The Response of *Eleutherodactylus* Populations, Crops, and Vegetation to Hurricane María in Coffee Agroecosystems

By

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ABSTRACT

The response of agricultural systems to natural disasters remains largely unexamined, despite the importance of these systems for food production and human welfare. To address the lack of literature surrounding agricultural ecosystem change after hazard events, this study evaluated the response of vegetative factors and populations of three common vertebrate predators, all coquí frogs (*Eleutherodactylus antillensis, Eleutherodactylus brittoni,* and *Eleutherodactylus coqui),* to Hurricane María (September 16, 2017, to October 2, 2017) in Puerto Rican coffee agroecosystems within the Cordillera Central region. We compared vegetative and coquí population data taken in May of 2017 before Hurricane María and again afterward in November of 2018. This comparison found that vegetative factors were highly negatively impacted by the natural disaster, whereas coquí populations remained stable. Our results suggest that *E. antillensis, E. brittoni, and E. coquí* may be resilient to hurricanes even while their agroecosystem habitats are dramatically altered.

INTRODUCTION

When the 2017 Hurricane María hit Puerto Rico, the grief of the global climate crisis was amplified to a horrifying degree. The hurricane took the lives of thousands of people, collapsed homes and infrastructure, and left a variety of tropical ecosystems shaken and uprooted (MURRAY, 2019; Smith & Rhiney, 2016; Spagat & van Weezel, 2020; Uriarte et al., 2019). As the climate crisis intensifies and hurricanes both become more frequent and more powerful, it is increasingly necessary to understand the full dynamics of anthropogenically-driven natural disasters (Collins & Walsh, 2017; Holland & Bruyère, 2014). By detailing the impacts of these catastrophes, potential adaptation and resilience strategies can be created, which will ultimately support both human and natural systems.

Ecosystems in the Caribbean are adapted to a certain amount of disturbance from hurricanes as they are common in the region (Gutiérrez del Arroyo & Silver, 2018). For example, by the mid 1980s it was estimated that Puerto Rico had been struck by hurricanes once every 22 years (Weaver, 1986). However, the increase in frequency and intensity of hurricanes due to anthropogenically-driven climate change has added a new level of challenge to ecosystem resilience (Collins & Walsh, 2017; Holland & Bruyère, 2014). This challenge is highly apparent in managed agroecosystems, where there is not only a need for conserving biodiversity and ecosystem function, but also the need for maintaining the productivity of the farm, and the wellbeing of farmers, and those dependent on their products (Rodríguez-Cruz et al., 2021).

Coffee in Puerto Rico has had a long history of economic importance, and remains one of the most important agricultural products grown on the island, especially in the Cordillera Central region (R. Borkhataria et al., 2012; Diaz & Hunsberger, 2018). Farmers often also plant citrus, plantain, and root crops in or alongside the coffee plants, increasing the production, diversity, and ecological importance of these farm system (Borkhataria et al., 2012; Perfecto et al., 2019).

Within coffee agroecosystems throughout the island, coquí frogs (*Eleutherodactylus spp.*) are abundant, and may act as a key invertebrate predator. Coquís are a group of nocturnal insectivorous frogs that are endemic to Puerto Rico (García-Rodríguez et al., 2010; Shiels et al., 2014). They are direct developing amphibians and are 2.5-5 cm in snout-vent length on average, with size varying between species (Beard, 2007). Though a single adult coquí only consumes 3-11 prey per night, in areas where coquí frogs reach high densities, they can collectively consume an average of 114,000 invertebrates during one forage period (Beard, 2007; Woolbright, 1996). Coquís are also culturally important in Puerto Rico and are the national symbol of the island (Balotta, 2011). The large amount of prey that coquí frogs consume, their major presence in coffee agroecosystems, and their cultural importance, makes these frogs key study organisms.

There are 17 species of coqui frogs in Puerto Rico, three of which are common in coffee farms (García-Rodríguez et al., 2010; Joglar et al., 2007). The Common coquí (*Eleutherodactylus coquí*), the Red-Eyed coquí (*Eleutherodactylus antillensis*) and the Grass coquí (*Eleutherodactylus brittoni*) all are present on the coffee farms of the Cordillera Central (Harmon, 2019; Monroe et al., 2017). Notably, the three species vary in both size and habitat preference. *E. coquí* is the largest and most sensitive to disturbance, and prefers pristine forested areas where they can take diurnal refuge up to 3 m from the ground (García-Rodríguez et al., 2010). *E. antillensis* is slightly smaller on average than *E. coqui* and is much less sensitive to disturbance, *E. antillensis* also prefers to be closer to the ground in its refugia (up to 1 m) (Barker et al., 2015). *E. brittoni* is the smallest of the three study species, and prefers wet, low refuges, as their common name, grass coquí, suggests.

Previous studies have examined the effects of simulated and historic hurricanes on coquí populations in natural ecosystems, but none have broadened this analysis to managed systems. When researchers in Luquillo Experimental Forest simulated a hurricane, it was found that the loss of canopy cover caused *E. coquí* populations to decrease, whereas, the addition of detritus from the simulated storm had no effect (Klawinski et al., 2014). The 1989 Hurricane Hugo also provided an opportunity to study the impact of hurricanes on coquís. A 1991 comparison of *E. coquí* populations, again in Luqillo Experimental Forest, before and after Hurricane Hugo showed that juvenile coquí initially decreased, but that the adult population stayed stable. However, a year after Hugo, the adult population density increased by four-times its pre-hurricane level, though adults were smaller on average than before the storm (Woolbright, 1991, 1996). A large review of longterm data taken in Luqillo Experimental Forest Data on the impacts of Hurricane Hugo on coquís were not taken in managed systems.

This study aims to fill the knowledge gap of hurricane impacts on managed systems and support climate science in agroecosystems by examining the influence of Hurricane María on vegetation and crop plants as well as the populations of these three species of coquí. By comparing data taken before the hurricane in 2017 with information collected after Hurricane María in 2018, this study aims to shed light on the potential impacts of the hurricane to these managed systems. On-the-ground vegetative survey techniques were employed to measure crop factors like stem counts, litter depth, herbaceous vegetation height, and more to determine how the hurricane impacted vegetation structure within Puerto Rican coffee farms. Bioacoustic monitoring was used to compare coquí populations before and after the catastrophe.

METHODS

2.1 - Study Sites

The study was conducted between June and September of 2017 and November and December in 2018 on 19 farms and 6 secondary forest sites in the Cordillera Central of Puerto Rico, including the municipalities of Utuado, Ciales, Jayuya, and Adjuntas (Figure 1.). The central mountains are the primary coffee-growing region on the island; the landscape is characterized by secondary forest, agriculture, and low-intensity development (Daly et al., 2003). Coffee farms in Puerto Rico are most often mixed polycultures with a combination of coffee (*Coffea* spp.) and one or more of the following crops: plantain/banana (Musa paradisiaca, vars.) (hereafter plantain), citrus species (*Citrus* spp.), and malanga and yautia (*Colocasia esculenta* and *Xanthosoma sagittifolium*) (herein root crops). Other crops commonly planted include papaya (*Carica papaya*), avocado (*Persea americana*), guava (*Psidium guajava*), pineapple (*Ananas comosus*), and pigeon peas (*Cajanus cajan*). Farm sites were chosen to represent a range of management styles and crop combinations. Elevation ranged from 272 m to 704 m asl at farm sites and from 371 m to 764 m asl in forest sites. Mean elevations were 536 m and 548 m asl respectively. Average farm size was roughly 3 ha with a minimum farm size of 0.36 ha and maximum size of 16.38 ha.

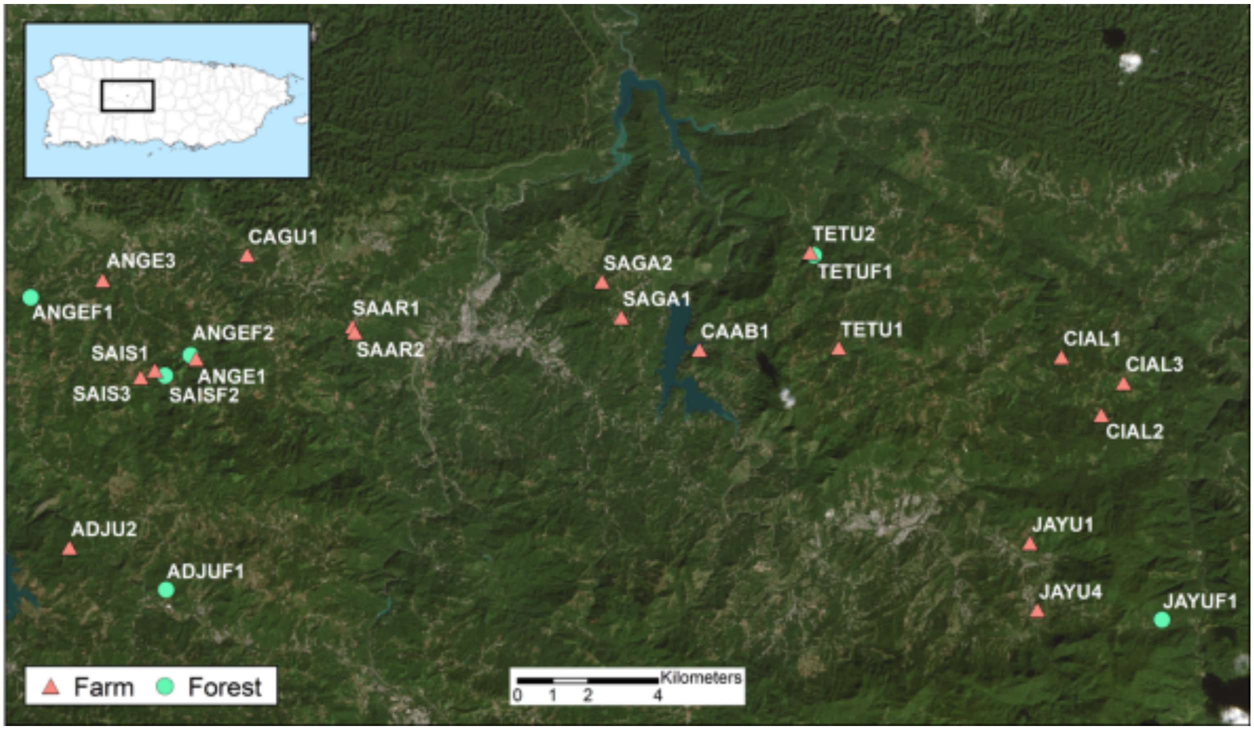

Figure 1. Study area in the Cordillera Central of Puerto Rico (inset). Recorder locations are marked with orange triangles at farm sites and green circles at forest sites. Sites were within the municipalities of Adjuntas, Ciales, Jayuya, and Utuado.

2.2 - Vegetation Surveys

Vegetation was surveyed at twenty 10 m-diameter points at each of the 29 farm sites. Survey points were constrained within farm boundaries and located up to 75 m from the center of sites. When possible, 10 of the points were selected from locations at which coquís had been observed while the remaining 10 points were generated randomly using ArcMap (ESRI, 2017) to sample farm vegetation at both random locations and points known to be used by coquís. All points were at least 10 m apart. Survey points were divided into quadrants using 5 m lengths of rope tied to a central stake to minimize counting errors and delineate the point boundary. Vegetation and management data collected within each point included: percent canopy cover; number and diameter at breast height (DBH) of shade trees; number of stems of coffee, plantain, citrus, root crops, and other crops, as well as a stem count of woody trees in the system, and whether herbicide had been applied, non-crop herbaceous vegetation height, leaf litter depth, percentage of exposed soil. The distance between each shade tree as well as the minimum distance between trees in a plot was also recorded to give secondary data about canopy cover. Coffee and plantain seedlings below 0.5 m in height were not included since they are neither mature enough to bear fruit nor large enough to shelter coquís. Crop stems were summed, and variables were averaged across points for each farm. A farm management intensity index (FMI) was adapted from the methods of Mas and Dietsch (2003). Percent shade cover, number of shade trees, DBH of shade trees, number of crop stems, percentage of plots with herbicide application, non-crop herbaceous vegetation height, leaf litter depth, percentage of exposed soil, and percentage of plots where plantain leaves had been removed were used in the creation of the index. Each of the nine variable was assign a value from 0 to 1 and summed to calculate the total FMI. Because lower values for the shade variables, vegetation height, and litter depth reflect a higher management intensity, these components were calculated with 1 as the lowest index value and 0 as the highest. Remaining variables were calculated so that 1 represented the highest index value for that variable while 0 represented the lowest. The FMI had a maximum possible value of 9.

2.3 - Bioacoustic Monitoring Methods

We employed ARBIMON portable acoustic recorders, described by Campos-Cerqueira et al. (2013), to record *Eleutherodactylus* vocalizations at all study sites. Farm site recorders were placed at least 150 m apart to avoid overlap in audio recordings and ensure independent vegetation sampling points. Forest site recorders were placed at least 75 m from the edge of the forest and were located between 150 m and 3.6 km from the nearest farm recorder. The recorders were deployed for a period of 4.5 days at each site. Sixty seconds of audio were collected every 10 minutes for a total of 144 recordings/site/day. To focus on the most active calling times for *Eleutherodactylus* and minimize overlap with avian vocalization periods, the recordings used in analyses were limited to those taken between 18:00 and 6:00 (72 recordings/site/day) (García-Rodríguez et al., 2010; Hilje & Aide, 2012; Joglar et al., 2007). The microphones on the recorders have an operational distance of approximately 50 m (Aide et al., 2013). On large farms (dimensions > 100 m), recorders were placed at least 50 m from farm boundaries to avoid recording frogs calling from outside of farms. For small farms (dimensions < 100 m), recorded calls potentially originating outside the farm were excluded from analyses by adding white noise to the recordings in post-processing using the program Audacity (Audacity Development Team, 2019). The white noise masked all frog calls below a specified decibel level associated with the boundary of a particular farm. *Eleutherodactylus coquí*, the amphibian with the loudest known call, calls at a frequency of approximately 2.5 khz at a volume of up to 90 dB (Beard & Pitt, 2005; Drewry & Rand, 1983). Threshold levels for each small farm were established by first playing test tones with a portable speaker at 90 dB and 2.5 khz at 10 m intervals from the recorder to the farm boundary. The decibel levels the microphones captured from the tones decreased as distance from the recorder increased. The decibel level detected at the farthest interval within farm boundaries formed the threshold for analysis, as calls captured at lower volumes could belong to individuals beyond farm limits.

2.4 - Data Analysis

2.4.1 - Bioacoustic Surveys

Audio recordings were analyzed for *Eleutherodactylus* presence using the ARBIMON II software platform, which incorporates Hidden Markov Models in automated species identification (Aide et al., 2013). Species detection models were built using training data from farm and forest recordings. Creating training sets included isolating species calls as regions of interest and manually identifying each species as present in 100 or more recordings and as absent in 200 recordings. Presence and absence recordings were each divided evenly between fitting and validation in model creation. All recordings were then analyzed using the species identification models. Positive detections in model outputs were visually validated for accuracy. For each species within a site, the night with the highest detection rate out of the four sampling nights was used in subsequent statistical analyses. Fogarty and Vilella (2001) found that call counts of *E. coquí* were correlated with the density of calling males in Puerto Rico. We modeled the frequency of species detections in audio recordings using frog encounter data with the beta regression function in the package betareg (Cribari-Neto & Zeileis, 2010). Beta regressions were chosen because of the nature (bounded proportions) and overdispersion of the bioacoustic data. In order to use beta regressions, which do not allow for [0, 1] values, acoustic detection data were transformed using the formula $x' = [x'(N-1)+0.5]/N$, in which N is the sample size (Verkuilen & Smithson, 2012).

2.4.3 - Vegetation and coquí population change between 2017 and 2018

To determine the difference between measured factors before and after Hurricane María paired Mann-Wilcoxon tests were conducted for each variable using RStudio version 1.4.1103. The Mann-Wilcoxon test was used because none of the variables were normally distributed. Some uncertainty was introduced because only 29 farms were measured, thereby reducing the statistical power of the test. The Mann-Wilcoxon test compared each variable as measured in 2017 for each farm with the values for 2018 for each farm. Results for each test were considered statistically significant if the p-value ($\propto$) was less than 0.05.

2.4.4 - Mixed models

Linear mixed effect models were run using RStudio version 1.4.1103 packages “lme4” and “lmerTest” to determine how coquí populations were impacted by vegetative factors, distance to Hurricane María’s cental path, and farm management intensity (FMI). Mixed models were utilized because the data is paired (2017 and 2018) within farms and is therefore not independent. All effects were treated as random except farm identity, which was treated as a fixed variable.

RESULTS

3.1 - Vegetative Change between 2017 and 2018

Several variables were found to have significantly changed from 2017 before Hurricane María to 2018, after the hurricane. Overall, vegetation significantly decreased. Figure 2. demonstrates the per farm change in crop composition and stem count. The average stem count across 19 farms in 2017 was 735 crop stems. In 2018, the average crop stem count was 518 per farm, demonstrating an average loss of 217 crops per farm due to Hurricane María and resultant variables.

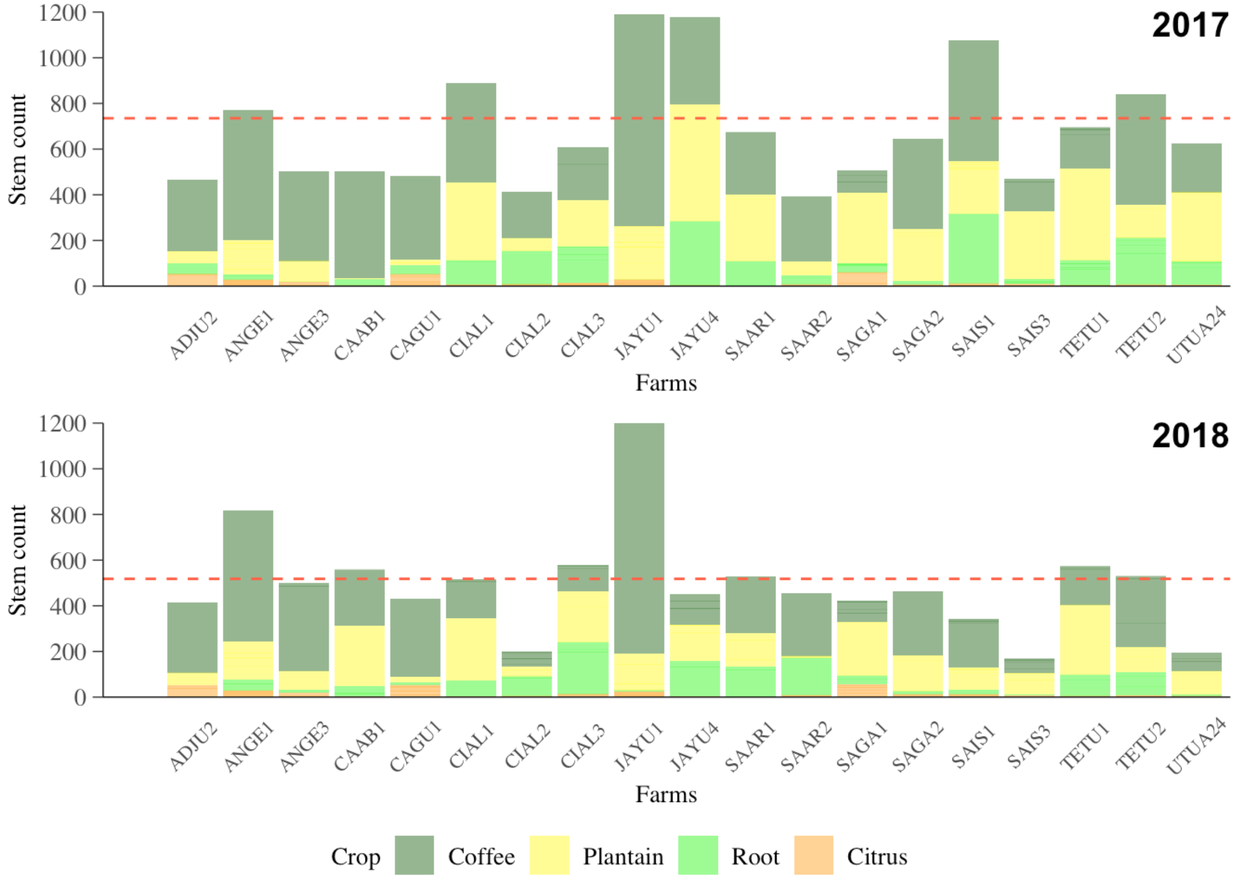

Figure 2. Stem counts of important crops, coffee, plantain, root crops, and citrus, within the 19 study farms in 2017 and 2018. Red line denotes average total crops in each year. For 2017 this average was 735 crops per farm, and in 2018 it was 518 crops per farm. Farm IDs can be matched to Figure 1. Map for spatial reference.

Table 1. indicates which variables were significantly different when comparing pre- with post-hurricane samples. The average total number of trees in each farm as well as the total number

coffee bushes, total plantains, and total number of root crops significantly decreased after Hurricane María in 2018 (Figure 3 and 4). The average density of crops in each farm, and depth of litter on the farm floor also significantly decreased (Table 1, Figure 4). Only the average percent of citrus plants, and herbaceous vegetation height significantly increased in 2018 as compared to 2017. The total citrus and other crops, percentage composition of citrus, plantain, root crops, and other crops did not show significant change. Figures 3 and 4 demonstrate the data range of each variable in 2017 and again in 2018.

Table 1. Paired Mann-Wilcoxon ranked signed test results for vegetative factors. More positive V statistics indicate a greater difference between pre- and post-hurricane values. See boxplots (Figure 3 and 4) for data distribution.

Factor	*V*	*p*	Significance
Total Trees	11,700.0	0.0000024	***
Total Citrus	8,875.5	0.4289999	
Total Coffee	98,214.0	0.0000000	***
Total Plantain	58,604.0	0.0000000	***
Total Other Crops	632.5	0.2300000	
Total Root Crops	15,303.0	0.0034800	***
Percent Citrus	11,388.0	0.1759999	
Percent Coffee	65,651.0	0.0545000	*
Percent Plantain	42,546.0	0.8020000	
Percent Other Crops	691.5	0.1449999	
Percent Root Crops	11,944.0	0.9929999	
Average Plantain Height	24,492.0	0.0000000	***
Bare ground	71,768.0	0.0000000	***
Crop Density	114,218.0	0.0000000	***
Herbaceous Vegetation Height	29,900.0	0.0000000	***
Litter Depth	81,794.0	0.0000000	***

* < 0.01, ** < 0.05, *** < 0.01

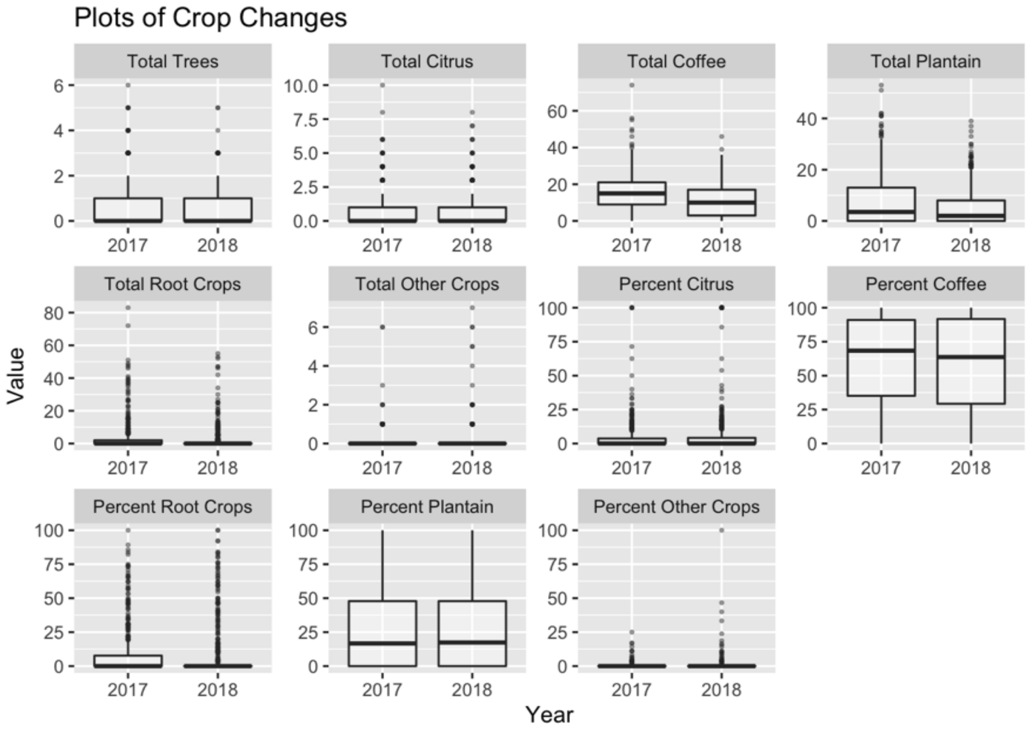

Figure 3. Boxplots comparing each crop variable in 2017 to 2018. These plots demonstrate the change in each variable from before the disturbance to afterwards. Variables that were shown to have significantly decreased in 2018 by Mann-Wilcoxon tests are: total coffee, total plantain, and percent coffee. Y-axis values differ depending on the unit of measurement for the variable.

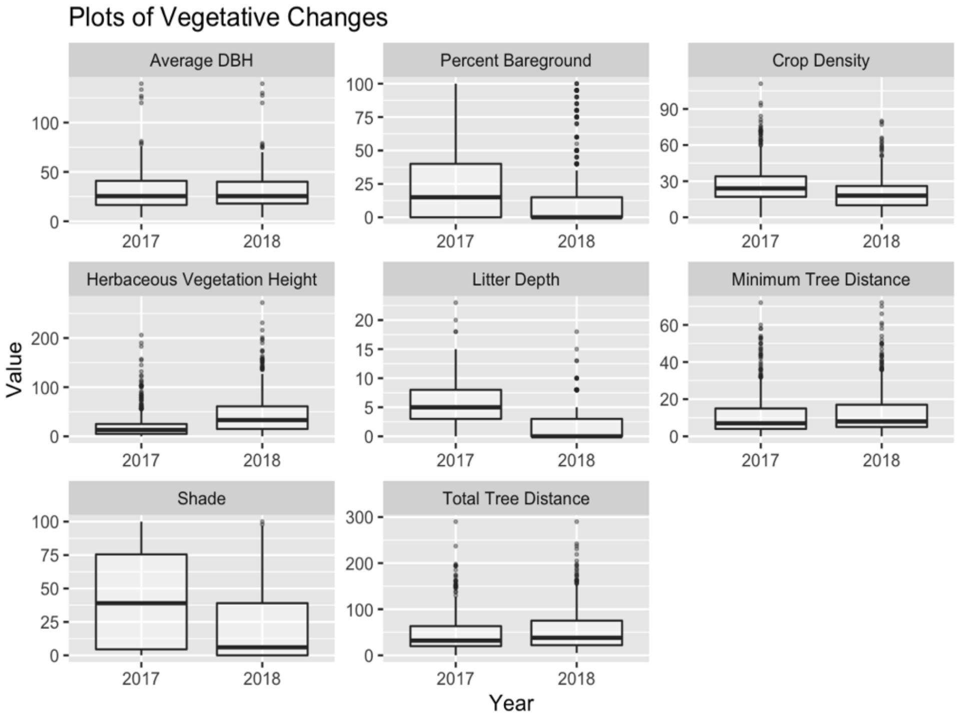

Figure 4. Boxplots comparing each non-crop vegetation variable to surveyed results in 2017 and again in 2018. Variables that were shown to have significantly decreased in 2018 by Mann-Wilcoxon tests are: percent bare ground,

crop density, and litter depth. Herbaceous vegetation was found to have significantly increased in 2018. Y-axis values differ depending on the unit of measure for the variable.

3.2 - Coquí Population Changes

The three species that were detected within the bioacoustic monitoring dataset were *E. antillensis, E. brittoni, E. coqui. E. whigtmanea* was also detected in the data but was only found in the forest plots, therefore, it was excluded from the rest of the analysis. None of the coquí populations (*E. antillensis*, *E. brittoni*, and *E. coquí*) changed significantly after the hurricane. The Mann-Wilcoxon tests found that populations of all three studied species, the *E. antillensis*, *E. brittoni*, and *E. coquí*, remained constant in both amount and composition from 2017 to 2018 (Table 2). Total and percent detected call on farms also had no change (Table 2).

Table 2. Paired Mann-Wilcoxon ranked signed test results for coqui call counts before and after Hurricane Maria. The lack of significant variables demonstrates that there was no significant change in coqui populations across study species.

Factor	*V*	*p*	Significance
Number of Species	2.0	0.3447	
Total Calls Detected	147.5	0.8996	
Total *E. antillensis*	96.0	0.5090	
Total *E. brittoni*	9.5	0.1383	
Total *E. coqui*	154.0	0.9218	
Percent *E.antillensis*	95.0	0.4870	
Percent *E. brittoni*	9.0	0.1235	
Percent *E. coqui*	155.0	0.8996	

* < 0.01, ** < 0.05, *** < 0.01

3.4 – Coquí Population mixed model results

Coquí populations and species composition did not significantly change between 2017 and 2018. However, mixed models examining the influence of various factors on coquí populations and species composition show some significant differences (Table 3). Notably, different factors were significant indicators for different species. The red-eyed coquí (*E. antillensis*) increased in 2018, with an average of 17.29 more calls detected on each farm in 2018 than in 2017. However, red-eyed coquís were also significantly impacted by litter depth; for each centimeter that litter depth decreased, 2.43 less red-eyed coquí calls were detected. The grass coquí (*E.brittoni*) also increased in 2018, and an average of 3.39 more calls were detected the year after the hurricane. Grass coquís were also related to bare ground, and calls detected increased as bare ground increased. The common coquí (*E. coquí*) was the only studied species to decrease in 2018 and 18 less common coquí calls were detected on average at each site. The common coquí was also significantly impacted by vegetation height, and populations decreased as herbaceous vegetation height increased. The total amount of coquí calls was found to increase in 2018 by 16.79 on average.

Variable	Factor	ß	SE	*p*	Significance Level
Total *E. antillensis*	2017 (Intercept)	203.058868	136.692738	0.15690	
	2018	17.286769	8.349254	0.03960	**
	Management Score	-11.171679	22.621855	0.62820	
	Distance from Maria	1.213900	5.814957	0.83720	
	Crop Density	-0.976734	6.800279	0.88590	
	Total Trees	-0.535647	4.039768	0.89460	
	Total Citrus	1.756860	7.543097	0.81610	
	Total Coffee	0.033627	6.809891	0.99610	
	Total Plantain	1.451091	6.819446	0.83170	
	Total Root Crops	0.705110	6.830067	0.91790	
	Average DBH	0.008705	0.150112	0.95380	
	Bare Ground	-0.117561	0.143909	0.41490	
	Vegetation Height	-0.185200	0.130848	0.15840	
	Litter Depth	-2.431845	1.147863	0.03530	**
	Shade	-0.009765	0.136182	0.94290	
Percent *E. antillensis*	2017 (Intercept)	32.906725	24.173744	0.19230	
	2018	3.069993	1.457301	0.03630	**
	Management Score	-1.667730	4.000795	0.68240	
	Distance from Maria	0.296825	1.028279	0.77650	
	Crop Density	-0.190863	1.186955	0.87240	
	Total Trees	-0.086253	0.705099	0.90280	
	Total Citrus	0.317619	1.316606	0.80960	
	Total Coffee	0.025993	1.188635	0.98260	
	Total Plantain	0.277304	1.190300	0.81600	
	Total Root Crops	0.143051	1.192154	0.90460	

Variable	Factor	ß	SE	*p*	Significance Level
	Average DBH	0.001847	0.026201	0.94390	
	Bare Ground	-0.020602	0.025119	0.41300	
	Vegetation Height	-0.031577	0.022838	0.16820	
	Litter Depth	-0.423396	0.200351	0.03570	**
	Shade	-0.001752	0.023770	0.94130	
Total *E. brittoni*	2017 (Intercept)	-62.076266	79.428045	0.44599	
	2018	3.385905	1.153300	0.00369	***
	Manageme nt Score	11.185192	13.164918	0.40817	
	Distance from Maria	2.264754	3.368324	0.51101	
	Crop Density	-0.503590	0.939860	0.59265	
	Total Trees	0.085221	0.557652	0.87869	
	Total Citrus	0.134293	1.042347	0.89761	
	Total Coffee	0.498689	0.941229	0.59679	
	Total Plantain	0.404188	0.942487	0.66847	
	Total Root Crops	0.487068	0.943954	0.60640	
	Average DBH	-0.008697	0.020725	0.67518	
	Bare Ground	0.037878	0.019890	0.05821	*
	Vegetation Height	-0.008197	0.018059	0.65036	
	Litter Depth	0.058685	0.158545	0.71164	
	Shade	-0.010512	0.018816	0.57696	
Percent *E. brittoni*	2017 (Intercept)	-12.418073	14.297675	0.39802	
	2018	0.566403	0.191705	0.00349	***
	Manageme nt Score	2.137191	2.369818	0.38061	
	Distance from Maria	0.450842	0.606307	0.46797	
	Crop Density	-0.088476	0.156227	0.57177	

Variable	Factor	ß	SE	*p*	Significance Level
	Total Trees	0.014279	0.092694	0.87772	
	Total Citrus	0.025711	0.173263	0.88217	
	Total Coffee	0.087928	0.156455	0.57471	
	Total Plantain	0.071857	0.156664	0.64694	
	Total Root Crops	0.085706	0.156908	0.58549	
	Average DBH	-0.001451	0.003445	0.67398	
	Bare Ground	0.006361	0.003306	0.05568	*
	Vegetation Height	-0.001326	0.003002	0.65919	
	Litter Depth	0.009909	0.026354	0.70729	
	Shade	-0.001807	0.003128	0.56415	
Total *E. coqui*	2017 (Intercept)	197.013620	189.604640	0.31430	
	2018	-18.006850	6.964000	0.01040	**
	Manageme nt Score	-1.011690	31.411660	0.97470	
	Distance from Maria	2.469630	8.049280	0.76290	
	Crop Density	-2.975110	5.674090	0.60060	
	Total Trees	-0.861190	3.368010	0.79840	
	Total Citrus	5.302420	6.293240	0.40040	
	Total Coffee	3.087360	5.682280	0.58750	
	Total Plantain	2.113100	5.689990	0.71070	
	Total Root Crops	2.787850	5.698850	0.62520	
	Average DBH	-0.078550	0.125160	0.53090	
	Bare Ground	-0.101400	0.120080	0.39930	
	Vegetation Height	-0.209640	0.109080	0.05590	*
	Litter Depth	-0.040270	0.957370	0.96650	
	Shade	0.113150	0.113610	0.32040	

Variable	Factor	ß	SE	*p*	Significance Level
Percent *E. coqui*	2017 (Intercept)	30.681090	33.308180	0.37073	
	2018	-3.191140	1.206020	0.00875	**
	Management Score	0.237700	5.518230	0.96618	
	Distance from Maria	0.554460	1.413980	0.70014	
	Crop Density	-0.532170	0.982640	0.58868	
	Total Trees	-0.143780	0.583270	0.80552	
	Total Citrus	0.936640	1.089860	0.39108	
	Total Coffee	0.552640	0.984060	0.57498	
	Total Plantain	0.383690	0.985390	0.69739	
	Total Root Crops	0.499610	0.986930	0.61322	
	Average DBH	-0.013500	0.021680	0.53423	
	Bare Ground	-0.018210	0.020800	0.38209	
	Vegetation Height	-0.035960	0.018890	0.05828	*
	Litter Depth	-0.005920	0.165800	0.97155	
	Shade	0.019870	0.019680	0.31374	
Calls Total	2017 (Intercept)	272.202570	188.740070	0.16870	
	2018	16.798980	7.539210	0.02690	**
	Management Score	-7.467200	31.265180	0.81430	
	Distance from Maria	0.872620	8.014380	0.91470	
	Crop Density	-3.855150	6.142510	0.53090	
	Total Trees	-1.096930	3.646370	0.76380	
	Total Citrus	4.576870	6.812860	0.50240	
	Total Coffee	3.147070	6.151360	0.60950	
	Total Plantain	4.112720	6.159730	0.50510	
	Total Root Crops	3.439600	6.169320	0.57770	

Variable	Factor	ß	SE	*p*	Significance Level
	Average DBH	-0.018460	0.135510	0.89180	
	Bare Ground	-0.037700	0.129990	0.77210	
	Vegetation Height	-0.166290	0.118090	0.16050	
	Litter Depth	-1.071780	1.036460	0.30230	
	Shade	-0.021730	0.122990	0.85990	

* < 0.01,
** < 0.05,
*** <0.01

DISCUSSION

Coquí frogs (*Eleutherodactylus spp.*) are important organisms both as a cultural symbol and as a major part of the Puerto Rican ecological system. 2017's Hurricane María was a devastating natural disaster that is likely to be soon repeated due to the intensification of the climate crisis. By understanding how hurricanes impact vegetation structure in agroforestry systems like coffee farms and simultaneously taking data on coqui populations, this study gained insights into how climatic events that are predicted to increase in intensity and frequency with global climate change, shape the ecology of managed systems.

4.1 – Vegetative Change between 2017 and 2018

Vegetative factors were, overall, much more impacted by Hurricane María than coquí populations. Most vegetative variables were significantly negatively impacted by the hurricane. The few vegetative factors that were not significantly changed were the total amount of citrus trees and other crops, the farm composition accounted for by citrus trees, plantains, root crops, and other crops. The percentage of coffee plants within farms changed to a significance of 0.1. Therefore, farm composition overall did not drastically change after the hurricane hit, but the total amount of each plant except for citrus did. This is visualized in Figure 2. This finding of general crop decrease is further supported by the decrease in crop density.

A potential reason that citrus trees were not lost to the same extent as other crops is that they are woody where plantain, and root crops are herbaceous, and coffee is woody but more fragile than citrus (Feng et al., 2020). Previous studies have found that Hurricane María was more harmful to taller and more mature trees (Feng et al., 2020). The average plantain tree is taller than an average citrus tree in our study system, and therefore, our finding that citrus trees remained constant after the hurricane corroborates Feng et al.'s results. Further, the increase in height of herbaceous vegetation and decrease in percent bare ground after the hurricane suggests that smaller herbaceous plants were not negatively impacted by the hurricane and benefited from lower densities of coffee, plantain, and root crops post hurricane.

The finding that citrus trees were more resilient to the hurricane than other crops may provide a strategy for improving overall economic resilience in coffee production systems. This diversification may be able to provide ecosystem benefits such as increased canopy cover and soil nutrients and may also increase the economic resilience of farmers. However, previous work has found that citrus planting may also have negative effects on coquí populations, as coquís are sensitive to citric acid (Tuttle et al., 2008). However, there is no indication in this study that citrus planting negatively impacts coquí populations. More work may be needed to examine the effects of intercropping dynamics and food web impacts, and to predict the influence that farmers increasing citrus planting may have on both ecological and economic systems.

4.2 - Coquí Population Change between 2017 and 2018

Mann-Wilcoxon tests found no significant change in any of the coquí variables between 2017 and 2018. The total calls detected for all species combined, as well as the calls detected for each of the study species, *E. antillensis*, *E. brittoni*, and *E. coquí,* did not change significantly (Table 1). The percentage of calls detected of each species also did not significantly change. These results suggest that populations of coquí in coffee agroforests were not significantly harmed by Hurricane María. It is unknown how these small frogs escaped dramatic harm from the natural disaster, though it is locally thought that coquís were able to hide in their diurnal refugia (commonly inside of leaf furls, bromeliads, and other moisture retaining vegetation). Because of coquís' light body mass, they may have been able to be protected within their refugia, even if it became airborne for a brief time. The feasibility of this refugia protection has not been proven. We suggest that future work examines the mechanisms by which coquís survive these disturbances, as it may give key insights into resilience indicators for all species.

4.4 - Coquí Population Mixed Models

Though coquí populations were not found differed significantly between 2017 and 2018 by the Mann-Wilcoxon test (Table 2). However, linear models gave more insight into what factors were important for each of the study species. As shown in Table 2., each of the different coquí species had different vegetation factors that were significantly positively or negatively related to their populations and composition. These differences provide insight into the subtleties of coquí conservation and hurricane resilience.

Importantly, both *E. antillensis* and *E. brittoni* increased in 2018 as compared to the intercept of 2017, whereas *E. coquí* decreased in 2018, although these changes were not statistically significant. *E. coquí* is the largest of the three species and prefers undisturbed forested areas (García-Rodríguez et al., 2010). Decrease in *E. coquí* after the hurricane is likely due to the vegetative shifts seen throughout the farms, as most farms lost a significant amount of vegetation to the natural disaster. Further, *E. antillensis* and *E. brittoni*, unlike *E.coquí*, were found to increase in 2018 in the linear models. Both species are smaller and prefer more disturbed areas, especially *E. antillensis* (Barker et al., 2015). This community shift could impact insect numbers consumed by all coquí in the farms, as *E. antillensis* and *E. brittoni* have a smaller average size and therefore eat less than *E. coquí* (García-Rodríguez et al., 2010). However, they could potentially eat some of the insect pests in coffee (all of which are smaller insects and some of which, like the coffee leaf miner, are nocturnal). The shift may also have more intricate ecological impacts that we are not yet aware of.

E. coquí's preference towards habitats that are more pristine was also shown in the negative relationship between vegetation height and *E. coquí* populations. With every cm increase in vegetation height, an average of 0.2 less *E. coquí* calls were detected. As herbaceous vegetation height was the single vegetation variable that increased after the hurricane, it is likely that farms that were more disturbed had a higher vegetation height. Therefore, *E. coquí*'s slight decline from farms that had a higher vegetation height suggest that more disturbed farms became could be less favorable habitat. Common coquís have been previously found to be more impacted by canopy openness after a hurricane than leaf litter height, but this study found that shade was not a significant determinant of *E. coquí* populations (Klawinski et al., 2014).

E. brittoni was not impacted by vegetation height, but for each percentage of bare ground increase, an average of 0.04 more grass coquí calls were noted. This result does not align with the literature, as it would be expected that as leaf litter or vegetation increased, so would grass coquí populations (Vilella & Fogarty, 2005).

Litter depth was found to be the most related factor to *E. antillensis* populations. Each centimeter that litter depth decreased, an average of 2.426 less *E. antillensis* calls were detected. *E. antillensis* is a low-dwelling species, and our findings agree with Barker et al., 2015). Notably, the vegetative factor mixed model found that as farm management intensity increased, litter depth decreased. Therefore, less intensely managed farms may be better for *E. antillensis* as well as *E. coquí* and *E. brittoni*. This conclusion is in-line with many others which demonstrate that shade-farming is a more ecologically helpful method of farming coffee (R. Borkhataria et al., 2012; García-Barrios et al., 2017; Mariño et al., 2016).

CONCLUSION

Managed agroecosystems are uniquely vulnerable to the intensification of the global climate crisis due to their need for economic and ecosystem resilience. This study has found that important coffee, plantain, and tubers within coffee farms were dramatically reduced by Hurricane María. However, *Eleutherodactylus* frogs demonstrated population resilience through all three study species, *E. coqui*, *E. antillensis*, and *E. brittoni.* Though these results demonstrate that the intensification of natural disasters may not dramatically devastate populations of some organisms in agroecosystem food webs, these disasters could shift species composition even in the most well-adapted systems. The result that *E. antillensis* calls were detected with more frequency and *E. coqui* with less frequency after the disaster may have unknown implications for these coffee agroecosystems. More work on the intricacies of natural disaster resilience in agroecosystems is recommended, as even subtle changes in these systems could have effects on food systems, economies, and farmer livelihoods.

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