



# Impacts of a drought and hurricane on tropical bird and frog distributions

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**Abstract.** During the last few decades, much attention has focused on how global change is affecting the environment and species distributions. Land-use change is still the major cause of species declines worldwide, but changes in species distributions have been documented even in pristine and protected areas. Here, we document the distribution dynamics of 26 species of frogs and birds within a Caribbean protected area between 2015 and 2019. Specifically, we document species occupancy and detectability in 59 sites along three elevational transects within the El Yunque National Forest in Puerto Rico. Species were sampled using acoustic recorders, species identification algorithms, and post-classification validation. The study period included a severe drought (2015–2016) and a category 4 hurricane (2017). The distribution of most frog species did not change significantly during the study period. In contrast, the distributions of the bird species contracted between the 2015 and 2016 pre-hurricane surveys. This contraction coincides with a severe drought that peaked after the 2015 survey. The response of bird species after H. Maria was heterogeneous. Our results suggest that for many species, particularly birds, the 2015–2016 drought in Puerto Rico had a greater negative effect than H. Maria. The difference in the response of the bird and frog communities is likely related to their abundance at the site level, their ability to disperse, and temporal patterns of reproduction. If a site is occupied by a frog species, it could easily include 100s of individuals, and even if condition worsens, over a relatively short period the species will continue to occupy the site. In contrast, a site may only be occupied by one or a few individuals of birds. Birds have also higher dispersal abilities than frogs. Furthermore, Puerto Rican frogs reproduce year-round, whereas birds concentrate their reproduction during a few months in the wet season. Future climate scenarios predict a decrease in total precipitation and an increase in droughts for the region, which emphasizes the need to consider the diversity of changes that will be associated with future climate change.

**Key words:** ARBIMON; climate change; conservation ecology; detectability; elevation; occupancy; passive acoustic monitoring; population decline; tropics.

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## INTRODUCTION

Over the last 40 yr, one of the most important factors affecting species distributions has been deforestation and fragmentation (Sala et al. 2000, Laurance 2015). This has been particularly important in the tropics where some high

diversity habitats have lost more than 90% of forest cover (e.g., Atlantic forest; Saatchi et al. 2001). While few extinctions have been documented following this extreme level of deforestation, the population size and distributions of many species have been severely reduced (Paviolo et al. 2016). A major tool to combat deforestation and

conserve species has been the implementation of protected areas (PA; le Saout et al. 2013). Between 1980 and 2015, the global area of terrestrial PA has increased from <5% to ~15% (Butchart et al. 2015) and these efforts have helped to protect populations of thousands of species across the globe (Barnes et al. 2016).

Unfortunately, the effects of climate change are pervasive and transcend the borders of PA (Blake and Loiselle 2015). Some of the most notable changes have been shifts in species distributions (Chen et al. 2011). For example, the distributions of species as diverse as mangroves (Dangremond et al. 2020), cod (Spies et al. 2020), and spruce bark beetle (Økland et al. 2019) have increased by extending their distributions to higher latitudes. In other cases, species distributions are extending to higher elevations. For example, in the Andes, woody vegetation is colonizing high elevational grasslands and there are areas where glaciers are receding (Aide et al. 2019). For other species, the extent of their distributions has been reduced, and in some cases, it appears that species have gone extinct (Waller et al. 2017). Although it is often difficult to identify a single cause, increasing temperature and increasing intensity and extent of natural disturbances (e.g., hurricanes and droughts) are often important factors.

In the Caribbean, changing patterns of tropical cyclone (TC) activity could be a major factor affecting species' distributions. While increasing sea surface temperature (SST) might be expected to generate more hurricanes in the Atlantic, most modeling efforts agree that during the next 20–50 yr the frequency of TC will be the same or decrease (Choi et al. 2017). One explanation for the decrease in the frequency of TC is that increasing SST in the Pacific is likely to increase the frequency of El Niño events, which may reduce TC in the Atlantic (Krishnamurthy et al. 2016, Hosseini et al. 2018). In contrast, most models predict an increase in intensity in TC (Bhatia et al. 2019). For example, during the last 30 yr, four category 3 or greater hurricanes, H. Hugo (1989, category 3), H. Georges (1998, category 3), H. Irma (2017, category 5), and H. Maria (2017, category 4), have struck Puerto Rico. Less is known about droughts, especially in the tropics. Climate models predict less precipitation and more

frequent droughts for the Caribbean, and, for Puerto Rico, models have suggested that precipitation could decrease from 20% to 30% by 2100 (Bhardwaj et al. 2018).

Both hurricane and drought disturbances can produce direct and indirect effects on animal populations. Indirect effects include decreased availability of food resources, nest and roost sites, increased vulnerability to predation, and microclimate changes. Direct impacts included mortality as well changes in physiology, abundance, occurrence, diet, foraging habitats, and reproductive behaviors (Waide 1991, Woolbright 1991, Wauer and Wunderle 1992, Wiley and Wunderle 1993, Wunderle 1995, Lugo 2008, Lloyd et al. 2019). Furthermore, hurricane and drought events can create conditions favorable for secondary disturbance, such as wildfire (Saracco et al. 2018). Changes in soil biogeochemistry, greenhouse gas emission, and vegetation damage due to a recent drought and hurricane were related to elevation (Hu and Smith 2018, O'Connell et al. 2018). Consequently, we expect different responses of fauna along an elevational gradient due to extreme weather events. Despite the potential for major impacts on animal populations, little is known about the impact of hurricanes and drought on animal distributions.

To address these issues, we describe the changes in the species distribution of 26 species of frogs and birds within the El Yunque National Forest (EYNF) in Puerto Rico between 2015 and 2019, which included an extreme drought and Hurricane Maria (category 4). Specifically, we document species detectability and occupancy in 59 sites along three elevational transects. These data are used to address the following question: How do species distributions change through time and along the elevational gradient? In addition, we tested for changes in rates of occupancy among years to assess the relative impact of the drought and hurricane on species distributions.

## MATERIALS AND METHODS

### *Study area and recent disturbances*

The study was conducted in El Yunque National Forest (EYNF) in north-eastern Puerto Rico (Fig. 1). The EYNF is the largest PA (115 km<sup>2</sup>) in Puerto Rico (Lugo 1994). The EYNF includes a strong elevational gradient that affects

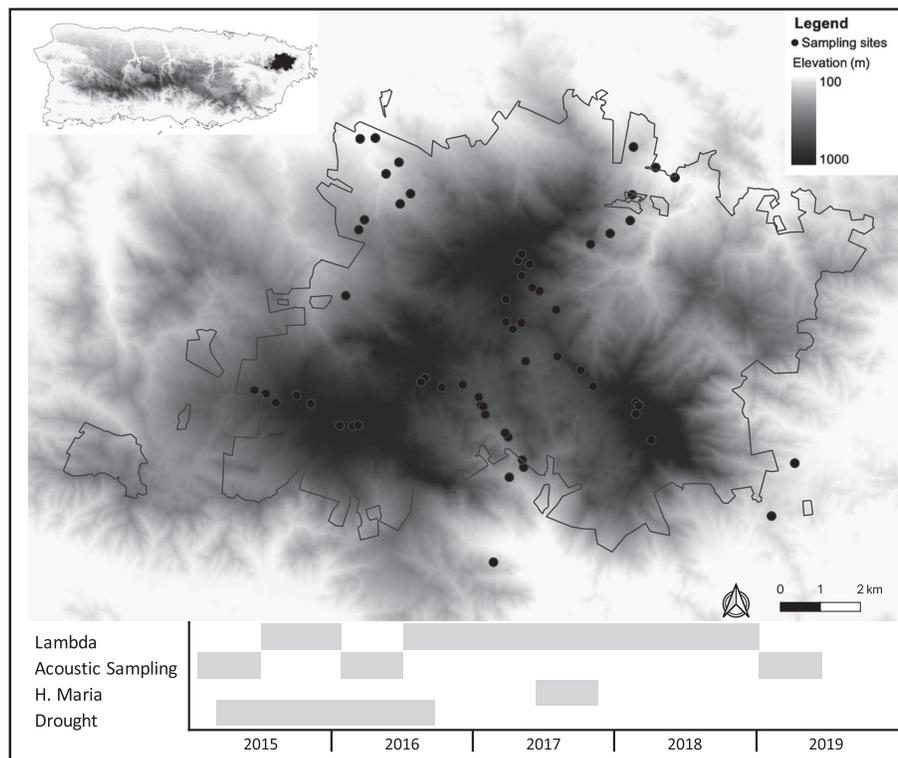


Fig. 1. Study sites ( $n = 59$ ) and sampling dates relative to environmental disturbances.

temperature, precipitation, humidity, and the distribution of plants and animals (García-Martín et al. 1996, Wang et al. 2003, Gould et al. 2006, Willig et al. 2012, Weaver and Gould 2013). Annual rainfall ranges from 2450 mm/yr at lower elevations to over 4000 mm/yr at higher elevations (Waide et al. 2013).

There are four main forest types along the elevational gradient: Tabonuco forest which is dominated by *Dacryodes excelsa* and occurs between 150 and 600 m, Palo Colorado forest which is dominated by *Cyrilla racemiflora*, and occurs between 600 and 950 m, Elfin forest which is dominated by *Tabebuia rigida* and *Eugenia boriquirensis* and occurs above 950 m, and Sierra Palm forest, which is dominated by *Prestoea montana* and can occur anywhere along the elevational gradient. In addition to the four major forest types, EYNF has a considerable area of old secondary forest (>40 yr) that occurs mostly at low elevations near the border of the reserve. During the last 80 yr, there has been no deforestation or selective logging within the PA. On average, hurricanes pass over Puerto Rico every

21 yr between July and December (Waide et al. 2013), and the EYNF study region has experienced hurricanes every 50–60 yr (Scatena 1995).

Between May 2015 and August 2016, Puerto Rico experienced the most severe drought since 1950 (Herrera and Ault 2017). Total precipitation in EYNF in 2015 was 48% below the long-term average (2004–2013; O'Connell et al. 2018). The impacts of the drought included changes in vegetation cover (Schwartz et al. 2019), a decrease in streamflow, an increase in invasive aquatic species (Ramírez et al. 2018), and an increase in organic phosphorus and soil carbon dioxide (O'Connell et al. 2018).

In September 2017, two hurricanes impacted the EYNF. H. Irma passed ~100 km to the northeast of EYNF as a category 5 hurricane on 6 and 7 September. Damage to the north-facing side of EYNF was extensive. Two weeks later on 20 September, H. Maria passed directly across Puerto Rico as a category 4 hurricane. The eye of the hurricane passed to the southwest of EYNF. The damage to the forest was much greater than with H. Irma. Hurricane Maria doubled tree

mortality relative to other major storms (Uriarte et al. 2019), and vegetation damaged was most severe at higher elevations (Hu and Smith 2018).

### Sampling design

Sampling sites were established along three elevational transects with 20 sampling sites per transect (Fig. 1). Along each transect, two recorders, separated by at least 200 m, were deployed at ~100-m elevational interval (from 95 to 1074 m). All recorders were placed more than 200 m from any road. One site could not be accessed in 2019, and thus, the analyses presented here are based on the 59 sites with audio recordings from each of the three sampling periods (March–April 2015, March–April 2016, and March–April 2019).

In the 2015 and 2016 sampling periods, we used ARBIMON recorders which consisted of a LG smartphone enclosed in a waterproof case with an external Monoprice microphone. During the 2019 sampling period, we used AudioMoth recorders. In all sampling periods, the recorders were placed on trees at a height of 1.5 m and were programmed to record 1 min of audio every 10 min 24 h per day for a total of 144 1-min recordings per day. Playback experiments within the study area found that most understory bird and frog species were detected up to ~50 m; therefore, for most species, the detection area is ~1 ha. A total of 75,966 recordings were collected in 2015, whereas 48,875 recordings were collected in 2016 and 106,914 recordings were collected in 2019. All recordings were uploaded and analyzed within the ARBIMON platform, and the recordings are available within the <https://arbimon.rfcx.org/project/luquillo-long-term-monitoring/dashboard> project in the ARBIMON platform<sup>1</sup>.

### Species-specific identification models

Species-specific identification models were created for each of the 11 frog and 15 bird species to determine their presence or absence in each audio recording. First, a template of a call or song was created for each species. This was done by reviewing the field recordings and choosing a representative example with low levels of background noise and without overlapping calls of other species. Next, two playlists were created as follows: (1) all diurnal (05:00–18:00 hours) recordings from the three sampling years and (2)

all nocturnal (18:00–05:00 hours) recordings from the three sampling years. All bird templates, except for *Megascops nudipes* (Puerto Rican screech owl), were applied to the diurnal playlist, and all frog templates and *M. nudipes* templates were applied to the nocturnal playlist. The classifications were based on a pattern matching procedure (LeBien et al. 2020) that searches through each recording and detects regions that have a correlation with the template above a given threshold. For these analyses, we used a correlation threshold of 0.1. This low threshold generated many false positives, but it reduced any false negative ensuring that we detected the species if it occurred in a site. Regions of interest (ROIs) with values above the correlation threshold are presented as potential detections. In the ROI classification inspection display, we used the filter “best match per site per day.” This filter shows the ROI with the highest correlation with the template for each day that recordings were collected. In that way, there can only be a maximum of one detection per day for each sampling site. These detections (i.e., ROIs) were all manually inspected by the co-author (MC-C) to eliminate any false positives. This procedure led to a present/absent matrix for all species for all days that were included in the study.

### Occupancy models

The species-specific detection matrices were used to create hierarchical dynamic occupancy models (MacKenzie et al. 2003) using the package unmarked in R (Fiske and Chandler 2011). Dynamic occupancy models estimate species distributions in the landscape and provide inferences about how changes in occurrence are driven by colonization and extinction while accounting for imperfect detection (Appendix S1: Table S1). Our design included three primary periods, that is, each of three years, 2015, 2016, and 2019. For each sampling period, detections were summarized by day, resulting in 14 secondary occasions in 2015, 13 secondary occasion for 2016, and 16 secondary occasion for 2019.

We evaluated eight a priori candidate models (Appendix S1: Table S2). We allowed elevation to influence initial occupancy, colonization, and extinction because this variable is known to affect occurrence of bird and frog species in the study area (Campos-Cerqueira et al. 2017,

Campos-Cerqueira and Aide 2017a, b). In the most parameterized model, the first-year occupancy parameter was modeled as a function of elevation (second polynomial function of elevation), and colonization and extinction parameters were modeled as an interaction function with elevation (second polynomial function of elevation) and year (full time-dependence), whereas the detection parameter was modeled as function of year. We created a scaled elevational vector (i.e., changing meters to kilometers) before the analyses.

To determine how species distribution across the elevational gradient changed relative to the disturbances, we constructed an elevational profile effect for each species in each year using the parameters of the top model ( $\Delta\text{AIC} = 0$ ). To do this, the intercepts and the elevational coefficients were allowed to change with year. We estimated the precision of the elevational effect (i.e., 95% confidence intervals) with 1000 bootstraps iterations. Although we provide measures of uncertainty associated with the elevational profiles among the years, we chose to draw our inferences about changes in occupancy along the elevational gradient based on point estimates for simplicity.

To estimate the rate of change in occupancy through time, we used two approaches. First, we estimated the proportion of sampling sites that were occupied in each year by using the projected-based estimate of occupancy from the top model. Standard errors of the projected estimates of occupancy probability during each year were computed using 1000 non-parametric bootstraps iterations. Second, we calculated lambda prime ( $\lambda'$ ; Appendix S1: Table S1) using the best overall model ( $\Delta\text{AIC} = 0$ ) of each species (Appendix S1: Tables S3, S4). This metric is the ratio of the probability of occupancy at time  $t$  vs. at time  $t + 1$  ( $\lambda' = (\psi_{(t+1)}/1 - \psi_{(t+1)})/(\psi_t/1 - \psi_t)$ ). It can be interpreted as the amount that the probability of occupancy at time  $t$  would be multiplied by to get the probability of occupancy at time  $t + 1$ . A stable set of populations should have an estimated  $\lambda'$  of approximately 1.0, a declining population  $<1$ , and an increasing population  $>1$  (MacKenzie et al. 2003). Here, we use a more conservative approach: lambda 0.95–1.05 stable,  $<0.95$  declining, and  $>1.05$  increasing.

We have estimated three lambdas during the study period: The first lambda ( $\lambda_1$ ) measures the population growth between the first and second years (2015–2016) which coincides with an extensive drought period, the second lambda ( $\lambda_2$ ) measures the population growth between the second and third years (2016–2019) which encompass the additional effect of H. Maria, and the third lambda ( $\lambda_3$ ) measures the population growth between the first (2015) and the last year (2019). We computed 95% confidence intervals for each lambda using 1000 bootstraps. Nevertheless, lambda estimates are not independent from each other, and in our case, they are often highly positively correlated. Therefore, individual confidence intervals can overlap, but the lambdas can still be significantly different. Therefore, we calculated all pairwise lambda differences and the uncertainties associated with the differences (i.e., 95% confidence interval). We first calculated the difference in the lambda prime values, and then, we created bootstrap percentile confidence intervals for the differences for each species. In the bootstrap process, we took the standard deviation of the differences as the estimate of the standard error of the difference, following the general annotation:  $\sqrt{(\text{Var}(\lambda_1) + \text{Var}(\lambda_2) - 2 \times \text{Cov}(\lambda_1, \lambda_2))}$ . Therefore, if the confidence interval intervals do not include zero, then that is equivalent of a test of equality and finding a significant difference.

Given the high uncertainty associated with individual estimates of lambdas, we assess the relative impact of each weather event on species occupancy in two different ways: (1) by accessing the directionality of lambda across the three years, and (2) by assessing if there were significant differences among the lambdas ( $\lambda_1, \lambda_2, \lambda_3$ ).

To determine a possible trend in population growth in each time period, we focused on the sign of lambdas point estimates among years. If species populations are resistant to natural weather events such as droughts and hurricanes, we would expect that lambdas would be close to 1.0 (i.e., stable population,  $\lambda = 0.95\text{--}1.05$ ) between each time period and across the entire study period. However, if the drought had a negative effect on population growth, we expected  $\lambda_1$  (2015–2016)  $<0.95$  reflecting a declining population. Similarly, if H. Maria had a negative effect on population growth, we expected  $\lambda_2$  (2016–

2019)  $<0.95$  reflecting a declining population. If  $\lambda_3$  (2015–2019)  $<0.95$ , this would suggest that both the drought and hurricane had a negative effect on population growth.

To test for significant differences in population growth between years, we compared the differences among lambdas estimates from all time periods (2015–2016 vs. 2016–2019, 2015–2016 vs. 2015–2019, 2015–2016 vs. 2015–2019). If species populations are resistant to natural weather events such as droughts and hurricanes, we would expect to find no significant change in lambdas across the years. However, if the drought had a negative effect on species populations, we would expect that the lambda between the first and second years (2015–2016) would be significantly smaller than lambdas between the second and third year (2016–2019). Similarly, if H. Maria had a negative effect on growth rate, we expected that the lambda between the second and third year (2016–2019) would be significantly smaller than lambdas from the first and second years (2015–2016). A combined negative effect of the drought and hurricane on growth rate would be expected when lambdas from the entire study period (2015–2019) are smaller than lambdas from 2015 to 2016 and lambdas from 2016 to 2019.

Differences in detection probability were calculated by comparing the logits of the detection probabilities from the best model of each species. First, we obtained the estimates of detection probability from each year along with the covariance matrix. Then, we conducted pairwise comparisons among the three years and used a two-tailed two-sample *t* test (Bonferroni correction applied).

## RESULTS

### Frog community

Overall species detectability was high (~80%) for all frog species (Appendix S1: Table S5). Furthermore, even though two types of recorders were used during the study and the hurricane changed forest structure, there was no difference in detectability among years for the majority of the species (8/11; Appendix S1: Table S5). A significant difference in detection probability was detected for two species between 2015 and 2016, one species between 2016 and 2019 and three

species between 2015 and 2019 (Appendix S1: Table S5). Occupancy varied greatly among the 11 frog species (Fig. 2A). *Eleutherodactylus coqui* was the most common species; it was detected in all sites during the three sampling periods. Other common species included *Eleutherodactylus unicolor* and *Eleutherodactylus portoricensis* with estimated occupancies around 50% in each of the three years. Four forest species (*Eleutherodactylus wightmanae*, *Eleutherodactylus gryllus*, *Eleutherodactylus richmondi*, and *Eleutherodactylus locustus*) were rare with occupancy  $<20\%$ , and except for *E. gryllus*, occupancy point estimates declined over the four-year period for the other three species. The occupancy of two open-habitat species increased during the study period from 0.34 to 0.42 for *Eleutherodactylus brittoni* and 0.03–0.17 for *Eleutherodactylus antillensis*. The population expansion of these two species is supported by the sign of the lambdas ( $\lambda > 1$ ; Table 1) and a significant difference in lambdas between each time period (Table 2; Appendix S1: Table S6).

There was no community-level trend in the directionality of the lambdas between 2015 and 2016 (drought), 2016–2019 (hurricane), or 2015–2019 (drought and hurricane; Fig. 2B, Table 1). Five frog species had a negative lambda during the drought (2015–2016), and five species had a negative lambda following the hurricane (2016–2019), whereas six species had a negative lambda across the entire study period (2015–2019). Two forest specialist species, *E. wightmanae* (0.74) and *E. richmondi* (0.73), had the lowest lambda estimates during the drought period (2015–2016). Three forest-specialist species, *E. wightmanae* (0.75), *E. richmondi* (0.74), *E. gryllus* (0.68), and one forest-edge species, *E. locustus* (0.65), had the lowest lambda estimates following the hurricane (2016–2019). *Eleutherodactylus hedricki* (0.80), *E. locustus* (0.74), *E. wightmanae* (0.56), and *E. richmondi* (0.54) had the lowest lambda estimates for the entire study period (2015–2019).

Despite the lack of a clear trend in the directionality of lambdas at each time period (Table 1), population growth rate from 2015 to 2016 significantly changed from 2016 to 2019 for seven frog species (Table 2; Appendix S1: Table S6). Five frog species (*E. portoricensis*, *E. wightmanae*, *E. brittoni*, *E. antillensis*, and *E. richmondi*) had significantly lower population growth rate during the drought (2015–2016) than

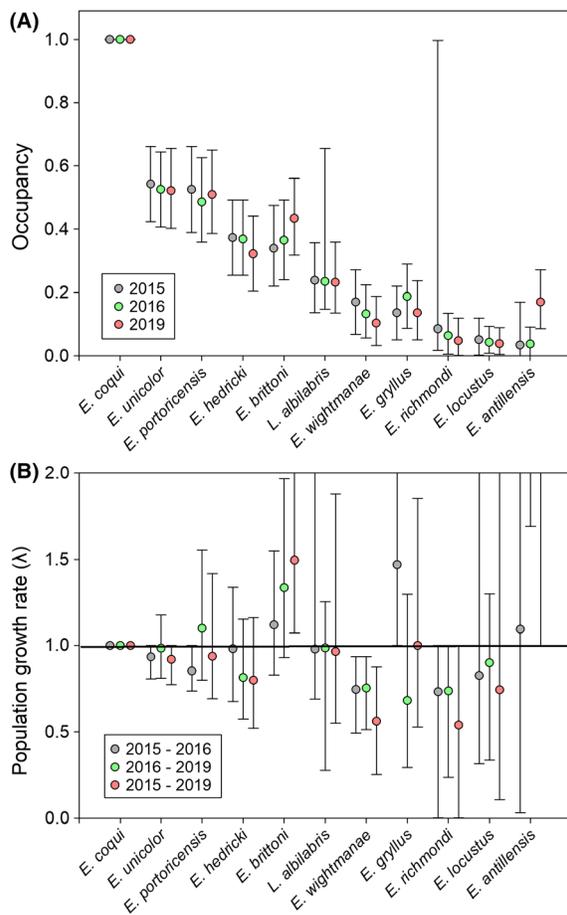


Fig. 2. (A) Probability of occupancy and 95% confidence intervals for each frog species during the three sampling periods (2015, 2016, and 2019). The species are order based on their occupancy in 2015, (B) estimate lambda (i.e., population growth rate for three time periods between the 2015–2016, 2016–2019, and 2015–2019 sampling periods). A lambda of 1.0 reflects a stable population, while values above 1.0 or below 1.0 reflect an increasing or decreasing population, respectively.

after the H. Maria (2016–2019). In contrast, two canopy frog species (*E. gryllus* and *E. hedricki*) had significantly lower population growth after the hurricane (2016–2019). The population growth rate from the entire study period (2015–2019) was significantly smaller than population growth rate at either time period (2015–2016, 2016–2019) for only two frog species (*E. wightmanae* and *E. hedricki*), indicating a negative and

combined effect of drought and hurricane. In contrast, the population growth rate from the entire study period was significantly higher than population growth rate at either time period (2015–2016, 2016–2019) for two open-area frog species (*E. brittoni* and *E. antillensis*) indicating a positive and combined effect of drought and hurricane.

With a few exceptions, the distributions of the frog species along the elevational gradient did not change across the years even after two extreme weather events (Fig. 3; Appendix S1: Fig. S1). Occupancy was low (<25%) and constant along the elevational gradient during the three years for four species (*E. wightmanae*, *E. richmondi*, *E. locustus*, and *Leptodactylus albilabris*). These species were relatively rare; they occurred in less than 14 sampling sites. Despite great uncertainty of the point estimates, the probability of occupancy of *E. portoricensis* decreased at lower elevations (<500 m) and increased at higher elevations (>700 m). In contrast, following the H. Maria in 2017, the probability of occupancy of *E. gryllus* decreased at higher elevations. Previous to H. Maria, *E. antillensis* had only been detected below 300 m, but following the hurricane the probability of occupancy increased in areas up to 600 m. Nevertheless, there is high uncertainty in the occupancy estimates for 2015 and 2016 data for *E. antillensis* (Appendix S1: Fig. S1). This species was detected in only two sites in 2015 and 2016 and increased to 10 sites in 2019.

#### Bird community

Detectability for bird species (mean = 0.5, range 0.13–0.83) was lower and more variable in comparison with the frogs (Appendix S1: Table S5). Furthermore, there was no obvious pattern among years in detectability (Appendix S1: Table S5). There was a significant difference in detection probability for eight species. Five species had significant differences in detection probabilities between 2015 and 2016, five species between 2016 and 2019, and four species between 2015 and 2019 (Appendix S1: Table S5). Occupancy varied greatly among the 15 bird species (Fig. 4A). *Coereba flaveola* was the most common bird species; it was detected in most of the sites during the three sampling periods. Other common species included *Patagoniaea*

Table 1. The lambdas signs for the two inter-sampling periods and the entire study period.

Species	Diet	Foraging strata	Lambda 2015–2016	Lambda 2016–2019	Lambda 2015–2019
Frogs ( <i>n</i> = 11)					
<i>Eleutherodactylus coqui</i>	Insectivore	Understory	=	=	=
<i>Eleutherodactylus unicolor</i>	Insectivore	Terrestrial	–	=	–
<i>Eleutherodactylus portoricensis</i>	Insectivore	Understory	–	+	–
<i>Eleutherodactylus wightmanae</i>	Insectivore	Understory	–	–	–
<i>Eleutherodactylus gryllus</i>	Insectivore	Canopy	+	–	=
<i>Eleutherodactylus brittoni</i>	Insectivore	Understory	+	+	+
<i>Eleutherodactylus hedricki</i>	Insectivore	Canopy	=	–	–
<i>Eleutherodactylus antillensis</i>	Insectivore	Understory	+	+	+
<i>Eleutherodactylus richmondi</i>	Insectivore	Terrestrial	–	–	–
<i>Leptodactylus albilabris</i>	Insectivore	Terrestrial/water	=	=	=
<i>Eleutherodactylus locustus</i>	Insectivore	Understory	–	–	–
Birds ( <i>n</i> = 15)					
<i>Vireo altiloquus</i>	Insectivore	Canopy	–	+	+
<i>Coereba flaveola</i>	Nectarivore	Canopy	–	=	–
<i>Setophaga angelae</i>	Insectivore	Canopy	–	–	–
<i>Patagonias squamosa</i>	Frugivore	Canopy	–	+	+
<i>Loxigilla portoricensis</i>	Frugivore	Canopy	+	–	–
<i>Spindalis portoricensis</i>	Frugivore	Canopy	+	–	–
<i>Nesospingus speculiferus</i>	Omnivore	Canopy	–	–	–
<i>Margarops fuscatus</i>	Omnivore	Canopy	–	+	+
<i>Megascops nudipes</i>	Carnivore	Canopy	–	+	+
<i>Tyrannus caudifasciatus</i>	Insectivore	Canopy	=	+	+
<i>Turdus plumbeus</i>	Omnivore	Canopy	–	+	–
<i>Todus mexicanus</i>	Insectivore	Canopy	–	=	–
<i>Coccyzus vieilloti</i>	Insectivore	Canopy	–	+	+
<i>Melanerpes portoricensis</i>	Omnivore	Canopy	–	+	+
<i>Geotrygon montana</i>	Frugivorous	Understory	–	+	–

Note: Population growth rate (i.e., lambda) was increasing (+) if lambda was >1.05, stable (=) if lambda was between 0.95 and 1.05, and declining (–) if lambda was <0.95.

*squamosa*, *Nesospingus speculiferus*, *Spindalis portoricensis*, and *Loxigilla portoricensis* with estimated occupancies around 0.8 in each of the three years. Occupancy estimates of many bird species declined between the 2015 and 2016 sampling periods, and *Todus mexicanus* (0.67–0.49) and *Geotrygon montana* (0.38–0.07) were the most dramatic. In contrast, between the 2016 and 2019 sampling, occupancy of most species increased, and *M. nudipes* (0.43–0.71) and *Coccyzus vieilloti* (0.33–0.53) were the most dramatic. Analyses of difference between lambda estimates support these findings given that nine of 15 bird species (60%) had a population growth rate significantly lower in 2015–2016 than between 2016 and 2019. The probability of occupancy of *Setophaga angelae*, a Puerto Rican endemic with one of its two populations in EYNF, declined from 0.35 in 2015 to 0.30 in 2019, and there was a significant

difference between lambdas from 2015 to 2019 to lambdas from 2015 to 2016, which indicates a population declining across the study period (Table 2). A similar pattern of population decline across the study period was observed for *N. speculiferus*.

Contrary to the results in the frog community, there was a clear community-level trend in the directionality of the lambdas for the bird community (Table 1, Fig. 4B). Lambdas during the drought period (2015–2016) were less than 0.95 for the majority of the bird species (12/15). It is highly improbable that the results would arise from chance under a true null hypothesis: If the sign of lambda followed a binomial distribution with probability of success 0.5, the overall result of 12 successes in 15 trials would have a probability of approximately 0.014. In contrast, the population growth rate after the hurricane was

Table 2. Differences between lambdas across all inter-sampling periods.

Species	Difference between lambdas		
	2015–2016 to 2016–2019	2015–2019 to 2016–2019	2015–2019 to 2015–2016
<b>Frogs (n = 11)</b>			
<i>Eleutherodactylus coqui</i>	Not determined	Not determined	Not determined
<i>Eleutherodactylus unicolor</i>	Increased	<b>Decreased</b>	Decreased
<i>Eleutherodactylus portoricensis</i>	<b>Increased</b>	<b>Decreased</b>	Increased
<i>Eleutherodactylus wightmanae</i>	<b>Increased</b>	<b>Decreased</b>	<b>Decreased</b>
<i>Eleutherodactylus gryllus</i>	<b>Decreased</b>	<b>Increased</b>	<b>Decreased</b>
<i>Eleutherodactylus brittoni</i>	<b>Increased</b>	<b>Increased</b>	<b>Increased</b>
<i>Eleutherodactylus hedricki</i>	<b>Decreased</b>	Decreased	<b>Decreased</b>
<i>Eleutherodactylus antillensis</i>	<b>Increased</b>	Increased	<b>Increased</b>
<i>Eleutherodactylus richmondi</i>	<b>Increased</b>	Decreased	Decreased
<i>Leptodactylus albilabris</i>	Decreased	Decreased	Decreased
<i>Eleutherodactylus locustus</i>	Increased	Decreased	Decreased
<b>Birds (n = 15)</b>			
<i>Vireo altiloquus</i>	<b>Increased</b>	<b>Decreased</b>	<b>Increased</b>
<i>Coereba flaveola</i>	<b>Increased</b>	<b>Decreased</b>	Increased
<i>Setophaga angelae</i>	Increased	Decreased	<b>Decreased</b>
<i>Patagionas squamosa</i>	<b>Increased</b>	<b>Decreased</b>	<b>Increased</b>
<i>Loxigilla portoricensis</i>	<b>Decreased</b>	<b>Increased</b>	<b>Decreased</b>
<i>Spindalis portoricensis</i>	<b>Decreased</b>	Increased	<b>Decreased</b>
<i>Nesospingus speculiferus</i>	<b>Decreased</b>	<b>Decreased</b>	<b>Decreased</b>
<i>Margarops fuscatus</i>	<b>Increased</b>	<b>Decreased</b>	<b>Increased</b>
<i>Megascops nudipes</i>	<b>Increased</b>	<b>Decreased</b>	<b>Increased</b>
<i>Tyrannus caudifasciatus</i>	Not determined	Not determined	Not determined
<i>Turdus plumbeus</i>	<b>Increased</b>	<b>Decreased</b>	Increased
<i>Todus mexicanus</i>	<b>Increased</b>	<b>Decreased</b>	<b>Decreased</b>
<i>Coccyzus vieilloti</i>	<b>Increased</b>	<b>Decreased</b>	<b>Increased</b>
<i>Melanerpes portoricensis</i>	<b>Increased</b>	<b>Decreased</b>	<b>Increased</b>
<i>Geotrygon montana</i>	Increased	Decreased	Increased

Notes: Significant differences are denoted in bold. Values for estimated differences and confidence intervals can be found in Appendix S1: Table S6.

greater than 1.05 for the majority of bird species (9/15; Table 1, Fig. 4B). This increase in occupancy between 2016 and 2019, which included H. Maria, was most obvious in the only native woodpecker in the island the Puerto Rican woodpecker (*Melanerpes portoricensis*), in two of the most common species, the bananaquit (*C. flaveola*) and the scaly-naped pigeon (*P. squamosa*), and in two predator species, the Puerto Rican screech owl (*M. nudipes*) and the Puerto Rican lizard cuckoo (*C. vieilloti*). In contrast to the other bird species, population growth (i.e., lambda) of the Puerto Rican bullfinch (*L. portoricensis*) and the Puerto Rican spindalis (*S. portoricensis*) was high between 2015 and 2016 and then decreased between 2016 and 2019.

Population growth rate during the drought (2015–2016) was significantly different from

population growth rate after H. Maria (2016–2019) for 12 bird species (Table 2; Appendix S1: Table S6). Nine bird species (*Vireo altiloquus*, *C. flaveola*, *Patagionas squamosa*, *Margarops fuscatus*, *M. nudipes*, *Turdus plumbeus*, *T. mexicanus*, *C. vieilloti*, and *M. portoricensis*) had significantly lower population growth rate during the drought (2015–2016) than after the H. Maria (2016–2019). In contrast, three bird species (*L. portoricensis*, *S. portoricensis*, and *N. speculiferus*) had significantly lower population growth after the hurricane (2016–2019) than during the drought (2015–2016). The population growth rate from the entire study period (2015–2019) was significantly smaller than population growth rate at either time period (2015–2016, 2016–2019) for only three bird species (*N. speculiferus*, *S. angelae*, and *T. mexicanus*), indicating a negative and combined effect of drought

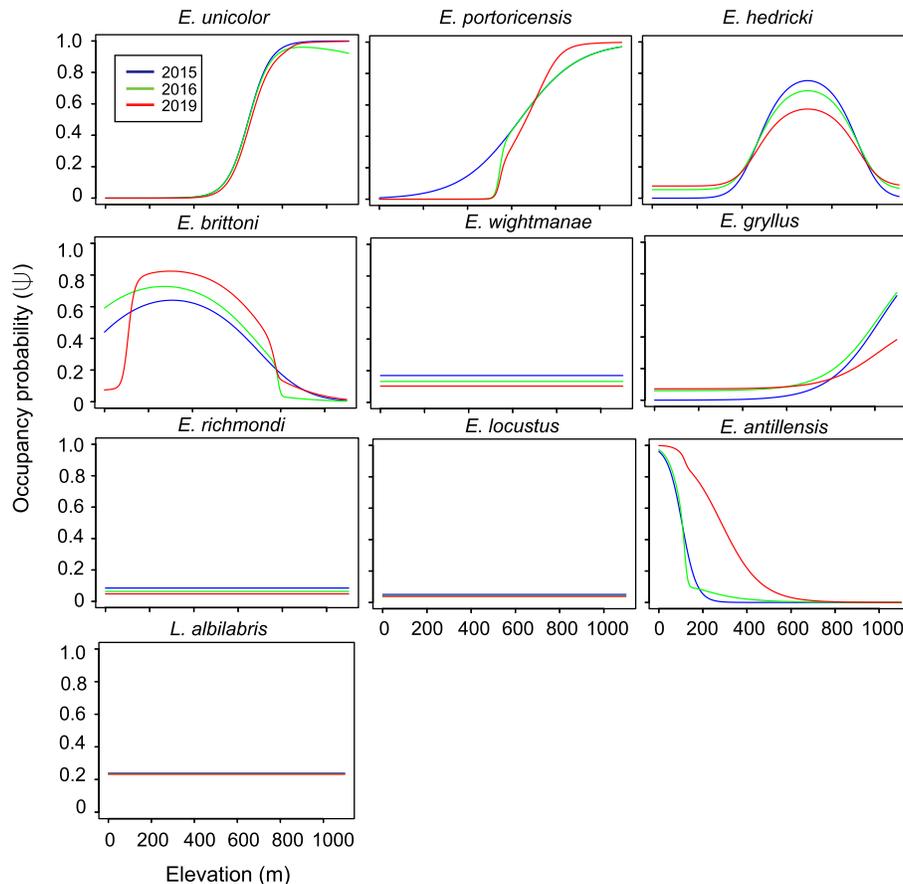


Fig. 3. Predicted relationship between occupancy and elevation for each frog species during each sampling period. We did not include the common coqui in the occupancy models since this species occur in all but one sampling site during the three years. 95% confidence intervals can be found on Appendix S1: Fig. S1.

and hurricane. Despite a significantly increase in population growth rate for the majority of bird species (9/15) after the hurricane (2016–2019), the population growth associated with the entire study period (2015–2019) for these nine bird species was still significantly smaller than the population growth observed after the hurricane (2016–2019) for all but *L. portoricensis*. In contrast, the population growth rate from the entire study period (2015–2019) was significantly higher than population growth rate during the drought (2015–2016) for six bird species (*V. altiloquus*, *P. squamosa*, *L. portoricensis*, *M. fuscatus*, *M. nudipes*, *C. vieillot*, and *M. portoricensis*) indicating a combined effect of drought and hurricane.

The elevational distributions of the bird species varied considerably in EYNF (Fig. 5;

Appendix S1: Fig. S2). The distribution of most species did not change much during the study period and the uncertainty was high (Appendix S1: Fig. S2), but occupancy point estimates suggest that the distributions of three species (*M. fuscatus*, *C. vieillot*, and *M. nudipes*) shifted up the mountain following H. Maria in the 2019 sampling period. In contrast, the distribution of *G. montana* shifted down the mountain. This loss of the highland populations first occurred between the 2015 and 2016 sampling periods. By 2019, there was an increase in occupancy in the lowland areas (<300 m), but there was no recovery in the highlands. The change in the elevational distribution of *T. plumbeus* was unique in that it was the only species where the occupancy in the lowlands (<400 m) declined.

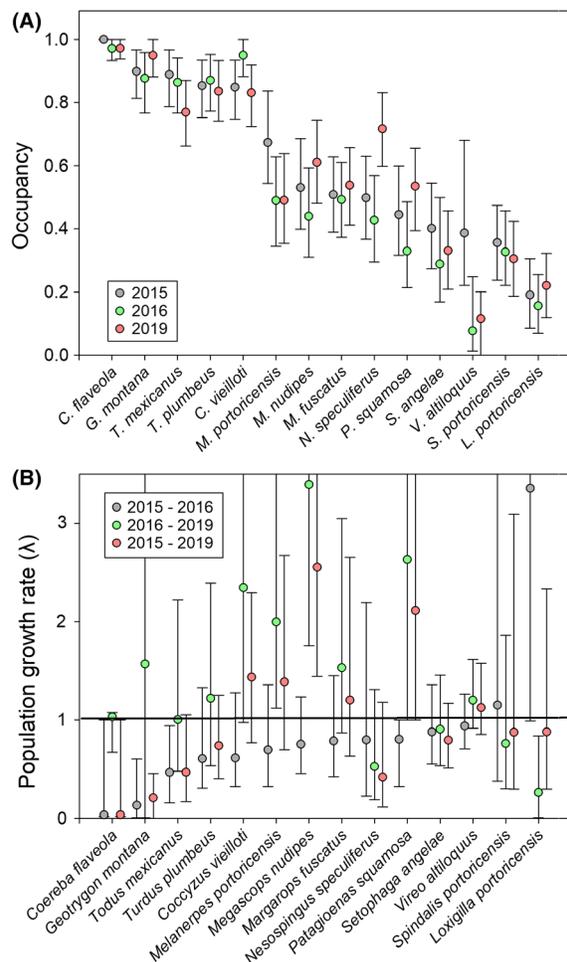


Fig. 4. (A) Probability of occupancy and 95% confidence intervals for each bird species during the three sampling periods (2015, 2016, and 2019). The species are order based on their occupancy in 2015, (B) estimate lambda (i.e., population growth rate for the three time periods between the 2015–2016, 2016–2019, and 2015–2019). A lambda of 1.0 reflects a stable population, while values above 1.0 or below 1.0 reflect an increasing or decreasing population, respectively.

Initially (i.e., 2015), the occupancy <400 m was >0.8, but by the 2016, it had declined to <0.7 and there was no sign of recovery by the 2019.

## DISCUSSION

All studies on the impact of transient disturbances on animal species suffer from the absence of temporal and spatial replications and lack of

control populations, which can limit inferences about the causes of changes in occupancy. Long-term monitoring across large spatial scales can greatly improve these limitations. Unfortunately, for many species, particularly species with limited distributions, it is not feasible to include control population because hurricane and droughts can impact the entire species distribution. Given these limitations, there are two lines of evidence that strongly support the inference that these disturbances were responsible for a large proportion of the changes in occupancy. First, the populations of 12 of the 15 bird species declined during the 2015–2016 period, which corresponded with the most severe and prolonged drought since 1950 (Herrera and Ault 2017). This drought spanned two reproductive cycles, and the lack of rainfall before the reproduction cycle can decrease breeding success and population size (Faaborg 1982). Second, the increase in bird occupancy after H. Maria is consistent with the increase in resource availability (e.g., food and nesting locations) during the recovery stage following a hurricane (Wiley and Wunderle 1993, Wunderle 1995, 1999).

## Frog community

Compared with the bird community, the response of the frog community to the severe drought and hurricane was less pronounced, but five of the 11 frog species did show a decline in population growth following the drought. Little is known about the effect of drought on frog communities in Puerto Rico but given that in general frogs occur in humid habitats, prolonged droughts are expected to have a significant negative impact. For example, long periods of drought can negatively impact the abundance of *E. coqui*, particularly juveniles (Stewart 1995). Drought can also force frogs to aggregate in humid refuges, increasing frog vulnerabilities to disease, such as the chytrid fungus (Joglar and Burrowes 1996, Burrowes 2009, Longo and Burrowes 2010, Langhammer et al. 2014). Despite the small changes in occupancy, our results indicate that about half of the frog species had a significant smaller growth rate during the drought (2015–2016) than after the hurricane (2016–2019) which indicates their vulnerability to droughts.

In contrast, the effects of hurricanes on frog populations have been well studied. Low levels

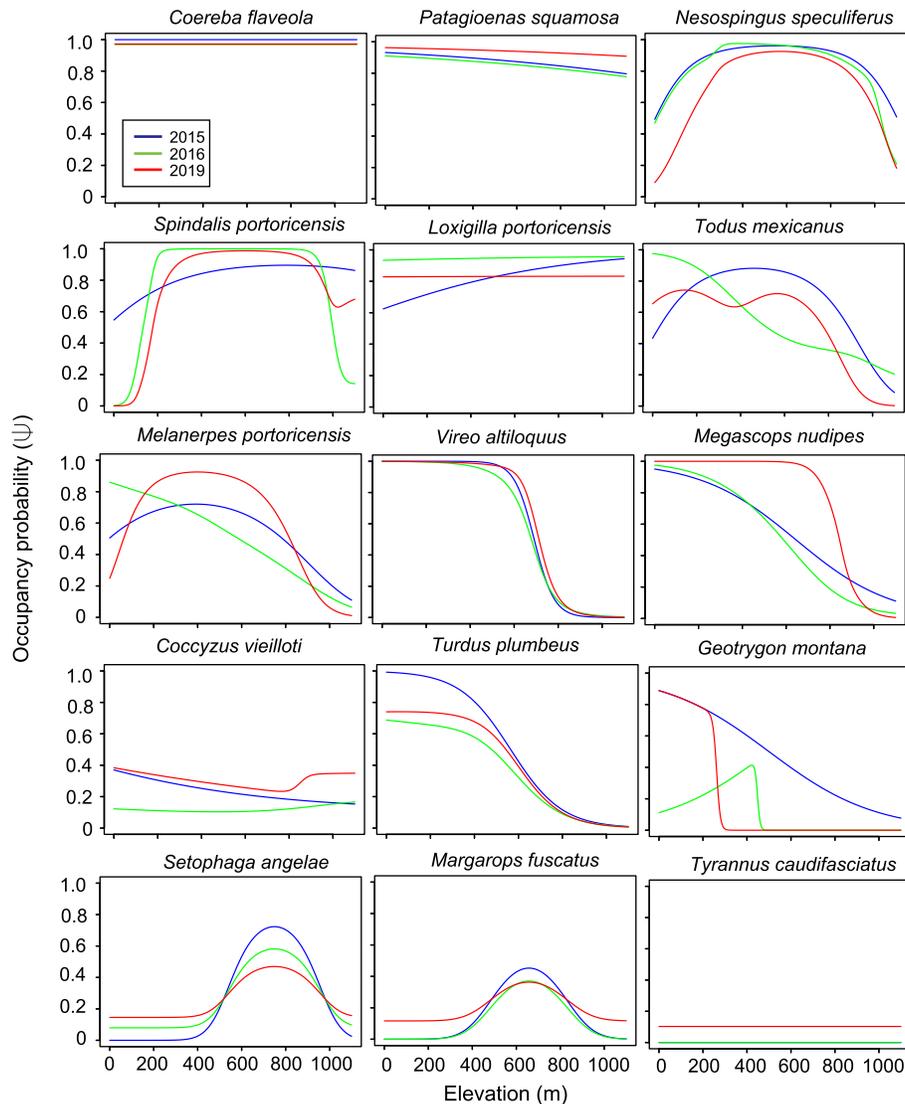


Fig. 5. Predicted relationship between occupancy and elevation for each bird species during each sampling period. 95% confidence intervals can be found on Appendix S1: Fig. S2.

of mortality in adult frogs were observed in EYNF after H. Hugo (1989), but lower humidity in the understory post-hurricane had a negative effect on juveniles of *E. coqui* (Woolbright 1991). Nevertheless, one year after the hurricane, the number of adults and juveniles of *E. coqui* rapidly surpassed those in pre-hurricane surveys, probably due to an increase in retreat sites, a decline in predators, and an increase in humidity as the canopy closed (Woolbright 1991). The high resilience of most *Eleutherodactylus* frogs to

environmental disturbances and their ability to reproduce throughout the year (Woolbright 1991, Joglar 1998) are characteristics that help explain the limited response of these species to a severe drought and a category 4 hurricane in the present study. There are three non-exclusive explanations for the high resilience of frog species to these large-scale disturbances compared to birds. First, aspects of their natural history, particularly the microhabitat use, period of activity, and reproductive behavior, may favor the persistence

of frog populations in the landscape. Except for *E. hedricki* and *E. gryllus*, all the other frog species in this study occur on or near the ground. Contrary to birds in our study area, which are mainly canopy species, most of the frog species occur in the forest understory and are most active at night. Even during a drought, the understory of tropical rainforest will still maintain relatively high levels of humidity during the night when frogs are most active. Furthermore, all species in the genus *Eleutherodactylus* are characterized by direct development and calling and reproductive activity occurs year-round (Pough et al. 1983, Woolbright 1985, Stewart 1995, Joglar 1998). Coquis hatch directly from the eggs, and there is no tadpole stage; thus, their development does not depend on bodies of water (e.g., ponds or puddles). The ability of the coqui species to reproduce year-round provides another advantage. Consequently, coqui species could breed as soon as environmental conditions are again favorable, as demonstrated by the rapid increase in adults and juveniles of *E. coqui* after H. Hugo in 1989 (Woolbright 1991).

Second, frogs have poor dispersal ability compared to birds. Both males and females of the common coqui, for example, are strongly territorial, and they rarely move more than five meters from their retreat sites (Woolbright 1985, 1996, Gonser and Woolbright 1995, Joglar 1998). Contrary to birds that can rapidly colonize other suitable sites, coqui species need to cope with environmental disturbance through shifts in behavior and physiology.

Third, patterns of species occurrence at the site level are different for birds and frogs; consequently, our occupancy estimates may have a different meaning for birds and frogs. Given that frogs hold a much smaller territory than birds, audio recorders can detect an entire subpopulation of frogs. Therefore, to be able to detect an extinction from one site, the entire frog subpopulation must be extirpated from that location. As such, there could be an extreme decrease in abundance, but presence would remain unchanged.

Although the distributions of the majority of frog species did not change much during the study period, there were some notable exceptions. Both, *E. brittoni* and *E. antillensis*, are primarily associated with open areas, shrubs, and

grass vegetation, and this could explain the increase in their occupancy in 2019 following H. Maria. The same pattern of expansion of these two species following H. Maria was also observed in the Cayey Mountains in Puerto Rico (M. Campos-Cerqueira et al., unpublished data). In addition, *E. hedricki* and *E. gryllus* are both species associated with the canopy, and this could explain lower lambdas after H. Maria (2016–2019) compared with the drought period (2015–2019). Despite the lack of a strong response by the frog community, *Eleutherodactylus* frogs in Puerto Rico can be particularly vulnerable to climate and land-use change given that almost all species are endemic, endangered, have lost many populations in the lowlands (Campos-Cerqueira and Aide 2017b), and currently occur only in a few localities inside PA in Puerto Rico (Joglar 1998).

#### *Bird community*

In contrast to the frog community, the bird community showed a strong negative response during the 2015–2016 period, which included a severe drought, with  $\lambda < 0.95$  in 12 of the 15 species, suggesting that the populations of 12 bird species contracted. But during the 2016–2019 period, which included H. Maria,  $\lambda > 1.05$  for nine of the 15 species suggesting that the drought had a more adverse effect on the bird community than did the hurricane. This pattern is supported by a significant lower lambda of nine bird species during the drought (2015–2016) compared with after H. Maria (2016–2019). Similar to frogs, little is known about the effect of droughts on birds. Severe and prolonged drought in Australia (1997–2009) led to population declines in several bird species, and these declines were not related to species ecological traits (Bennett et al. 2014). The only study that has accessed the impact of drought on birds in Puerto Rico was conducted in a dry forest and showed a population decline of 40% in 1974 (Faaborg 1982). The decline was related to drought conditions through 1973–1975. Frugivorous and insectivorous flycatchers were the most negatively affected species.

In contrast, the impact of hurricanes on birds has been well documented, and overall, their response has been heterogeneous. Several studies reported declines in abundance and occurrence

for bird species that have a diet based on nectar, fruit, and seeds, but these declines were not related with direct mortality from hurricanes and were most apparent in the months following the hurricane (~6 months after the hurricane; Waide 1991, Wiley and Wunderle 1993, Lloyd et al. 2019). In contrast, the population of omnivorous and insectivore species seems to be less affected by hurricanes. Nevertheless, population changes after H. Hugo in Puerto Rico were not strongly related to the trophic guild. Instead, shifts in foraging strata and changes in diet were observed (Wunderle 1995). Canopy species were frequently observed foraging in lower vegetation strata, consuming different insect prey, shifting to early successional habitat patches, and consuming a larger proportion of fruits (Waide 1991, Wunderle 1995). In addition, high reproduction success was observed for some species in the second breeding period following a hurricane (Wunderle and Arendt 2011) likely as a result of an increase in forest primary productivity (Scatena 1998).

There are three non-exclusive explanations for the different responses of birds to drought and hurricanes. First, the strong negative response observed during the 2015–2016 drought period may be associated with the time of the event in relation to the peak of bird reproduction. The drought lasted 80 weeks, beginning on 5 May 2015 and ending on 8 November 2016.<sup>2</sup> This period encompasses at least two reproductive seasons (March–June), when food availability is high, for most terrestrial birds in Puerto Rico (Castro-Prieto et al. 2020). Given that we sampled during the bird breeding season, we were able to measure short-term changes in occupancy influenced by the drought.

Second, with the exception of *S. angelae*, *N. speculariferus*, and *G. montana*, all bird species from this study are generalists in terms of habitat use, occurring in both dry-open and wet-closed forests. Thus, the population expansion after the pass of the hurricanes may be related to an increasing habitat heterogeneity, creating successional habitats with new food availability (e.g., fruits and insects; Wiley and Wunderle 1993). For instance, bird species had higher capture rates in pre-existing gaps relative to the forest after H. Hugo (1989) because some plant species responded quicker and many bird species took

advantage of the increase in fruits (e.g., *Hirtella rugosa*; Waide 1991, Wunderle 1995, 1999). In addition, outbreaks of insect populations in EYNF following H. Hugo also provided additional resources for birds (Torres 1992). Furthermore, contrary to the aftermath of H. Hugo there was an increase in precipitation after H. Maria, which may have provided even more food resources for birds.

Third, the fauna of Puerto Rico has evolved in habitats periodically disturbed by hurricanes, but may not be as well adapted to prolonged droughts amplified by human-induced climatic changes. With the exception of *S. angelae*, *N. speculariferus*, and *G. montana*, which are only found in montane forests in Puerto Rico, all other bird species from this study are generalists in terms of habitat use, occurring in both dry-open and wet-closed forests, and therefore, these species may be more tolerant of the changes to forest structure associated with hurricane damage.

The dramatic occupancy declines of *G. montana* were related to its sensitivity to forest disturbances and drought. In the Amazon, this species avoids small fragments (<1 ha), areas lacking forest canopy, and its abundance was positively correlated with rainfall in the previous year (Stouffer and Bierregaard 1993). In Puerto Rico, there was a sharp population decline of this species after H. Hugo (1989; Wunderle 1995). In the present study, the combination of the drought followed by the hurricane may explain the species decline.

*Setophaga angelae* and *N. speculariferus* were the only bird species with negative lambdas in both periods. In addition, the population growth rate from the entire study period (2015–2019) for these two species was also significantly smaller than population growth rate from 2015 to 2016. These may represent the most specialist species in terms of habitat requirements. The distributions of both species are restricted to mountain forested habitats which could make them more vulnerable to environmental disturbances (Betts et al. 2019). The consistent decline in the distribution of *S. angelae* is an alarming result given that this endangered species only occur in two isolated populations in Puerto Rico (Anadón-Irizarry et al. 2017).

Hurricane Maria caused extensive damage to the forest, which could explain the increase in

the occupancy of some species. For example, defoliation will increase prey (e.g., insects, frogs, and lizards) detectability and could explain the increase in occupancy of two predators, *M. nudipes* and *C. vieillot*. *Melanerpes portoricensis* may also have expanded its distribution after H. Maria by taking advantage of the increase in food and nesting resources as consequences of changes in forest structure. H. Maria tripled stem breaks and doubled tree mortality relative to other major storms (Wiley and Wunderle 1993), increasing availability of tree holes for nesting and increasing termites and other insects feeding on dead trees. Changes in vegetation structure, particularly the loss of canopy cover, may also explain the appearance of *Tyrannus caudifasciatus*, an open-area species, in the study area only after H. Maria. This shift in distribution has also been observed in gray kingbirds, *Tyrannus dominicensis*, which is rarely found in mature forests, but became common in forest gaps following a hurricane in Dominica (Wiley and Wunderle 1993).

## CONCLUSIONS

Hurricane and droughts are natural disturbances that influence the structure of communities. Nevertheless, there are still many uncertainties related to the magnitude and the interaction of these disturbances and their impacts on the abundance and distribution of fauna. The decline in bird occupancy during the drought and an increase in occupancy following H. Maria suggest that droughts can have a greater negative impact on birds than hurricanes. The rapid responses of birds suggest that they are good indicators of climate change, which may include drier conditions in the future. Even small changes in occupancy will likely reshape the fauna and flora communities because of the disproportional importance of bird and frogs in the Puerto Rican food web, as top predators, seed dispersers, and pollinators (Knutson et al. 2008). Climate models indicate a possible decline in hurricanes frequency (Msadek et al. 2016), but an increase in hurricane intensity (Masson-Delmotte et al. 2018). Models also predict an increase in droughts due to human-induced climate changes in many parts of the world (Khalyani et al. 2016, Bhardwaj et al. 2018). Future projections of precipitation

in the Caribbean vary greatly; however, all models agree with an overall reduction in rainfall and an increase in droughts for Puerto Rico (Khalyani et al. 2016, Bhardwaj et al. 2018). Given the climate model predictions and the variability in species-level responses, we urgently need to improve the way we monitor fauna around the world by establishing extensive, frequent, and long-term monitoring. Long-term monitoring can be especially useful for disentangling the effects and interactions of different weather events (e.g., droughts, hurricanes) on species population growth and their distributions. Furthermore, it is essential to have information across the distributions of the species to understand where to focus management action.

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## NOTES

<sup>1</sup><https://bit.ly/39IqNc2>

<sup>2</sup><https://www.drought.gov/drought/states/puerto-rico>

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