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Can artificial retreat sites help frogs recover after severe habitat devastation? Insights on the use of "coqui houses" after Hurricane Maria in Puerto Rico

[1,*]Patricia A. Burrowes, [1]Ábner D. Hernández-Figueroa, [1]Gustavo D. Acevedo,
[1]Junángel Alemán-Ríos, and [2]Ana V. Longo

[1]*Department of Biology, P.O. Box 23360, University of Puerto Rico, San Juan, Puerto Rico 00931* [2]*Department of Biology, P.O. Box 118525, University of Florida, Gainesville, Florida 32605 USA*

***Abstract.*—On September 2017, Hurricane Maria swept over Puerto Rico as a Category 4 storm. Severe canopy loss, augmentation of forest floor debris, and a significant increase in temperature and light reaching the understory were among the most evident changes at El Yunque National Forest, where a population of *Eleutherodactylus coqui* frogs has been monitored over the past 30 years. When sampling was re-established, the frogs could be heard calling, but it was very difficult to find them among the complexity of vegetation in the forest floor. We inferred that canopy disturbance had left frogs without optimal arboreal habitats for retreat, nocturnal perching, feeding, and reproductive activities, and wondered whether they would use artificial habitats placed in the forest understory. To test this, two types of artificial habitats (i.e., "coqui houses") were introduced in the forest understory, consisting of either open PVC pipes or single-entrance natural bamboo shoots. Surveys were conducted twice a month for 15 months in an experimental transect with coqui houses, and a control transect without them. Data were collected on the occupancy rate of the artificial sites, type of usage, time of day occupied, and the number of *E. coqui* observed. The effects of time since the hurricane, microhabitat temperature, type of coqui house, and seasonality on the occupancy rate were also evaluated. Results showed that coquis used bamboo houses mostly during daytime as retreat and nesting sites, whereas the PVC houses were used mostly at night as calling sites. Daytime occupancy of coqui houses showed a significant bell-shaped pattern over time since the hurricane. This may be explained by a steady increase in usage after severe forest damage, a peak during the stressful cool-dry season, and a decline afterwards as the forest began to recover. No differences were found in frog counts between experimental and control transects, probably because the coquis could also hide among the fallen vegetation, but either disparities in forest conditions or inappropriateness of the methods for estimating population numbers may have overshadowed this effect. Coquis used artificial houses more often during the most stressful environmental conditions, suggesting that these shelters may serve to enhance habitat quality for amphibians after extreme weather events.**

Keywords. Amphibians, conservation, *Eleutherodactylus*, extreme events, habitat augmentation, retreat sites

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Introduction

Trends of recent climate change (1961–2010) in the Caribbean region show evidence of an increase in the frequencies of warm days, warm nights, and extreme high temperatures with a corresponding decrease of their cooler equivalents (Stephenson et al. 2014). An increase in minimum temperatures is significant at regional (Peterson et al. 2002; Stephenson et al. 2014) and local scales, such as the Puerto Rican eastern highland forests (Burrowes et al. 2004). While precipitation patterns for the Caribbean are not as clear, some studies have shown a significant drying trend (Nurse and Sem 2001; Neelin et al. 2006). In addition, the frequency of extreme events, like hard rains and hurricanes, has increased significantly in the last decade, and the International Panel for Climate Change (IPCC) anticipates further increases in the future (Peterson et al. 2002; IPCC 2014, 2018; Oppenheimer et al. 2019). Due to factors intrinsic to the biology and physiology of amphibians, these patterns of climate change represent a threat to these animals. For example, many tropical ectotherms are thermoconformers, having

Correspondence. **pburrowesupr@gmail.com*

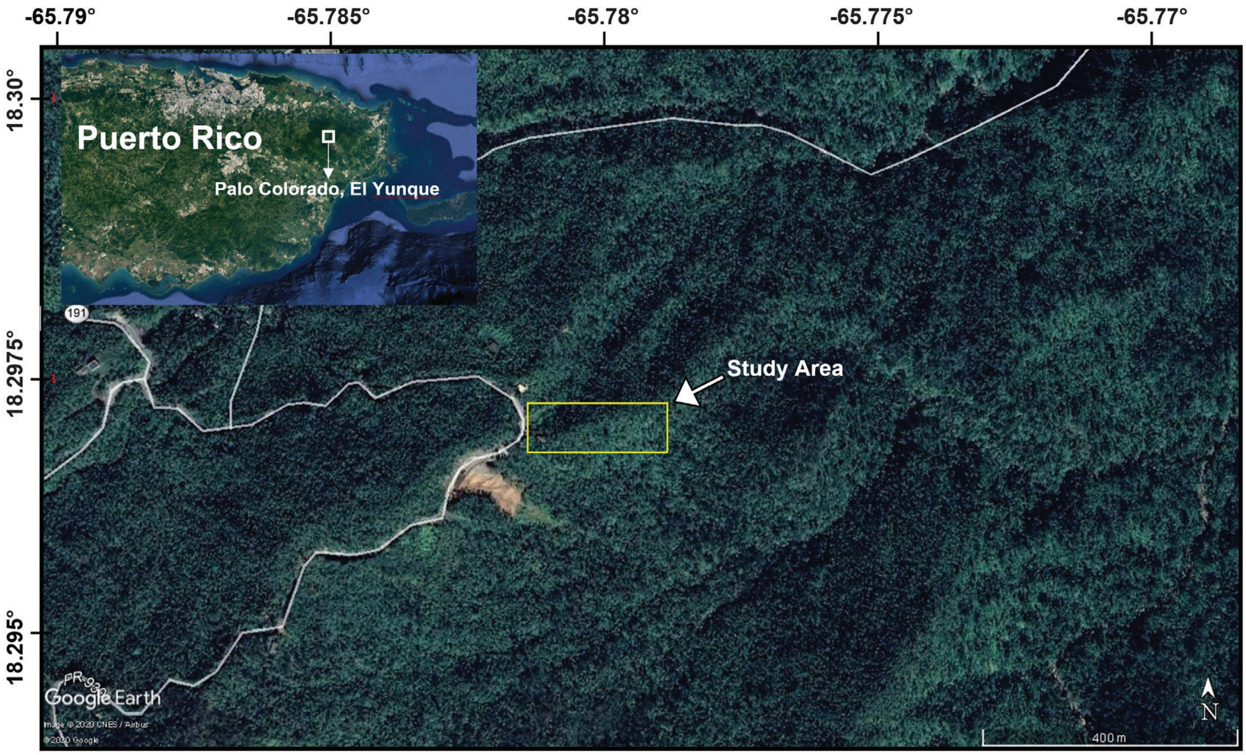

Fig. 1. Map showing the location of El Yunque National Forest in Puerto Rico, and the location of the study transects.

a reduced ability to thermoregulate compared to other vertebrates adapted to the climatic heterogeneity of higher latitudes (Navas 1996a,b; Huey et al. 2009). For the anurans in the genus *Eleutherodactylus*, which represent an important component of the endemic vertebrate fauna of the Caribbean (Hedges 1999; Duellman 1999; Joglar 2005), this may pose an additional challenge because amphibians lack epidermal protection that can reduce evapotranspiration rates during hot days. Thus, global climate change patterns for the Caribbean pose a risk for the *Eleutherodactylus* of Puerto Rico (locally known as "coquis"), which are already dealing with other threats such as the pathogenic chytrid fungus (*Batrachochytrium dendrobatidis* Longcore, Pessier and Nichols, 1999) that causes chytridiomycosis (Burrowes et al. 2004, 2008a,b, 2017; Longo and Burrowes 2010; Longo et al. 2013).

Extreme atmospheric events, such as strong hurricanes, can affect coqui populations by changing local temperature regimes and habitat structure. A study on the effect of Hurricane Hugo (Category 3 in 1998) on a population of *Eleutherodactylus coqui* at the Luquillo Experimental Forest (LEF) of Puerto Rico, revealed an increase in adults, albeit at a smaller body size, and a decrease in juveniles (Woolbright 1991, 1996). The proliferation of adults was attributed to a greater availability of retreat sites among the fallen debris and a decrease in invertebrate predators, while the reduction of juveniles was explained by a decrease in reproductive activity due to changes in microclimate (Woolbright 1991). Another study experimentally evaluated the effect of two consequences of hurricanes, canopy disturbance and increased deposition of debris in the forest floor, on a population of coquis in the LEF in Puerto Rico (Klawinski et al. 2014). In contrast to the results of Woolbright (1991), this study found that while canopy disturbances were detrimental to *E. coqui* abundance in experimental plots, an increase in forest debris had no effect (Klawinski et al. 2014).

In September 2017, Hurricane Maria hit Puerto Rico as a strong Category 4 storm with maximum sustained winds of 155 mph (~250 km/hr). High energy winds spread at 280 km/hr over the island along with heavy rainfall resulting in catastrophic flooding in many areas (NOAA 2017). As a consequence, critical damage to the island's infrastructure occurred and Puerto Rico was declared a disaster area by the Federal Emergency Management Agency (FEMA). Natural ecosystems were also severely affected. At El Yunque National Forest in the eastern highlands of the island (Fig. 1), most large trees were defoliated and lost medium to large branches, while others were snapped or uprooted by Hurricane Maria's strong winds. A large amount of vegetative debris accumulated on the forest floor causing an increase in structural complexity at that level. These changes and other complex consequences of hurricanes to ecosystems were discussed by Lugo (2008). Considering the negative effects of Hurricane Hugo on *E. coqui* populations (Woolbright 1991; Klawinsky et al. 2014), and with the knowledge that Hurricane Maria had been much stronger, we were concerned about the response of the population of coqui frogs that we have been monitoring for over 30 years at higher elevations in El Yunque National forest (Burrowes et al. 2004; Longo and Burrowes 2010).

We obtained permission from the U.S. Forest Service to evaluate our working area at El Yunque in December 2017, but due to security measures, we were not allowed to conduct nocturnal work in the forest until March 2018. At that time, finding our transects and clearing a path through forest debris to re-establish amphibian monitoring was arduous work. Initial surveys of the coqui population revealed that male frogs were still calling, but adults were difficult to observe because they were not active in their typical understory nocturnal sites, and juveniles, common in pre-hurricane surveys, were undetected. This was probably due to the absence of arboreal vegetation such as bromeliads and palm-frond axils which fell with the hurricane winds, as well as the loss of moss-covered tree trunks and branches that were concealed by leaves overhanging from the canopy before the hurricane, providing ideal hiding places for active frogs. Thus, the objective of this study was to provide artificial habitat in the form of "coqui houses" in the forest understory and quantify how much the frogs would use them for their regular activities, as well as the factors that may be associated with their usage. The data obtained could also serve to evaluate the potential of this strategy as a mitigation tool in the face of severe forest devastation.

The placement of artificial habitats has been used to increase reproductive activity and success of other vertebrate species of conservation concern. For example, Grubb and Bronson (1995) used artificial nesting sites made of PVC tubes to increase reproductive activity and success of Passeriformes birds (chickadees) in Ohio, USA. They found that when using artificial nesting sites, the survival of juveniles of one species of chickadees increased to 100%, and that birds used artificial nesting sites even in areas where natural nesting sites were abundant (Grubb and Bronson 1995). In Baja California, ospreys were observed using artificial nesting sites within a development area, resulting in an increase in reproductive activity and population size (Ortega-Rubio 1995). For the European Storm Petrels, for which the abundance of nesting sites is considered a limiting factor, the placement of artificial nesting sites proved to be effective at increasing population growth and density (De León and Mínguez 2003). Among amphibians, a study in Australia showed that water dams in farmlands supported a similar number of species as natural ponds, and highlighted the role of well-designed artificial habitats in frog conservation (Hazell et al. 2004). In Puerto Rico, Stewart and Pough (1983) placed artificial nest houses constructed from bamboo shoots in selected plots at "El Verde" in the LEF (350 m asl), and studied their effect on a population of *Eleutherodactylus coqui*. The authors found that the bamboo houses were often used as retreat and nesting sites, and resulted in significant increases in reproductive activity and population numbers. They concluded that retreat sites were a limiting factor for *E. coqui* population abundance (Stewart and Pough 1983).

Based on the positive results obtained by Stewart and Pough (1983), we expected that coqui frogs confronting the habitat devastation caused by Hurricane Maria would use artificial habitats placed on trees in the forest understory as retreat, calling, perching, mating, and nesting sites. If so, we hypothesized a consequent increase in nocturnal frogs counts in experimental versus control transects because the coqui houses would encourage reproductive activity. The factors that influenced occupancy rate and the type of uses given to different types of artificial coqui houses were also investigated in an attempt to determine their potential effectiveness for mitigating the effects of habitat loss. Understanding the patterns of species responses to dramatic changes in habitat is important in order to develop effective conservation practices (Gascon 1993). The results of this work may guide future management strategies to help the recuperation of amphibians and/or other species after severe forest damage due to extreme climatic events.

Materials and Methods

Study Area

This work was conducted at El Yunque National Forest at 661 m asl in the Luquillo mountains of Puerto Rico. The study transects were located within the Palo Colorado Forest formation (18°18'5.8"N, 65°47'7.4"W; Fig. 1), characterized by the tree with the same name, *Cyrilla racemiflora,* as well as the Sierra Palm, *Prestoea montana* (Ewel and Whitmore 1973; Harris et al. 2012). Other species, such as *Micropholis garcinifolia* (Caimitillo Verde), *Calycogonium squamulosum* (Jusillo), and *Croton poecilanthus* (Sabinón), are also common trees in the Palo Colorado Forest, and epiphytic bromeliads in the genus *Guzmania*, which are an important habitat for *Eleutherodactylus* frogs (Joglar 1998), are abundant (Stephenson et al. 1999; Harris et al. 2012). The average minimum temperature (nocturnal) and daily precipitation at the Palo Colorado Forest are 21.5 °C and 9.9 mm, respectively, but vary with the marked seasonality of Puerto Rico—being cooler and drier from January to April and warmer and wetter from May to December (Longo et al. 2010). Three species of *Eleutherodctylus, E. coqui*, *E. hedricki,* and *E. portoricensis,* can be found within the transect in the Palo Colorado forest. Following Hurricane Maria in 2017, the transect sites within this forest exhibited considerable canopy cover change. Table 1 shows an attempt to broadly categorize the stages of forest damage and chronological recuperation based on field notes and photographs (Fig. 2). The initial damage level was approximately 90–99% devastation, with a large proportion of that being vegetation accumulated in the forest floor, which then progressed to a considerable recuperation of up to 50% of the canopy cover by the end of 2019**.** The chronology presented in Table 1 may seem rather rapid, but research has shown that forest recovery after hurricane damage is faster in the tropics than in temper-

Fig. 2. Change in forest structure in the Palo Colorado forest transect (El Yunque) due to Hurricane Maria and corresponding damage/recovery stages according to Table 1. **(A)** Before the hurricane. **(B)** Same site after the hurricane, stage 1. **(C)** Moderate recuperation, stage 3. **(D–E)** Canopy dominated by Sierra Palm fronds showing signs of further recuperation of original understory vegetation, stage 4.

ate zones (Canham et al. 2010). In Puerto Rico, forests tend to recover basic structure within 10 to 20 years after hurricane blowdowns (Walker 1991; Lugo and Helmer 2004), and may achieve a tree size and density similar to those of primary forests after 40 years of recovery (Aide et al. 1996).

Study Species

The biology and ecology of *E. coqui* (Fig. 3) was extensively reviewed by Joglar (1998); thus, only some details that are pertinent to this study will be highlighted here. The species is native to Puerto Rico where it is widely

Table 1. Stages of forest changes describing the timeline of hurricane damage and gradual recovery. These stages are based on personal observations and field notes during daytime monitoring of coqui-houses at the Palo Colorado Forest (661 m) in El Yunque, Puerto Rico.

Stages of hurricane damage (1 = greatest)	Forest description	Approximate time-frame
1	90–99% of the forest canopy gone; remaining standing trees 90–95% defoliated; vegetation fallen from the canopy accumulated in the floor	Hurricane Maria, Sep 2017–Sep 2018
2	85–90% of the forest canopy gone; palm trees grow back their fronds; canopy vegetation decomposing and understory vegetation growth dominated by herbaceous vegetation and opportunistic fast-growing plants that tolerate sunlight; recuperation of standing trees very limited	Oct 2018–Jan 2019
3	70–85% of forest canopy gone; standing trees growing leaves on branches, and native understory vegetation becomes apparent with new saplings restricting light and limiting the growth of herbs and opportunistic plants	Feb 2019–May 2019
4	50–70% of forest canopy gone; standing trees recuperating leaves to about 70%, and native understory vegetation growing with new saplings at about 5 m high; forest understory clear of herbs and other light-loving plants; canopy dominated by sierra palm fronds	Jun 2019–Dec 2019

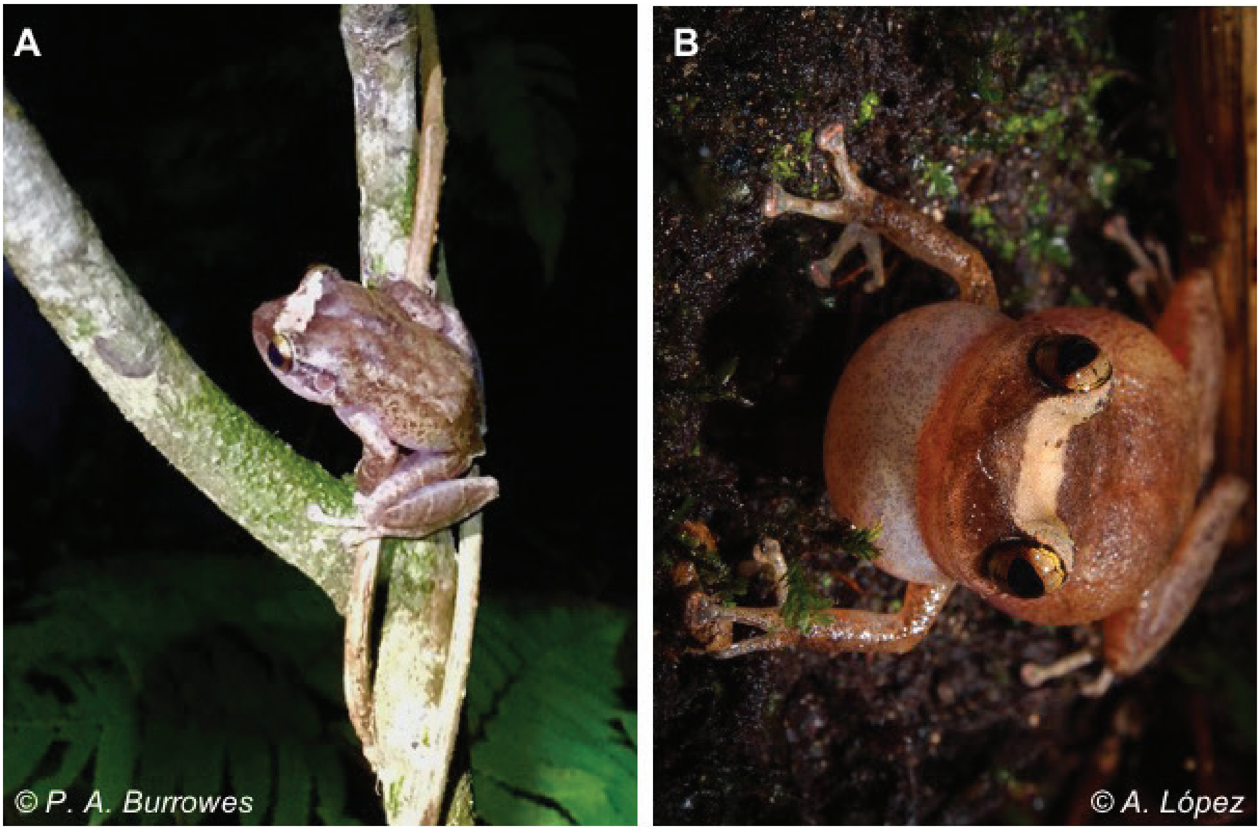

Fig. 3. *Eleutherodactylus coqui* perching on natural habitat. **(A)** Female on branch. **(B)** Male on tree trunk.

distributed from urbanized to pristine areas, and from sea level to highland wet forests (0–1,189 m asl). It is an important nocturnal predator which consumes a variety of prey, predominantly arthropods (Woolbright 1991). The size of *E. coqui* varies considerably with the elevation, with individuals from higher elevations being the largest (Narins and Smith 1986). At the study site (661 m asl), the mean size of adult females measured as the snout-to-vent length (SVL) is 46.4 mm and that of adult males is 36.4 mm (Joglar 1998). Similar to other *Eleutherodactylus* species in Puerto Rico, *E. coqui* females are larger, presumably due to the cost of producing clutches of heavily-yolked, direct-developing eggs (Townsend and Stewart 1986; Woolbright and Stewart 1987). The common coqui uses various substrates as daytime retreats, including leaf litter, rock cavities, palm axils, and bromeliads. As nesting sites, they may use arboreal bromeliad axils, cracks within the bark of tree trunks, curled palms fronds, or large *Cecropia* leaves. It is common to observe males calling at night from vegetation 1–3 m above the ground. Reproductive activity is present all year around, but it is more frequent during the warm-wet season (Woolbright and Stewart 1987; Joglar 1998). During mating encounters, males call to attract females to a protected nesting site where amplexus takes place. Mating behavior usually lasts between 8.5–12 hours, and in contrast to most anurans, eggs are fertilized internally (Townsend et al. 1981). Males offer parental care to the clutch, which can last from 16 days in the higher temperatures typical of lowlands, or up to 27 days in cooler, highland temperatures (Townsend and Stewart 1986).

Field Work

For this study, two 50 m x 3 m transects were sampled, an experimental transect where coqui houses were placed, and a control left unmanaged, approximately every two weeks for 15 months from August 2018 to October 2019. These transects are located only 100 m apart at the study site and have been monitored over many years to estimate population fluctuations and study the responses of coqui frogs to chytridiomycosis (Burrowes et al. 2004, 2017; Longo et al. 2010; Longo and Burrowes 2010). Visual encounter surveys were used to count the number of adult frogs active from the middle of the transects to a distance of 1.5 m at each side of the forest (Heyer et al. 2014) while also monitoring coqui houses for occupancy. Both transects were sampled simultaneously starting shortly after dusk (1830–1900 h) for approximately 2.5 hours by two or three trained people. This time range was chosen because it is the peak time of activity for *E. coqui* (Drewry 1970; Woolbright 1985). If a frog was found in one of the coqui houses, its behavior was recorded to infer the particular uses made of the artificial habitats, such as for retreat, calling, mating, or nesting and parental care. To determine potential differences in occupancy of coqui houses during daytime versus nighttime, coqui houses were checked twice, first at approxi-

Fig. 4. Artificial coqui houses built with **(A)** bamboo shoots and **(B)** PVC tubes.

mately 1600 h and then at night during the regular survey as described above. Juvenile frogs (SVL 5–18 mm) were not considered for this study because debris and invasive plant vegetation heavily covered the forest floor and the lower vegetation where young coquis are active at night (Burrowes et al. 2017). Thus, it was impossible to say with certainty whether juveniles truly decreased, or if their absence was an artifact of the difficulty in sampling.

Two different kinds of "coqui houses" (Fig. 4) were used: (A) bamboo houses made of natural bamboo cylinders cut at a node to provide a floor and a small opening carved into the lower part of the cylinder as a single entrance point (Stewart and Pough 1983); and (B) open-ended, hollow, white PVC pipes. The length of the cylinders for both kinds of houses was 6.4 cm, and the diameter did not exceed 4 cm. The top of the bamboo houses was closed with strong duct tape such that frogs could not get in or out, but they could be easily checked for occupancy by peeling the tape back (Fig. 4). In the experimental transect, a total of 22 bamboo houses and 22 PVC houses were deployed. One of each type was placed every 5 m in the understory, tied to trees or branches 1.5–2.0 m above ground in the forest understory (Fig. 4). Similar types of coqui houses are used to trap invasive *E. coqui* in Hawaii (Control of Coqui Frogs in Hawaii 2008; Pitt et al. 2012).

In order to document the changes in temperature associated with forest cover loss after Hurricane Maria and the structural damage caused to the forest canopy, HOBO® data-loggers were used to monitor ambient air temperature in the understory of the transects during the 15 months of this study. Because microhabitat temperatures are routinely monitored with dataloggers for other studies in these transects, one datalogger was deployed during the hurricane that allowed us to track the temperature changes during the storm itself (Fig. 5A).

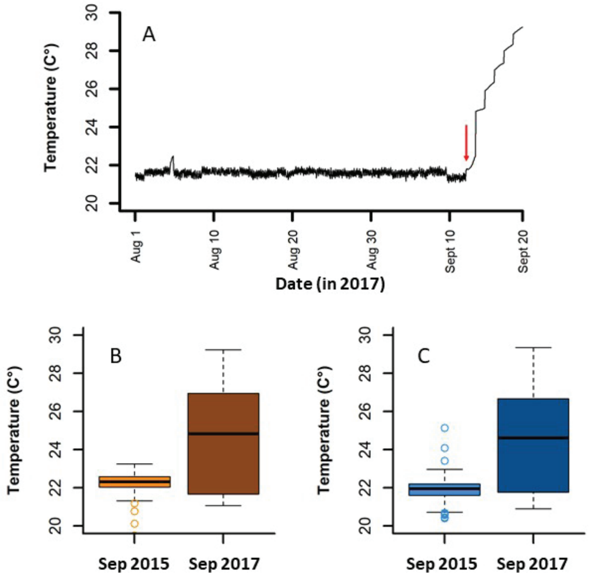

Fig. 5. Drastic changes in temperature at the transects in the Palo Colorado forest of El Yunque as a consequence of Hurricane Maria. **(A)** Ambient temperatures registered by HOBO data logger in the forest understory before, during, and shortly after Hurricane Maria. **(B–C)** Box plots showing variation in forest microhabitat temperature by day and at night during the month of September in 2015 (a non-hurricane year), and in 2017, the year that Hurricane Maria hit Puerto Rico.

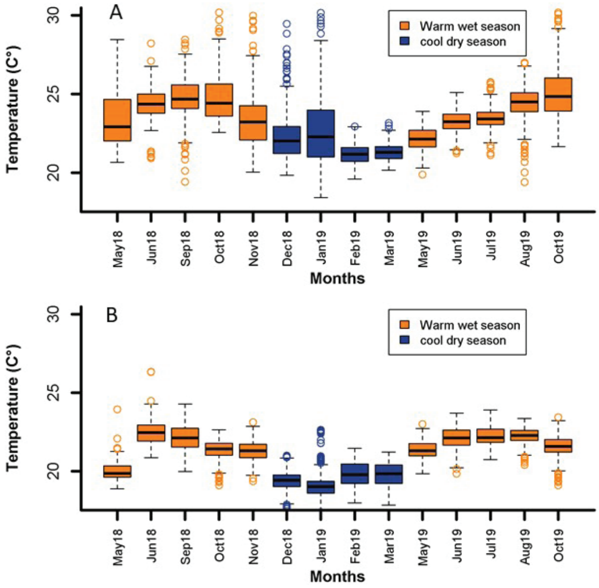

Fig. 6. Variation in operative temperatures measured by frog agar models in typical forest microhabitats after Hurricane Maria, showing a significant decrease during the cool-dry season (in blue) during midday **(A)**, and nighttime **(B)**.

The HOBO® data-loggers were also used in the bamboo coqui houses to record microhabitat temperature in the forest understory during the duration of this study. The thermal coupler was inserted into agar models designed to mimic coqui frogs (Rowley and Alford 2010; Burrowes et al. 2020) such that the microhabitat temperatures would reveal the operative temperatures that frogs would encounter at these sites (i.e., equilibrium body temperatures that the animal experiences in its habitat (Bakken and Gates 1975)). Temperature readings taken in the same manner in this transect during the year 2015 allowed the assessment of changes in the specific months before and after Hurricane Maria.

Analyses

Bar graphs are used to illustrate the frequency of usage of coqui houses by type and time of day through the sampling surveys or time since the hurricane, and boxplots are used to illustrate changes in temperature patterns. A Generalized Mixed Linear Model (GLM) was applied to evaluate factors that best predicted occupancy rates of the artificial habitats. In the model, date of sampling and coqui house number were considered random effects, and time (days) since Hurricane Maria, microhabitat temperature (mean of five days: four days immediately before and sampling day), and the type of coqui house (PVC versus bamboo) as fixed effects. Mann-Whiney or *t*-tests were conducted to test for differences in temperature in forest habitat that may be attributed to post hurricane damage, and ANOVA was used to determine whether mean frog counts were associated with transects where coqui houses were placed and whether differences in mean microhabitat temperatures were associated with seasons. Chi-square was used to test for independence on the type of coqui house used by day versus night, as well as particular behaviors. Finally, a quadratic regression model was fitted to evaluate the predictive effect of time since the hurricane on the daytime usage of coqui houses. Statistical analyses were performed with Minitab Release 1.5.3 (https://www.minitab.com/) and R statistical package (http://www.R-project.org/).

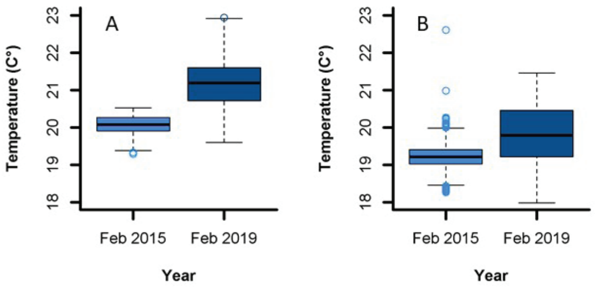

Fig. 7. Box plots showing variation in forest microhabitat temperature by day **(A)** and night **(B)** during the cool-dry season (February) of 2015 (a non-hurricane year), and in 2019, 17 months after Hurricane Maria hit Puerto Rico.

Results

Temperature Changes in the Forest

As an immediate result of canopy cover loss due to Hurricane Maria, a drastic increase in the ambient temperature was registered by a data logger left in the forest until its battery was drained shortly after (Fig. 5A). In the microhabitats, a significant increase and high variability in temperature was found when comparing a non-hurricane year (September 2015) with that of September 2017, the year of Hurricane Maria (Fig. 5B–C). This pattern was evident both at mid-day when frogs are in retreat sites ($W = 46{,}697$, $P < 0.001$), and at night when they are active ($W = 310{,}949$, $P < 0.001$) (Fig. 5B–C). Temperature data taken during this study showed that after Hurricane Maria, frogs confronted operative temperatures spanning 22–28 °C during midday, and 18–24 °C at night in forest microhabitats (Fig. 6A–B). These temperatures are alarming because they were measured at retreat sites where frogs are protected from direct sunlight, and yet, are on average 2 °C higher than air temperatures registered in a previous study during 2005–2007 in the same forest transects (Longo et al. 2010). As expected, microhabitat temperatures post-Maria were significatively associated with seasonal changes, where higher temperatures corresponded to the warm-wet season and lower temperatures to the cool-dry season ($F = 79.47$, df = 13, $P < 0.001$; Fig. 6A–B). A comparison of the mean operative temperatures recorded in the same manner in February 2015 during the cool-dry season of a non-hurricane year, with those of February 2019 (17 months after Hurricane Maria), showed a significant increase in the microhabitat temperature during the day ($\bar{x} = 1.08$, $T = -5.34$, df = 300, $P < 0.0001$) and at night ($\bar{x} = 0.56$, $T = -11.09$, df = 368, $P < 0.0001$) (Fig. 7A–B).

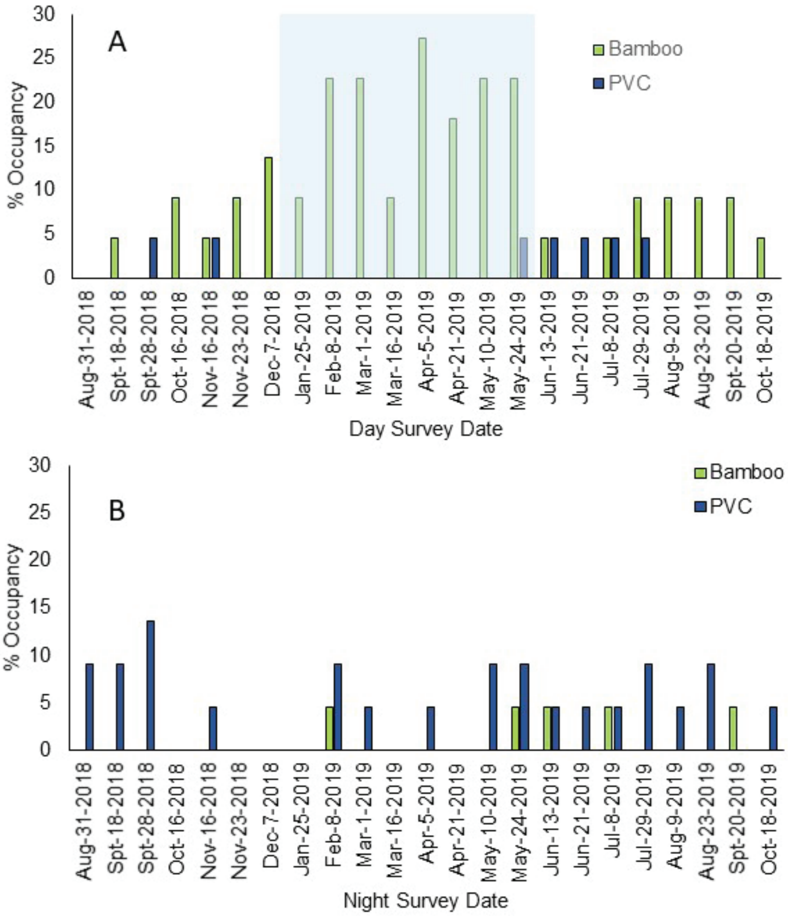

Fig. 8. Bar graphs showing coqui house occupancy rate by *Eleutherodactylus coqui* during the length of this study by daytime **(A)**, and by nighttime **(B)** surveys. The shaded area in **(A)** denotes sampling in months during the cool-dry season.

Coqui House Occupancy Rates

The results of a general mixed model revealed that (1) time since the hurricane as a proxy of forest recovery, (2) microhabitat temperature, (3) house type, and (4) the interaction between time since the hurricane and microhabitat temperature were all significant predictors of occupancy rate of artificial coqui houses by *E. coqui* (Table 2).

Over the study period frogs that used these artificial habitats were found more often during the day with an occupancy rate up to 27.3% (mean 10.64, SD ± 4.23), and somewhat less during the night with a maximum occupancy of 13.6% (mean 4.94, SD ± 2.20) during any sampling event (Fig. 8). The time at which frogs occupied one of these artificial habitats was not independent of the type of coqui house ($X^2 = 104.05$, df = 1, $P < 0.001$). Bamboo houses were used mostly during the day, as retreat and nesting sites, while PVC houses were used mostly at night for perching and/or calling ($X^2 = 115.94$, df = 1, $P < 0.001$, Fig. 9).

The number of frogs occupying coqui houses during the day was found to be inversely related to the mean midday (1200–1600 h) temperature at the microhabitats ($Y = -0.68x + 18.35$, $P = 0.0185$ and $R^2 = 37.13$). Accordingly, frogs occupied bamboo coqui houses significantly more often in the cooler dry season (shaded box) than in the warmer wet months (*F* =

Table 2. Results of Generalized Mixed Linear Model (GLM) to determine the effects of several factors on occupancy of the artificial coqui houses. The number of asterisks (*) indicates the level of statistical significance (α = 0.05).

Fixed effects	Estimate	Standard error	*Z* value	*P* (>|*z*|)	
Intercept	-38.21	6.549	-5.835	0.000	***
Time (days since hurricane)	0.068	0.0097	6.937	0.000	***
Temperature	1.525	0.277	5.496	0.000	***
House type PVC	-1.323	0.519	-2.546	0.011	*
Time: temperature interaction	-0.003	0.0004	-7.221	0.000	***

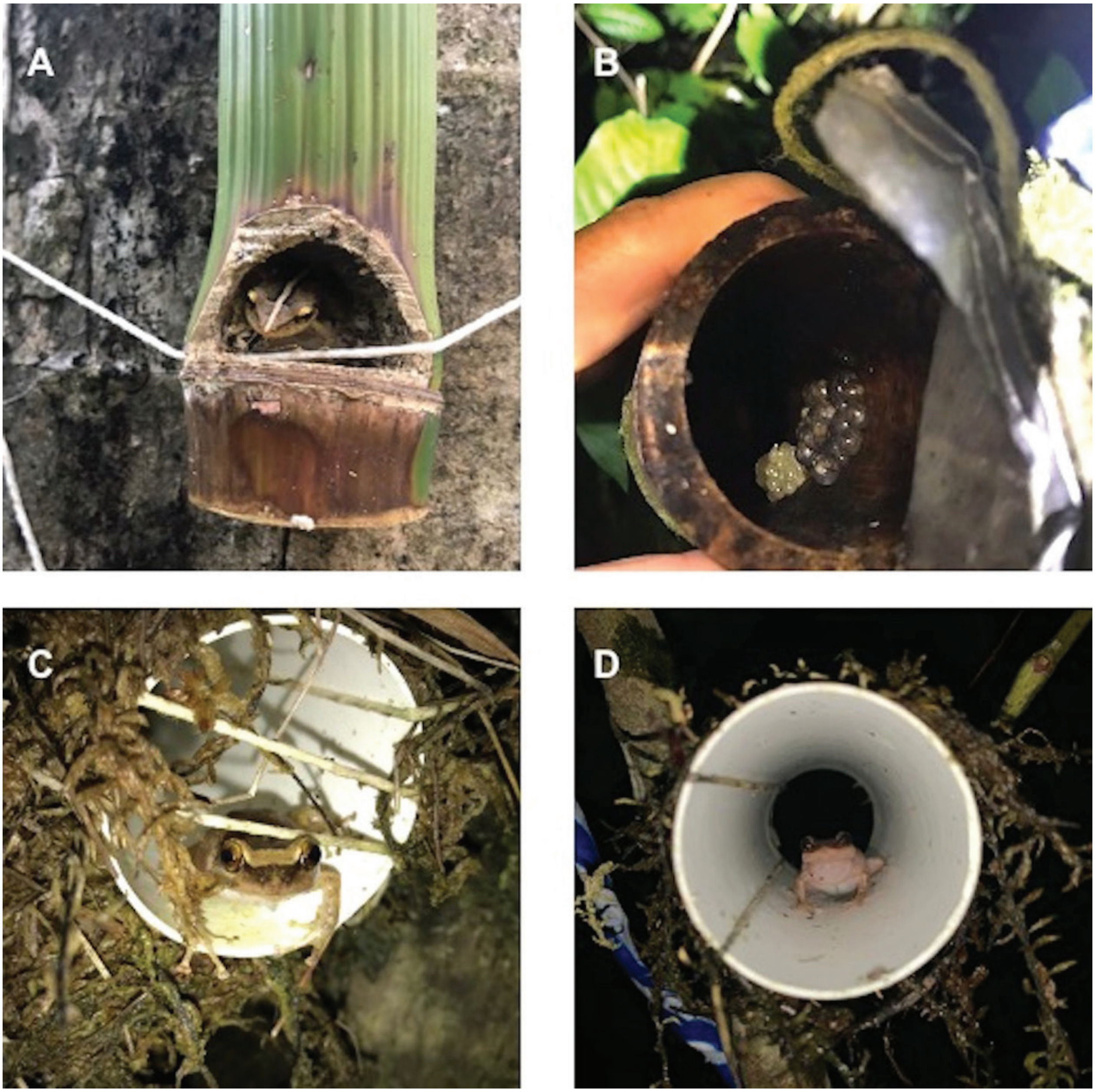

Fig. 9. Different uses ascribed to the two types of artificial habitats (=coqui houses) placed in the forest. **(A)** Coqui frog using bamboo house as retreat site during the day. **(B)** Bamboo house used as nesting site with a double clutch. Note that eggs are observed but the guarding male jumped away as the photo was taken. **(C)** PVC house used by a coqui as a nocturnal perching site. **(D)** PVC house used by a coqui as a calling site during the night.

5.90, df = 13, $P = 0.0258$, Fig. 8A). The frequency of daytime usage (i.e., occupancy rate) of coqui houses through time since the hurricane, which serves as a proxy of forest recovery (Table 1), fits a bell-shaped curve that was explained by a quadratic model ($y = -0.0004x^2 + 0.426x - 102.24$, $P = 0.0026$ and $R^2 = 0.40$, Fig. 8A). No pattern in the nocturnal usage could be associated with time after the hurricane; nonetheless, the coqui houses (especially PVC) were used consistently throughout the study (Fig. 8B). On four occasions, bamboo houses were used for nesting/parental care, and during this period the males stayed inside day-and-night for approximately 27 days until the eggs hatched and the juveniles dispersed (Fig. 9).

Contrary to what we expected, the mean number of adult frogs observed per survey night was slightly greater in the control transect (18.43 ± 5.98) than in the experimental transect (17.93 ± 5.54; Paired $T = -0.313$, $P = 0.7599$; Fig. 9). The higher variance associated with the abundance of frogs in the control transect may reflect greater habitat heterogeneity in this part of the forest (Fig. 10).

Discussion

Hurricanes have many effects on forest ecosystems, ranging from the physical damage to the forest and its functional consequences to biodiversity and ecosystem

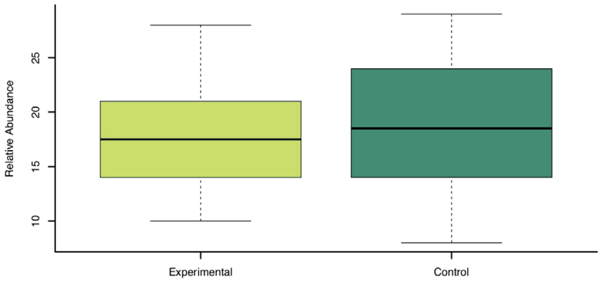

Fig. 10. Comparison of the relative abundance, measured as the number of adult *Eleutherodactylus coqui* observed per sampling night in the experimental transect where artificial coqui houses were made available, versus the control.

processes, to the opportunity for evolutionary change (Lugo 2008). Herein the thermal and structural changes that Hurricane Maria caused to a highland forest in Puerto Rico are documented, and results are presented on the responses of coqui frogs to the placement of artificial coqui houses on trees in the forest understory from which their traditional habitat had been displaced.

The drastic effect of Hurricane Maria's blowdown over the study site at El Yunque was evidenced by a 6 °C increase in ambient temperature in September 2017, right after it passed over Puerto Rico (Fig. 5A). A comparison of microhabitat temperatures in the months of September 2015, 17 years since the previous hurricane (Georges in 1998) and September 2017, show a significant increase in temperature attributable to the loss of forest canopy caused by Hurricane Maria (Fig. 5B–C). A similar comparison of microhabitat temperatures in the months of February in 2015 and 2019 (Fig. 7A–B), revealed that 17 months after the hurricane, when the forest is considered to be on recovery stage 3 (Table 1), frogs in the understory still confronted operational body temperatures approximately 1.0 °C higher than in non-hurricane years. The observed increase in temperatures by day and night associated with the loss of canopy are expected to bring about an increase in wind speed and a corresponding decrease in relative humidity within the forest (Tanner et al. 1991; Lugo 2008). These thermal changes may exacerbate the already stressful environmental conditions for coqui frogs as their operative body temperatures rise and the risk of dehydration from evaporative water loss increases. The fine interaction between local temperature and its impact on the frog's ability to maintain moisture is a key to amphibian homeostasis (Navas 1996a,b) and may result in unpredictable outcomes (Burrowes et al. 2020). In fact, temperature was a significant predictor of coqui house occupancy (Table 2), and the data revealed that frogs occupied artificial habitats significantly more often during the cool-dry season (Fig. 7A, shaded box). Low temperatures and drought are unfavorable conditions for tropical frogs, especially terrestrial direct-developers that depend on ambient moisture for rehydration (Duellman and Trueb 1994; Navas 1996b). Studies in Puerto Rico have shown that both nocturnal activity and reproduction of *E. coqui* decrease during the dry season (reviewed by Joglar 1998) and that dry periods negatively affect their response to pathogens such as the chytrid fungus (Longo et al. 2010). Thus, we infer that the use of artificial retreats, such as the bamboo houses provided in this study, may have contributed to mitigating the effects of the hurricane.

Bamboo houses by day had a higher occupancy rate (Fig. 8), suggesting that the need for arboreal understory habitat that would serve as daytime retreat and nesting site was of higher demand than the nocturnal perching sites for which the PVC houses were used (Fig. 9). Thus, the results show that although coquis can survive hurricane devastation by hiding in the complexity of fallen vegetation (Woolbright 1991), they will use arboreal habitat if available. The preference for the more enclosed and protected bamboo houses during the daytime (when temperatures are higher, and the risk of dehydration is greater) is expected under the devastated canopy conditions caused by Hurricane Maria. Although PVC houses were used less often (Table 2), they were used at night throughout this study, often at an occupancy rate of 10% (Fig. 8B), suggesting that these open cylinders provided a sheltered perching site that may also benefit coqui males by, for example, amplifying calling sound at a time when other natural microhabitats were unavailable (Fig. 9).

Time since the hurricane, which is a proxy of forest recuperation, was also a predictor of the occupancy rate of coqui houses (Table 2), resulting in a significant bell-shaped response in daytime usage (see Fig. 8A). A rapid increase in usage at the beginning of the study, despite a potential learning curve to discover the "new habitats," highlights the role of coqui houses in providing arboreal retreats and nesting sites soon after hurricane damage (recovery stages 1–2, Table 1). However, the peak in frequency of usage occurs later, in the midst of the cool-dry season when environmental conditions are most stressful to the frogs (Fig. 8A, shaded box). The gradual decrease in usage by the end of the study may be related to forest structure recovery since the hurricane. This pattern is confirmed by the significant interaction of temperature and time since the hurricane as predictors of the occupancy rate of artificial coqui houses (Table 2). With field notes and photographs, a chronological succession of the forest was documented, from over 90% canopy depletion to the recovery of foliage in standing trees to over 70%, and then to the replacement of invasive understory vegetation by native saplings that contribute more structure and shade by the end of 2019 (Table 1, Fig. 2). As the forest recuperates from the initial severe damage, restored natural habitat in standing trees is expected to serve as appropriate calling, perching, retreat, and nesting sites, and thus, the frogs would have a lesser need to occupy artificial habitats.

The rate of usage of bamboo houses by coqui frogs after Hurricane Maria (13–27%) was similar to that found in other studies that were successful in using artificial nesting sites as conservation methods. For example, Grubb and Bronson (1995) obtained 25% usage with the Carolina Chickadee birds in Ohio, USA; and in Benidorm, Spain, the European Storm Petrels used 29% of the artificial nesting sites (De León and Mínguez 2003). However, in Puerto Rico, a previous study showed that coqui frogs used up to 46% of the bamboo houses placed to enhance habitat in the lowland forests (Stewart and Pough 1983). With that amount of usage in undamaged forest (Stewart and Pough 1983), we expected to see a greater effect of artificial houses on the abundance of coquis in the experimental transect versus the control after Hurricane Maria. However, this was not the case (Fig. 10) probably because retreat sites are not a limiting factor for coquis after hurricane disturbances (Woolbright 1991). The increase of vegetative debris on the forest floor may have provided hiding places that were good alternatives to arboreal sites, allowing the frogs to cope with the other stressful conditions that the lack of canopy imposed. Other methodological caveats of this study may have contributed to the inability to show an effect of coqui houses on the number of frogs active at night. Since quantitative methods were not used to accurately compare the degree of canopy devastation between transects immediately after the hurricane, it is possible that the control transect had better conditions for the coquis in terms of perching, retreat, and reproduction sites than the experimental transect. It is also plausible that the number of coqui houses provided in this study was too few; while 44 coqui houses were set in 150 m^2, Stewart and Pough (1983) placed 100 of them in 100 m^2 plots. A greater number of artificial habitats may be needed, perhaps as a threshold, before a positive impact on population numbers can be observed. Finally, visual encounter surveys may not be the best way to count frogs after hurricane devastation of the habitat, particularly for a generalist species like *E. coqui,* because adults and especially juveniles can hide amongst the fallen debris where they would remain undetected.

Conclusions and Perspectives

This project aimed to determine whether a tropical forest frog population affected by an environmental catastrophe, such as a category 4–5 hurricane, would use artificial habitats set to augment arboreal forest structure. The findings reveal an increase in the forest temperature as a consequence of canopy blowdown, provide a description of the initial damage and early recovery stages of the forest (Table 1, Fig. 2), and highlight the importance of time since the hurricane, local climate, and the type of habitat on the frequency of usage of artificial habitats by coqui frogs. Although the data did not confirm that this kind of management intervention would result in an increase in the number of frogs, they did show that artificial habitats were used, and that occupancy rate increased significantly during the most stressful environmental conditions, i.e., early after the hurricane and during the cool and dry season (Fig. 7A), which highlights their potential as a mitigation strategy after extreme events. Unfortunately, we missed the opportunity to study the immediate effects of Hurricane Maria on coqui frog populations because safety reasons prevented us from sampling in our transects for several months. Thus, whenever safe and feasible, we recommend beginning studies on the impact of environmental disasters as soon as possible in order to record the full range of their consequences and the responses of the organisms in question.

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Patricia A. Burrowes is a Professor in the Department of Biology at The University of Puerto Rico in San Juan. She received her Ph.D. at the University of Kansas under the mentorship of W.E. Duellman, and her early-career research interests included community ecology, reproductive behavior, and population genetics of tropical amphibians. Given the precipitous decline of amphibian populations worldwide, Patricia has been dedicating her efforts to the study of the factors involved in this crisis, particularly the ecology of chytridiomycosis under enzootic conditions and the responses of tropical amphibians to climate warming.

Ábner D. Hernández-Figueroa (left) is a recent graduate from the Environmental Sciences program at the University of Puerto Rico in San Juan. Abner's interests and research experiences as an undergraduate focused on the conservation and ecological restoration of amphibians and coral reefs, which are being challenged by severe environmental changes as a consequence of global climate change.

Gustavo D. Acevedo-Vélez (right) recently obtained his B.S. in the Environmental Science program at the University of Puerto Rico in San Juan. His research interests include the behavioral and population ecology of amphibians and aquatic invertebrates. Currently Gustavo is a field technician for a stream flow reduction study on community composition and dynamics at the Luquillo LTER (Long-Term Ecological Research) site.

Junángel Alemán-Ríos (middle) is an undergraduate student at the University of Puerto Rico in San Juan, where he is currently completing a double major in Biology and Environmental Sciences. His research interests include the behavioral ecology of amphibians and wildlife diseases, and Junangel expects to continue his studies in veterinary medicine.

Ana V. Longo is an Assistant Professor in the Department of Biology at the University of Florida in Gainesville, Florida, USA. At every step of her academic career (from Master's degree to Postdoc), Ana has had the unique opportunity to be mentored and supported by three outstanding women herpetologists: Patricia Burrowes, Kelly Zamudio, and Karen Lips. Ana's research program aims to identify and quantify the ecological factors and evolutionary processes that allow amphibians to interact with their pathogens, parasites, and symbionts. She actively seeks to broaden the participation of underrepresented minorities in the fields of ecology and evolution through collaborations, student mentoring, and training.