (Myers *et al.* 2000, Anadón-Irizarry *et al.* 2012). An increase in the frequency of high-intensity storms is an extinction threat for many regionally endemic birds, e.g., the Imperial Parrot (*Amazona imperialis*) and Cozumel Thrasher (*Toxostoma guttatum*), and mammals such as the Dominican Myotis (*Myotis dominicensis*) and Cozumel Raccoon (*Procyon pygmaeus*), amongst other species (IUCN 2021).

Hurricanes impact bird populations in two distinct ways: direct impacts from the storm and indirect impacts following the storm (Wiley and Wunderle 1993). Mortalities from direct impacts of hurricanes are predominately due to exposure to high winds, flying and falling debris, flooding, and storm surges. Initial losses are generally minimal for terrestrial species; for these species, the most severe impacts typically occur after the hurricane has passed (Wiley and Wunderle 1993, Collazo *et al.* 2003, Wunderle 2017). Hurricanes cause considerable changes in vegetation, which alters forest structure, changes successional patterns (which increases habitat heterogeneity), alters ecosystem processes (Walker *et al.* 1991), and decreases resilience to future extreme weather events (Dale *et al.* 2001). These changes can have lasting indirect impacts, including increased predation risk, breeding and foraging habitat loss (Wiley and Wunderle 1993), food shortages (Dobbs *et al.* 2009), and invasive species colonization (Bhattarai and Cronin 2014, van den Burg *et al.* 2020). These indirect impacts can lead to significant changes in the community structure of birds, particularly in forest habitats as survivors need to travel further or move to refugia in search of food and breeding sites (Rittenhouse *et al.* 2010). These long-lasting and sometimes permanent changes in habitats can lead to delayed extinction, also known as extinction debt. This is a particular threat for species with low reproduction rates and slow population growth (Kuussaari *et al.* 2009), such as the Imperial Parrot, which has a generation length of over 12 years (BirdLife International 2019), or where reproductive success is reduced due to inbreeding from a small population (Beissinger

et al. 2008).

Hurricanes can have substantial negative short-term impacts on some species, with different functional groups displaying varied responses (Walker *et al.* 1991). Hurricanes Emily and Wilma, which hit in short succession (three months apart) during the 2005 hurricane season, led to widespread damage throughout the Caribbean and into Mexico. Cozumel Island, off the northeast coast of the Yucatan Peninsula, was directly hit by both storms. Due to the very short timeframe between the storms, there was little opportunity for recovery to occur, and Perdomo-Velázquez *et al.* (2017) found significant shifts in bird species assemblages: i.e., a greater dominance of insectivorous and generalist species that persisted until the end of observations, two years post-hurricane. Similar changes were observed in two different locations in Puerto Rico following Hurricanes Irma and Maria (Wunderle 2017, Lloyd *et al.* 2019). Post-hurricane surveys in northeastern Puerto Rico found significant increases in populations of insectivorous species—more than an 1800% and 500% increase for residents and migrants respectively—following both storms (Wunderle 2017). In forested areas across Puerto Rico, occupancy of frugivorous species decreased while occupancy of habitat generalists and some insectivores remained unchanged (Lloyd *et al.* 2019). However, what drives these changes may vary, with some being the result of detectability changes or shifts in home range due to changes in resource availability (Wunderle 2017), while others are the result of actual changes in populations.

On 18 September 2017, Hurricane Maria made landfall on the the Commonwealth of Dominica (henceforth 'Dominica') as a Category 5 storm (Saffir-Simpson Hurricane Wind Scale), the strongest ever recorded on the island. Unlike the previous most destructive storm, Hurricane David (also Category 5), Hurricane Maria encompassed the entire island, with the storm passing southeast to northwest across the middle of the island (Hu and Smith 2018). Initial reports suggested that 30% of trees were felled and the remainder stripped of foliage (Palmer *et al.* 2018). The government's Post-Disaster Needs Assessment estimated 15–25% of trees were felled and 80–90% defoliated, with significant impacts on terrestrial wildlife (Government of the Commonwealth of Dominica 2017). Remote sensing assessments immediately following the hurricane showed a significant drop in the mean Normalized Difference Vegetation Index (NDVI) of forests on Dominica, suggesting a loss of vegetation or an increase in the amount of unhealthy vegetation, with some recovery in the following months (Hu and Smith 2018). Two years post-Hurricane Maria, significant damage remained, and large tracts of forest, particularly in core protected areas such as the Northern Forest Reserve, showed minimal recovery (AF pers. obs.).

Little is known about the impacts Hurricane Maria had on Dominica's bird communities. The immediate impacts on Dom-

inica's national bird, the Imperial Parrot, were very apparent and, following precedents in recorded population declines after Hurricane David (Evans 1991), it is likely that their numbers have dropped significantly (Palmer *et al.* 2018). Anecdotal reports regarding some species exist, which suggest varying levels of impact. For example, the Red-necked Parrot (*Amazona arausiaca*) population was reported to have increased over pre-storm numbers (Crask 2019), although this may also be explained by increased visibility due to population displacement and decreased canopy cover (Wunderle 2017).

The objective of our study was to determine how Dominica's forest bird communities were affected by Hurricane Maria. Specifically, we aimed to detect any changes in bird community structure and composition by using mist-netting to measure changes in abundance and richness and structural vegetation surveys to help explain any observed changes. We also aimed to determine if the community was returning to its pre-hurricane state or continuing to shift, which could give insight into how vulnerable the islands' birds are to further disturbances. We conducted these surveys as part of an ongoing biodiversity monitoring program on Dominica to build a detailed picture of the species assemblages in different forest structures and to monitor long-term trends. Biodiversity monitoring began at the research site approximately four months before Hurricane Maria, providing us with a unique opportunity to compare baseline quantitative data with subsequent surveys to statistically determine the extent of its impacts on the bird community.

Methods

Study Area

Dominica is a 751 km^2 volcanic island nation in the eastern Caribbean that falls between the French islands of Guadeloupe to the north and Martinique to the south (Fig. 1) and is home to ~71,000 people (Central Statistical Office 2011). It has a humid tropical marine climate with more pronounced seasonal varia-
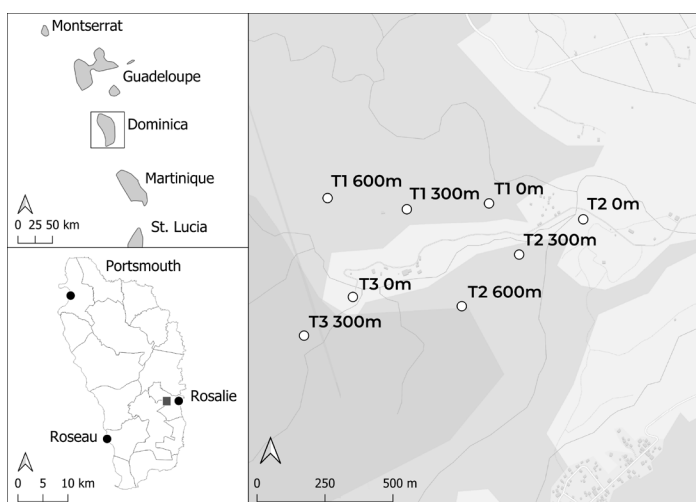
Fig. 1. Location map showing Dominica in the context of the Lesser Antilles and the location of the study site and survey points. The gray square on the Dominica inset represents the study area. © Map tiles by CartoDB, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

tion on the leeward (western) coast and more stable conditions on the windward (eastern) coast (Peel *et al.* 2007). Rainfall varies from 1,000 mm annually on the west coast to 2,000 mm annually on the east coast, with the interior of the island receiving 10,000 mm annually (Reading 1991). We sampled in the forests surrounding the Three Rivers Eco Lodge, Rosalie (15°22'25"N, 61°16'30"W), approximately three kilometres from the Atlantic coast. The site is characterized by lowland (average 120 m above sea level [asl]) mature and secondary rainforest bordering agricultural land composed of a mix of small gardens and plantations. Forests in Dominica are diverse, but dominant species in mature forest include the Genera *Dacryodes*, *Sloanea*, and *Amanoa* (Bell 1976). The average rainfall was 199.1 mm per month in 2016, 220.9 mm per month in 2017, and 154.9 mm per month in 2018 (Dominica Meteorological Service, pers. comm., June 2021). On 18 September 2017, the center of Hurricane Maria passed just south of our study site (Hu and Smith 2018).

Bird Sampling

We conducted mist net sampling over the course of three eight-week long fieldwork seasons between June and July in 2017, 2018, and 2019 (Appendix 1). We established three transects within our study area, two of which contained three mist-netting stations, and one which had two, with each station separated by a minimum of 250 m, following Barlow *et al.* (2007) and Martin *et al.* (2017), for a total of eight mist-netting stations (Fig. 1). The first stations on each transect were located on the forest edge bordering banana plantations and rivers, while subsequent points were located approximately 300 m and 600 m into the secondary forest bordering primary forest. We cut net lanes as near to the individual points as the surrounding terrain would allow and used a run of three 12 m long x 2.5 m high Ecotone mist nets. We used a mesh size of 36 mm, as this size is capable of capturing a wide range of species occurring in most ecosystems (Karr 1981). Mist-netting occurred between 0600 and 1100 to cover the first few hours after sunrise (~0630), the peak activity period for most Caribbean bird species (Wunderle 1994). We checked nets at a maximum interval of 30 minutes (Wunderle 1994, Martin *et al.* 2017) and sampled each station on two days each year with a minimum of 48 hours between samples. We did not sample on days with heavy rain or high winds and abandoned sampling if wind or rain caused net closures to occur for longer than 15 minutes (Wunderle 1994).

We banded all birds for which suitably sized bands were available (1.80 mm to 6.53 mm diameter) to account for recaptures, recording location, time caught, and band number. For most species, we recorded biometric measurements, including weight, age, molt status, and bill, tarsus, tail, and wing length using standard calipers, and wing and tail rules. We used the British Trust for Ornithology standards (Redfern and Clark 2001) in conjunction with Wolfe *et al.* (2010) for measuring and recording biometric data. We did not band hummingbirds or raptors and did not record biometrics for these birds to prevent the risk of duplication of data should the same, unmarked individual be caught again. We determined species and sex using Raffaele *et al.* (2003), James *et al.* (2005), and Arlott (2010) and identified functional group and habits of bird species using Arlott (2010), Billerman *et al.* (2020) and Pigot *et al.* (2020). We released birds

once all information was recorded.

Vegetation Surveys

We assessed the vegetation structure under 3 m in height surrounding each mist-netting station concurrent to the bird surveys on days when no mist-netting occurred to estimate density along understory flight paths. Survey methods, including the use of volunteer groups to rapidly generate high-quality data, followed those presented by Harrison *et al.* (2020). We established eight 20 x 20 m vegetation plots (400 m²) adjacent to bird sampling locations and surveyed them annually, with the exception of two sites (T2 0 m and T3 0 m) in 2017 (Fig. 1). We subdivided these vegetation plots into four 10 x 10 m subplots for measurement.

We determined understory density following methods described in Slater (2019) using a 300 cm touch-test pole divided into 50 cm sections. While holding the pole vertically at arm's length (~1 m) from the corners of each subplot (16 locations per plot), we recorded the number of contact points between live vegetation and the pole for each section, up to a maximum of 10 contact points, indicating vegetation density at each height interval above the forest floor.

Statistical Analyses

We calculated a Shannon diversity index and Pielou's evenness for each sampled site to assess the evenness and abundance of species present. We tested the variability between bird abundances and richness (per species and according to functional group) between the studied years using Kruskal-Wallis tests, with a Dunn's pairwise post-hoc test (Zar 1999).

To compare the dissimilarity of the bird communities pre- and post-Hurricane Maria, we used non-metric multidimensional scaling (nMDS) in combination with a non-parametric analysis of similarities (ANOSIM) (Clarke 1993) using the *metaMDS* and *anosim* functions of the R *vegan* package (Oksanen *et al.* 2019). The nMDS was based on a Bray–Curtis dissimilarity matrix of the bird community data between sites (Bray and Curtis 1957), for which the stress factor did not exceed 0.2 (0.162) (Dexter *et al.* 2018). For ANOSIM, *R* statistic values may vary between –1 and 1, where values closer to 1 indicate communities within years that are more similar to each other than to communities from other years. We excluded one site from the ANOSIM (T2 300 m in 2019) as no birds were caught. Following a global ANOSIM analysis, we conducted pairwise comparisons on subsets of the data (by year), with a Bonferroni correction applied to adjust for multiple comparisons. We identified indicator species for each year using the function *IndVal* in the R package *labdsv* (Roberts 2021). *IndVal* (Dufrene and Legendre 1997) gives a simple index for the determination of species importance for a given set of samples (i.e., bird communities across years). *IndVal* for each species is calculated by combining measurements of species specificity to each year with species fidelity within each year.

We carried out Wilcoxon signed-rank tests (Zar 1999) to test for statistical differences in weight across years for species caught at least three times for two or more consecutive years (Black-whiskered Vireo [*Vireo altiloquus*], Bananaquit [*Coereba flaveola*], Lesser Antillean Bullfinch [*Loxigilla noctis*], Black-faced Grassquit [*Melanospiza bicolor*], House Wren [*Troglodytes*

aedon] and Caribbean Elaenia [*Elaenia martinica*]). We tested for differences in the vegetation touch data by comparing the mean number of touches at each level between years using a pairwise *t*-test (Kassambara 2020).

Results

We completed 48 surveys across three years, capturing a total of 421 birds (408 individuals, 13 recaptures) of 18 species. Due to our standardized sampling method, capture effort remained the same each year. We recorded the greatest species diversity in 2017, before Hurricane Maria, when 16 species (171 birds) were caught. In 2018, we caught 15 species (169 birds), two of which were captured exclusively in that year (Scaly-breasted Thrasher [*Allenia fusca*] and Lesser Antillean Pewee [*Contopus latirostris*]). In 2019, we recorded the fewest individual birds (81), and the fewest species (10; Table 1). The first point on each transect (i.e., those nearest to the forest edge) had the highest overall avian abundance across all years (111 individuals in 2017, 81 in 2018, and 59 in 2019). However, there was some variation within the points and transects. Avian abundance at point T2 0 m in 2018 was lower (11 individuals) than both T2 300 m (17 individuals) and T2 600 m (19 individuals). In 2018, T1 600 m (the point deepest into the forest) had a greater avian abundance than all points except two of the forest edge points T1 0 m and T3 0 m.

Understory Structure

We found clear differences in the understory structure, particularly in the lower height strata (0–50 cm, 50–100 cm, and 100–150 cm), between both 2017 and 2018, and 2018 and 2019 (Pairwise t-test $p < 0.05$; Fig. 2). Thus, there was a significant increase in the lowest understory density in 2018. The understory in 2019 was more similar to 2017, showing a reduction in touches at the lower ranges between 2018–2019. We also observed an increase in understory density in the 250–300 cm band between 2018 and 2019, indicating further growth of the understory. Differences in understory density between 2017 and 2019 were marginal and not significant (Fig. 2).

Forest Bird Community

Community Composition.—Pairwise ANOSIM (Table 2) analyses identified highly significant differences between the bird communities of 2017 and 2018 (R = 0.44, $p < 0.01$), and a reduced (but still significant) difference between 2017 and 2019 (R = .42, $p < 0.05$). The bird communities of 2018 and 2019 were not significantly dissimilar. The nMDS analysis indicates distinct community clusters for 2017 and 2018, with 2019 having considerable overlap in species compositions across all years (Fig. 3). This was confirmed by the ANOSIM results (Table 2), which had a global R value of 0.318 ($p = 0.002$), suggesting the communities are clearly distinguishable between years.

Indicator species analysis identified Antillean Crested Hummingbird (*Orthorhyncus cristatus*) (d = 0.77, $p < 0.001$), Purple-throated Carib (*Eulampis jugularis*) (d = 0.56, $p = 0.022$), and Blue-headed Hummingbird (*Riccordia bicolor*) (d = 0.50, $p = 0.020$) as the species that were in relatively high abundance in 2017 but were recorded almost exclusively in that year compared to 2018 and 2019. No species were statistically significant indicators of 2018 or 2019 specifically, although Bananaquit was

Table 1. Summary counts of birds caught in mist-net surveys (*n* = 48) throughout 2017–2019 at eight sites in Dominica, West Indies. Numbers in parenthesis indicate relative abundance (percentage of community). All species are listed by the IUCN as Least Concern (IUCN 2021). Taxonomy follows HBW and BirdLife International (2019). Functional group determined using Arlott (2010), Billerman *et al.* (2020), and Pigot *et al.* (2020).

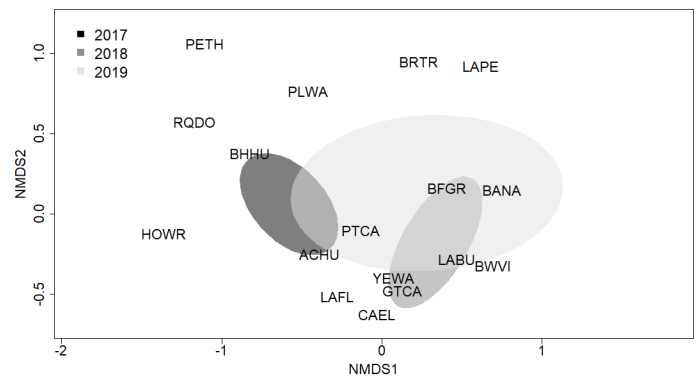| Scientific Name	Common Name	Functional Group	2017	2018	2019	Overall
Riccordia bicolor	Blue-headed Hummingbird	Nectarivorous	8 (4.7)	0 (0)	0 (0)	8
Eulampis holosericeus	Green-throated Carib	Nectarivorous	3 (1.8)	11 (6.5)	3 (3.7)	17
Eulampis jugularis	Purple-throated Carib	Nectarivorous	27 (15.8)	13 (7.7)	2 (2.5)	42
Orthorhyncus cristatus	Antillean Crested Hummingbird	Nectarivorous	22 (12.9)	2 (1.2)	1 (1.2)	25
Geotrygon montana	Ruddy Quail-Dove	Omnivorous	5 (2.9)	0 (0)	0 (0)	5
Vireo altiloquus	Black-whiskered Vireo	Omnivorous	6 (3.5)	8 (4.7)	9 (11.1)	23
Coereba flaveola	Bananaquit	Nectarivorous	28 (16.4)	80 (47.3)	46 (56.8)	154
Loxigilla noctis	Lesser Antillean Bullfinch	Omnivorous	19 (11.1)	29 (17.2)	9 (11.1)	57
Melanospiza bicolor	Black-faced Grassquit	Granivorous	16 (9.4)	8 (4.7)	3 (3.7)	27
Allenia fusca	Scaly-breasted Thrasher	Omnivorous	0 (0)	1 (0.6)	0 (0)	1
Cinclocerthia ruficauda	Brown Trembler	Omnivorous	1 (0.6)	1 (0.6)	2 (2.5)	4
Margarops fuscatus	Pearly-eyed Thrasher	Omnivorous	4 (2.3)	0 (0)	0 (0)	4
Setophaga plumbea	Plumbeous Warbler	Insectivorous	11 (6.4)	1 (0.6)	4 (4.9)	16
Setophaga petechia	Yellow Warbler	Insectivorous	2 (1.2)	1 (0.6)	0 (0)	3
Troglodytes aedon	House Wren	Insectivorous	11 (6.4)	3 (1.8)	2 (2.5)	16
Elaenia martinica	Caribbean Elaenia	Insectivorous	7 (4.1)	8 (4.7)	0 (0)	15
Myiarchus oberi	Lesser Antillean Flycatcher	Insectivorous	1 (0.6)	2 (1.2)	0 (0)	3
Contopus latirostris	Lesser Antillean Pewee	Insectivorous	0 (0)	1 (0.6)	0 (0)	1
		Totals:	171	169	81	421
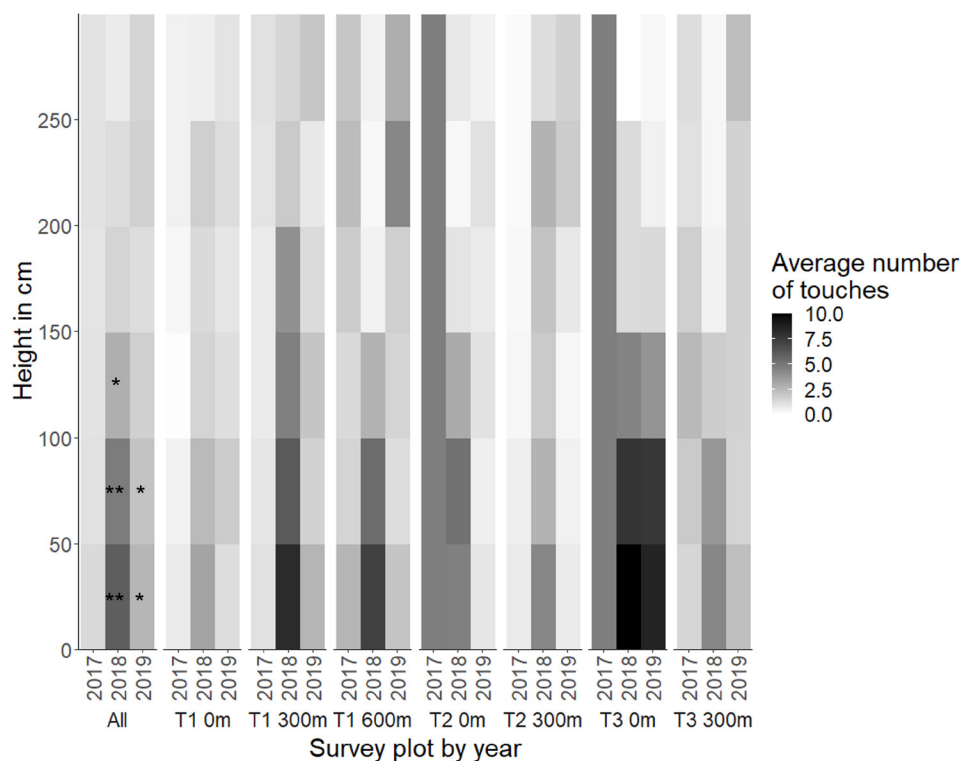
Fig. 2. Average number of touches for each height category by plot and year. Height is height above ground. T2 0 m and T3 0 m are both missing for 2017. All is the average for all sites. Asterisks represent a significant change over the previous year (Pairwise *t*-test). ** = *p* < 0.01; * = *p* < 0.05.

Table 2. Results of ANOSIM analyses testing dissimilarity in Dominican forest bird communities between survey years (2017–2019). R represents the degree of separation where values closer to one indicate a greater difference between the dissimilarity matrices based upon the communities present in each year compared. p. adjusted is Bonferroni corrected for multiple comparisons.

Comparison	*R*	*p*	*p* adjusted
Global	0.318	0.002	-
2017–2018	0.438	0.002	0.006
2018–2019	0.136	0.086	0.258
2017–2019	0.421	0.004	0.012

Fig. 3. Non-metric multidimensional scaling (nMDS) ordination plot indicating the compositional dissimilarity of bird communities at eight sites subject to surveys in 2017, 2018, and 2019. Species locations indicate their observed fidelity to any given year. Ninety-five percent confidence ellipses are displayed for each year based on the standard errors of the average axis scores for each sampled community. ACHU = *O. critatus*, BANA = *C. flaveola*, BFGR = *M. bicolor*, BHHU = *R. bicolor*, BRTR = *C. ruficauda*, BWVI = *V. altiloquus*, CAEL = *E. martinica*, GTCA = *E. holosericeus*, HOWR = *T. aedon*, LABU = *L. noctis*, LAFL = *M. oberi*, LAPE = *C. latirostris*, PETH = *M. fuscatus*, PLWA = *S. plumbea*, PTCA = *E. jugularis*, RQDO = *G. montana*, SBTH = *A. fusca*, YEWA = *S. petechia*.

marginally so for 2018 (*d* = 0.50, *p* = 0.09). Several species including Blue-headed Hummingbird, Ruddy Quail-Dove (*Geotrygon montana*) and Pearly-eyed Thrasher (*Margarops fuscatus*) were caught only in 2017. Others such as Green-throated Carib (*Eulampis holosericeus*), Lesser Antillean Bullfinch, and Caribbean Elaenia saw increases in relative abundance in 2018 but decreased in 2019 (Table 1). Average richness decreased each year post-hurricane, as did the average Shannon diversity index, which reduced significantly between years (Wilcoxon rank sum test 2017–2018, *W* = 55, *p* = 0.01; 2018–2019, *W* = 54, *p* = 0.02) and Pielou's evenness, which reduced significantly between 2017 and 2018 (Wilcoxon rank sum test 2017–2018, *W* = 55, *p* = 0.01; Table 3).

Functional Composition.—We observed changes in abundance between years and across all functional groups, with decreases in relative and absolute abundances of all groups except for omnivores (2017: 20.5% [31], 2018: 23.1% [39], 2019: 24.7% [20]) and nectarivores (2017: 51.5% [88], 2018: 62.7% [106], 2019: 64.2% [52]; Table 4). We also observed reductions in other groups between 2017 and 2018, which stabilized in 2019. Bananaquits, functional nectarivores, made up the greatest proportion of species caught across all years, comprising 16.4% (*n* = 28) of the birds caught in 2017, 47.3% (*n* = 80) in 2018, and 56.8% (*n* = 46) in

2019. Diet in birds can be complicated, and Bananaquits, for example, may readily feed on invertebrates (Poulin and Mcneil 1994, Waide 1996); therefore, we also analyzed the results with Bananaquits removed. When Bananaquits were excluded, increases in the proportion of omnivorous species was seen to a greater extent (21.68% in 2017 to 57.14% in 2019) and the decrease in hummingbirds was substantial (41.96% in 2017 down to 17.14% in 2019), with significant changes in relative abundance (Kruskal-Wallis post-hoc Dunn, *p* = 0.012; Table 4).

Biometric Analyses.—We found no significant changes in biometrics except for in the Bananaquit, which increased in

Table 3. Species richness, Shannon Diversity Index (SDI), and Pielou's Evenness values for bird communities at mist-netting stations in forest habitats on Dominica by year. Asterisks (*) represents significant change over previous year (Wilcoxon rank sum test *p* < 0.05).

Site	2017			2018			2019		
	Richness	SDI	Evenness	Richness	SDI	Evenness	Richness	SDI	Evenness
T1 0m	12	2.16	0.87	10	1.75	0.76	8	1.18	0.57
T1 300m	7	1.78	0.91	2	0.38	0.54	2	0.56	0.81
T1 600m	6	1.61	0.90	5	0.77	0.48	1	0	0.00
T2 0m	9	1.92	0.88	4	1.24	0.89	3	0.86	0.78
T2 300m	4	1.39	1.00	6	1.65	0.92	0	0	0.00
T2 600m	7	1.79	0.92	6	1.34	0.75	2	0.56	0.81
T3 0m	10	2.07	0.90	8	1.65	0.79	4	1.14	0.83
T3 300m	5	1.48	0.92	5	1.38	0.86	3	0.96	0.88
Mean	7.5	1.77±0.27	0.91	5.75	1.27±0.48*	0.75*	2.875	0.66±0.47*	0.58

Table 4. Relative abundance (in percent) by year for all functional groups captured during mist-netting surveys in forest habitats in Dominica between 2017 and 2019. Columns notated "a" include records of Bananaquit (*Coereba flaveola*) and columns notated "b" do not include Bananaquit. Asterisks (*) denotes the presence of significant differences between years (Kruskal-Wallis post hoc Dunn, *p* < 0.05).

Year	Omnivorous		Nectarivorous		Insectivorous		Granivorous	
	a	b	a	b	a	b	a	b
2017	20.47	24.48	51.60	42.00*	18.70	22.40	9.30	11.20
2018	23.10	43.80	62.70	29.20	9.50	18.00	4.70	9.00
2019	24.70	57.10	64.20	17.10*	7.40	17.10	3.70	8.60

weight in 2019 based on 42 individuals (Appendix 2). In 2017, the average weight was 10.19 g (*n* = 23) in 2017, 10.16 g (*n* = 70) in 2018, and 10.96 g (*n* = 42) in 2019. The difference in average weight between 2018 and 2019 was significant (Wilcoxon ranked sum, *p* = 0.029).

Discussion

Our study represents the first quantitative assessment of the impacts of Hurricane Maria on the forest bird communities of Dominica. We observed mixed responses by all functional groups, with some species faring better than others. In 2019, we recorded significantly fewer birds than in previous years, likely due to major changes in vegetation structure. The impacts of Hurricane Maria were most obvious in hummingbirds, which were identified as indicator species for the 2017 pre-hurricane community. Indeed, direct mortality of hummingbirds was observed immediately and for several days after the storm had passed (M. Lees and J. Winston, pers. comm., June 2018), with dead and dying hummingbirds seen on the ground. Mist-netting undertaken by Temeles and Bishop (2019) in the spring of 2018 at several sites across Dominica suggested that as much as 75% of the Purple-throated Carib population may have been lost in the weeks and months following Hurricane Maria. A decrease in the abundance of hummingbirds following major tropical storms is mirrored in the findings of other studies (Lynch 1991, Waide 1991a, Wauer and Wunderle 1992, Wiley and Wunderle 1993, Perdomo-Velázquez *et al.* 2017, Wunderle 2017, Lloyd *et al.* 2019). Fruit- and nectar-feeding species tend to be more vulnerable to hurricanes since their primary food sources are fragile, vulnerable to wind damage, and can take time to regenerate (Waide 1991a, Rathcke 2000). As such, annual flowering and fruiting cycles may take several years to return to normality, rendering food resources more heterogeneous and patchily distributed (Wunderle 1999). These cycles may be particularly disrupted following highly severe storms such as Hurricane Maria.

We did not record frugivorous species during any of the surveys. The larger fruit-eating species found on Dominica are generally considered canopy dwellers (Billerman *et al.* 2020), therefore making them difficult to capture in mist nets. Indeed, this is a limitation of mist-netting methods, as these groups are generally under-represented (Martin *et al.* 2017). With 80–90% defoliation (Government of the Commonwealth of Dominica 2017) and slow canopy recovery, any remaining frugivores may have moved to refugia or into plantations and farms where more food would have been available (Wunderle *et al.* 1992). Radio tracking of captive-reared Hispaniola Parrots (*Amazona ventralis*) in the Dominican Republic following hurricanes demonstrated that surviving birds increased their home ranges (Collazo *et al.* 2003, White *et al.* 2005), likely in search of resources made sparser by the storms. Conversations with several Dominican farmers in June and July of 2019 suggested that Red-necked Parrots were more prevalent on their farms and in and around the villages than before the storm (AF pers. obs.), leading to the assumption that frugivorous species are travelling further in search of resources. An increased home range may further reduce the number of frugivores available to be caught.

Notably, we observed an increase in Bananaquit relative abundance each year post-hurricane, although with a decrease in absolute abundance in 2019. Bananaquits, a functional nectarivore, were expected to decrease in number, similar to the hummingbird populations. Indeed, this is generally reflected in other regional studies (Askins and Ewert 1991, Waide 1991b, Wauer and Wunderle 1992, Rathcke 2000, Wunderle 2017, Lloyd *et al.* 2019). When we removed Bananaquits from our analysis, there was an overall decrease in the abundance of nectarivores each year. However, when retained, there was an increase from 2017 to 2019. While these results are not reflected by the majority of studies, others have observed similar increases in Bananaquit populations following hurricanes (Tossas 2006, Perdomo-Velázquez *et al.* 2017). Bananaquits reproduce quickly, as they have an average brood size of three and can breed multiple times per year (Billerman *et al.* 2020). While often considered a canopy species, they also have a preference for more open, disturbed, and scrubby habitats like gardens, plantations, and light woodland and are therefore less prevalent in dense forests (Billerman *et al.* 2020). Our study site borders an old banana plantation with a generally disturbed patchwork of small gardens, scrub, and larger areas of active plantation. The observed increase in relative and absolute abundance in 2018 may therefore represent an exploitation of the newly opened habitat, as indicated by the increase in understory growth. Further, a significant increase in Bananaquit weight between 2018 and 2019 (Appendix 2) could suggest that plentiful resources were available, which may in turn mean that the species gained a competitive advantage over other nectarivores whose populations decreased. Feeding and foraging behavior analyses of Bananaquits elsewhere suggest they may be more omnivorous than typically thought (Poulin and Mcneil 1994, Waide 1996, Mi-

chel *et al.* 2013). As such, their ability to exploit other resources may make them less susceptible to disturbance by hurricanes. Alternatively, both the increased abundance and weight could be explained by an influx of birds from higher altitudes, which have been shown to have a higher mean body mass than low-land birds (Wunderle 1995). Hu and Smith (2018) found the most substantial post-Hurricane Maria changes in NDVI values at higher altitudes, which suggests that the greatest damage to live vegetation occurred there. Surviving Bananaquits may have moved down-slope in search of food. Still, 2019 showed a major drop in absolute abundance compared to 2018. Bananaquits can be sensitive to drought conditions (Faaborg 1982); the year leading up to the 2019 field season was the driest of the three years, suggesting that climate may have influenced these species patterns. However, changes in the understory are a more likely cause, specifically an influx of tall grasses in 2019 (AF pers. obs.), which may have limited the number of birds in the understory and thus reduced the number captured by the nets.

Our results indicate that the only functional groups that fared well were the omnivores, which increased in abundance from 2017 to 2018 and remained stable between 2018 and 2019, and, when Bananaquits were included, nectarivores, which increased in abundance year on year. As with the decreases in hummingbirds, the increase and subsequent stability of omnivores is reflected in the literature and matches the population trends after Hurricanes Maria and Irma in Puerto Rico (Lloyd *et al.* 2019) and on Cozumel Island (Perdomo-Velázquez *et al.* 2017). This pattern is not unexpected, as omnivores can exploit a greater range of resources and would likely not be as impacted by changes in the distribution of resources or timing in resource availability compared to other functional groups. However, the apparent increase in omnivore abundance could be due to the displacement of birds normally feeding in the canopy. Wunderle (1995) observed an increase in omnivores from point counts and captures immediately following Hurricane Hugo that then decreased in subsequent months. Further, some omnivorous species may be sensitive to the impacts of hurricanes. We only recorded the Pearly-eyed Thrasher and the Ruddy Quail-Dove in 2017 and did not hear Ruddy Quail-Doves in the forests around the study site post-hurricane (AF pers. obs.). Wunderle (1995) demonstrated reduced catch rates of Ruddy Quail-Doves in Puerto Rico following Hurricane Hugo, and those that were caught had reduced body mass and fat scores. A population of Bridled Quail-Doves (*Geotrygon mystacea*), a relative of the Ruddy Quail-Dove, decreased significantly and remained low following Hurricanes Irma and Maria on St. Eustatius (Rivera-Milán *et al.* 2021). Ruddy Quail-Doves tend to feed on the ground, eating fallen fruits, seeds, and occasional insects (Kuecker *et al.* 2020). With a denser understory and debris on the forest floor, finding food may be more difficult. The combination of pre-existing pressures and functional traits may make this genus particularly sensitive to disturbance and changes in habitat caused by hurricanes.

While our results show a decline in the insectivore population, this is not a universally reported pattern. Several studies demonstrate a significant increase in insectivorous birds following hurricane events (Perdomo-Velázquez *et al.* 2017, Wunderle 2017, Lloyd *et al.* 2019). Wunderle (2017) suggested this could be due to increased detectability, with the lack of canopy dis-

placing some species and the reduction in foliage making them easier to see. Displacement due to the lack of canopy could have made more individuals prone to mist net capture, but since we observed a decrease in both richness and abundance, this may not be the case here. Still, birds may have been displaced outside our survey area due to increased understory density. Specifically, an apparent increase in understory grasses (AF pers. obs.) may have influenced the 2019 catch rates of insectivorous species. Where hurricanes cause major defoliation of the canopy, increased growth of the understory usually occurs; this influx of fresh leaves can have a positive impact on herbivorous insect populations (Walker *et al.* 1991, Angulo-Sandoval *et al.* 2004, Novais *et al.* 2018). An increase in deadwood resources following hurricanes may also have a positive effect on insect abundance (Novais *et al.* 2018). With increased resources, insectivorous bird populations would be expected to increase, as demonstrated in some insectivorous species (Angulo-Sandoval *et al.* 2004, Novais *et al.* 2018). However, changes to forest structure following disturbance events can destroy microhabitats favored by insectivores, impacting their ability to hunt, which has been shown to negatively impact their populations (Sodhi *et al.* 2004, Gray *et al.* 2007). We observed significant changes in understory density and structure in 2018 and 2019, which may have influenced insectivore behavior and caused reduced microhabitat availability.

Conclusion

Our work represents the first quantitative study regarding the impacts of Hurricane Maria on Dominica's forest bird community and adds to the growing body of knowledge on the impacts of hurricanes on island bird populations. We observed changes in richness, abundance, and community composition that show Dominica's forest birds vary in their response to severe hurricane events such as Hurricane Maria, and that these changes are still present two years following the storm. Our results further show that severe storms disproportionately impact some functional groups and that some species may be able to capitalize on the changes in habitat. There are some limitations to this study and opportunities for further research. First, it should be acknowledged that mist-netting as a method has biases that could be further influenced by changing conditions (Remsen Jr. and Good 1996). However, such biases are unlikely to have exerted a substantial influence on our findings. When standardized into a constant-effort format, as in this study, mist-netting is an effective tool for inferring abundance (Silkey *et al.* 1999, Wang and Finch 2002, Dunn and Ralph 2004), and our findings are in line with other regional studies utilizing different survey methods. Second, this study is limited to a small region of low-lying disturbed secondary and primary forest. Hurricanes cause significant changes to forest structure (Walker *et al.* 1991) and therefore the availability and distribution of resources required by birds. While possibly representative of similar regions throughout this island and others, our findings do not reflect changes in montane forests where rare species occur, such as the Forest Thrush (*Turdus lherminieri*), and Critically Endangered species, such as the Imperial Parrot. Additionally, our relatively modest sampling effort makes it difficult to determine robust demographic trends in less-common species within our study area. Third, continued

observation is necessary to gain an understanding of how bird communities change as the forest continues to recover and to maintain a baseline should another major storm event occur. Understanding how long it takes a bird community to recover from a severe storm event will give insight into how damaging more frequent major hurricane events could be, as would more detailed evaluation of impacts and recovery periods in different forest types supporting different bird community compositions (e.g., edge and secondary forests vs primary forest habitats). Finally, further work should examine the impacts of the hurricane on the rare, understudied, and globally threatened species of the island, so that targeted conservation efforts can be made.

Cover Page Illustration
Bananaquit (*Coereba flaveola*), photographed by Jack Baddams on 6 July 2016 at D-Smart Farm, Dominica.

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Appendix 1. Survey dates by site for all surveys conducted between 2017 and 2019. Missing dates are surveys where no birds were caught.

2017		2018		2019	
Date	Site	Date	Site	Date	Site
2017-06-29	T1 0 m	2018-06-11	T1 0 m	2019-06-17	T1 0 m
2017-07-10	T1 0 m	2018-06-14	T1 0 m	2019-06-20	T1 0 m
2017-06-15	T1 300 m	2018-06-19	T1 300 m	2019-06-25	T1 300 m
2017-07-11	T1 300 m	2018-06-25	T1 300 m	2019-07-02	T1 300 m
2017-07-07	T1 600 m	2018-06-28	T1 600 m	2019-07-08	T1 600 m
2017-07-17	T1 600 m	2018-07-10	T1 600 m		T1 600 m
2017-06-28	T2 0 m	2018-06-15	T2 0 m	2019-06-18	T2 0 m
2017-07-06	T2 0 m	2018-06-21	T2 0 m	2019-06-21	T2 0 m
	T2 300 m	2018-07-13	T2 300 m		T2 300 m
2017-07-04	T2 300 m	2018-07-17	T2 300 m		T2 300 m
2017-07-20	T2 600 m	2018-07-18	T2 600 m	2019-07-16	T2 600 m
2017-07-22	T2 600 m	2018-07-22	T2 600 m	2019-07-18	T2 600 m
2017-06-27	T3 0 m	2018-06-12	T3 0 m	2019-06-22	T3 0 m
2017-07-08	T3 0 m	2018-06-26	T3 0 m	2019-06-24	T3 0 m
2017-06-30	T3 300 m	2018-06-30	T3 300 m	2019-06-27	T3 300 m
2017-07-01	T3 300 m	2018-07-12	T3 300 m	2019-06-29	T3 300 m

Appendix 2. Average weight (g) of species caught at least three times for two or more consecutive years. *p*-values derived from Wilcoxon signed-rank test. a) *Vireo altiloquus*, b) *Coereba flaveola*, c) *Loxigilla noctis*, d) *Melanospiza bicolor*, e) *Elaenia martinica*, f) *Troglodytes aedon*.