Eleutherodactylus in coffee agroecosystems: Effects of farm management on vegetation selection, species richness, and abundances of Puerto Rican frogs

by

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A thesis submitted to the
SCHOOL OF NATURAL RESOURCES AND THE ENVIRONMENT
UNIVERSITY OF MICHIGAN

In partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE IN CONSERVATION ECOLOGY

November, 2019
Ann Arbor, Michigan
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Dedicated to my mother, who has quietly fostered my interest in the natural world for as long as I can remember.

ACKNOWLEDGEMENTS

This work would not have been possible without the shoulders that I stood upon and the hands that held me up along the way. I am deeply indebted to Ivette Perfecto and John Vandermeer for their role in my development as an ecologist and their guidance throughout this process; to my emotional support crews and comedic relief at 309 N Division and FFML who always kept laughter at hand and misery at bay; and to each of the previous research projects and field crews that I've been lucky enough to be a part of, each of which taught me a little bit more about how science gets done. I am also eternally grateful to the farmers that opened their homes and their lands to me; and to my parents, my family, and my partner Monique Picón, whose unwavering encouragement and love and support has been... everything.

ABSTRACT

Amphibians are declining globally as the combined threats of climate change, habitat loss, and infectious disease intensify and interact. Curbing species losses requires implementing conservation measures beyond natural or protected areas. Shaded coffee farms stand out among human-modified landscapes in their capacity to harbor high levels of biodiversity. In Puerto Rico, the ranges of most *Eleutherodactylus* frogs, many of which are endangered and declining, coincide with the primary coffee-producing region on the island. In this study we used a combination of radio telemetry, bioacoustic monitoring, GIS, and vegetation surveys to investigate the degree to which agricultural habitats at multiple spatial scales may contribute to *Eleutherodactylus* conservation. We compared frog species diversity and abundance between and among farm and forest sites and assessed the influence of farm management and landscape variables. To understand how a common species uses coffee agroecosystems as novel habitat, we tracked *Eleutherodactylus coqui* using radio telemetry and identified trends in vegetation use and microhabitat selection within farms. At the landscape scale, we found farms and forests harbored similar numbers of species but differed in their species composition, with no forest specialists detected in farm systems. Surrounding landcover did not impact farm-level richness or abundance. At the farm scale, *Eleutherodactylus* species varied in their responses to aspects of farm management, with the exception of uniformly negative responses to pesticide application and high densities of root crops which may concentrate pesticides. Within farms, *E. coqui* showed an affinity for plantain (*Musa spp*.), especially those with hanging dry leaves, for diurnal retreat sites. No vegetation preference was detected at night when frogs were active. We conclude that coffee farms in Puerto Rico provide suitable habitat for amphibians, yet may not be meeting the needs of forest specialist species. Within farms a generalist species was most abundant where microhabitats essential for shelter and reproduction were plentiful; such resources are likely lacking for species dependent on forests. Despite similar levels of diversity to nearby forests, coffee farms under current management regimes may not be useful habitat for species of conservation concern in Puerto Rico.

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CHAPTER 1

Coquí in coffee agroecosystems: Selection of farm vegetation as microhabitats for shelter and hunting by *Eleutherodactylus coqui* in Puerto Rico

ABSTRACT

Habitat loss through the conversion of land to agriculture and the simplification of previously diverse agroecosystems is contributing to amphibian species declines. Understanding how individual species use specific habitat components within agricultural systems can help identify keystone structures important for their persistence. *Eleutherodactylus coqui* is a hyper abundant species of frog found in all ecosystems in Puerto Rico, including coffee farms. This study examined the way in which *E. coqui*, a habitat generalist, used available farm vegetation within coffee agroecosystems. A total of 162 frogs were observed during visual encounter and farm vegetation surveys across 29 farm sites in the central mountains of Puerto Rico. An additional 20 individuals were tracked using radio telemetry for a period of four days. During the day, sheltering *E. coqui* showed significant preference for plantain (*Musa spp.*) over other vegetation. When frogs were active at night no vegetation preference was detected. Plantain with hanging dry leaves were particularly favored as diurnal retreat sites. These findings provide evidence that amphibian species, including generalists, prefer farm microhabitats similar in structure to commonly used retreat sites in natural settings. Such habitat resources are likely lacking for more specialized forest species, indicating that coffee agroecosystems under current management regimes may be limited in their conservation potential for forest amphibians in Puerto Rico.

1 | INTRODUCTION

Habitat loss and degradation are considered two of the greatest threats to global biodiversity (Arroyo-Rodríguez et al., 2013; Newbold et al., 2015; Phalan et al., 2013; Sala et al., 2000; Thomas et al., 2002) In the hyper-diverse tropics, the primary driver of habitat loss is the large-scale conversion of forests and intensification of agricultural systems (Donald, 2004; Gibson et al., 2011; Sala et al., 2000; Wright, 2005). As primary forests become more and more scarce the persistence of tropical forest biodiversity increasingly depends on the ability of species to make use of human-modified landscapes (Gardner et al., 2009; Harvey et al., 2008; Perfecto et al., 2007; Perfecto & Vandermeer, 2008, 2010; Perfecto et

al., 2009; Pineda & Halffter, 2004; Tscharntke et al., 2012; Vandermeer & Perfecto, 2007). The knowledge required to better manage these landscapes for biodiversity conservation is being generated at a slower rate than that at which habitat and species are being lost.

The suitability of agricultural systems as habitat varies depending on their floristic diversity and structural complexity as well as the requirements of individual species or functional groups (Galán-Acedo et al., 2019; Greenberg et al., 1997; Mendoza et al., 2015; Murrieta-Galindo et al., 2013b; Philpott & Bichier, 2012; Pineda et al., 2005; Tews et al., 2004). Shade coffee stands out among tropical agricultural systems in its ability to support forest biodiversity because it retains certain elements of forest ecosystems, such as vertical stratification and complex vegetative structure. Shade coffee can be viewed as part of a gradient stretching from primary and secondary forest to full-sun monocultures (Moguel & Toledo, 1999); biodiversity tends to decrease along this gradient as farms become more simplified and homogenous, causing canopy and understory microhabitats to disappear. This decrease in biodiversity is not even across or within taxonomic groups (Murrieta-Galindo et al., 2013b; Perfecto et al., 2003). A trend of coffee farm intensification across the tropics intended to increase yields is causing further habitat loss within agricultural landscapes (Borkhataria et al., 2012b; Perfecto et al., 1996; Perfecto et al., 2005).

Amphibians are experiencing much higher rates of extinction than other vertebrate taxa (Mendelson et al., 2006; Stuart et al., 2004; Whitfield et al., 2007). They are particularly vulnerable to habitat change due to low vagility coupled with specific requirements for temperature, humidity, and reproduction (Mendenhall et al., 2014; D. Robinson et al., 2013). Despite their vulnerability to habitat modification, amphibians are able to survive and reproduce in many tropical farming landscapes (Mendenhall et al., 2014; Meza-Joya et al., 2015; Monroe et al., 2017; Murrieta-Galindo et al., 2013a; Murrieta-Galindo et al., 2013b; Palmeirim et al., 2017; Pineda et al., 2005; Rathod & Rathod, 2013; D. Robinson et al., 2013; Santos-Barrera & Urbina-Cardona, 2011). Individual species or functional groups vary in their ability to exploit these landscapes. For instance large, pond-breeding amphibians in a modified landscape in Costa Rica preferred human-made ponds over natural habitats, while small, stream-breeding species and species with direct development depended more on forest attributes that were missing from farms (Mendenhall et al., 2014). Specific components of the physical habitat, or keystone structures, may be crucial to sustaining populations of some species (Tews et al., 2004). Within agroecosystems, habitat attributes ranging from remnant vegetation to manmade structures or local farming practices can impact amphibian life cycles, particularly reproduction. In temperate and tropical rangelands, artificial ponds and farm dams with particular physical characteristics can substitute natural wetlands as breeding habitat, and breeding may be enhanced by managing grazing regimes (Hazell et al., 2001; Pyke & Marty, 2005). Amphibian conservation in agricultural landscapes can be enhanced by identifying habitat elements that can meet the foraging, shelter, and reproductive requirements of individual species.

Eleutherodactylus coqui, or common coquí (herein coquí), is a nocturnal frog endemic to Puerto Rico and introduced to parts of the Caribbean, Florida, and Hawaii. It is widespread in Puerto Rico, occurring in all ecological life zones and elevations (Rivero, 1998), and consumes a wide variety of prey. Though a habitat generalist, *E. coqui* exhibits preferences for specific vegetation structures as shelter and nest sites (summarized in Joglar, 1998). These preferences are more pronounced during the day, when coqui take refuge, than at night, when coqui are known to forage on vegetation in approximate proportion to its availability on the landscape (Beard et al., 2003b). In all *Eleutherodactylus* species, eggs are laid on land and undergo direct development, making nest site selection important for reproductive success. Understanding the ways in which a non-forest habitat can meet the needs of a generalist species can inform the conservation of forest-dwelling amphibians and other forest specialists.

Previous studies of *Eleutherodactylus* frogs in Puerto Rico have evaluated habitat preferences and vegetation use in forest ecosystems (Beard et al., 2003b; Townsend, 1989; Woolbright & Stewart, 2008), yet few have examined these questions in a human-modified landscape (Monroe et al., 2017), and none have investigated *E. coqui* microhabitat preferences and vegetation use in an agricultural setting. In this study we surveyed *E. coqui* in cultivated areas using visual surveys and radio telemetry to identify important habitat components in coffee agroecosystems. We hypothesize that coquí inhabiting coffee farms select vegetation nonrandomly and predict that plantain and root crops will be favored as diurnal retreat sites because of their structural similarity to favored microhabitats in forested areas. We expect this preference to be stronger during the day than at night, when coquí are active and foraging. Differences in plantain management were examined to test a related hypothesis that the presence of senesced leaves on plantain stalks impacts the extent to which coqui use plantain. We predict that trimming dead plantain leaves will (a) reduce diurnal use of plantain as habitat, and (b) reduce the number of coquís found in an area by lowering the number of available retreat sites.

2 | METHODS

2.1 | Study Site

The study was conducted between June and September of 2017 on 29 farms 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 and the landscape is characterized by secondary forest, agriculture, and low-intensity development. Coffee farms in Puerto Rico are typically mixed polycultures with a combination of coffee (*Coffea spp.*) and one or more of the following crops: plantain/banana (*Musa spp.*) (herein plantain), citrus trees (*Citrus spp.*), and the root crops 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 elevation ranged between 272 m and 704 m asl. Mean farm elevation was 524 m asl. Average farm size was 5.5 ha, with a minimum farm size of 0.36 ha and a maximum size of 45.5 ha. Sites were selected to be representative of variation in elevation and size as well as management, crop varieties, and crop abundances.

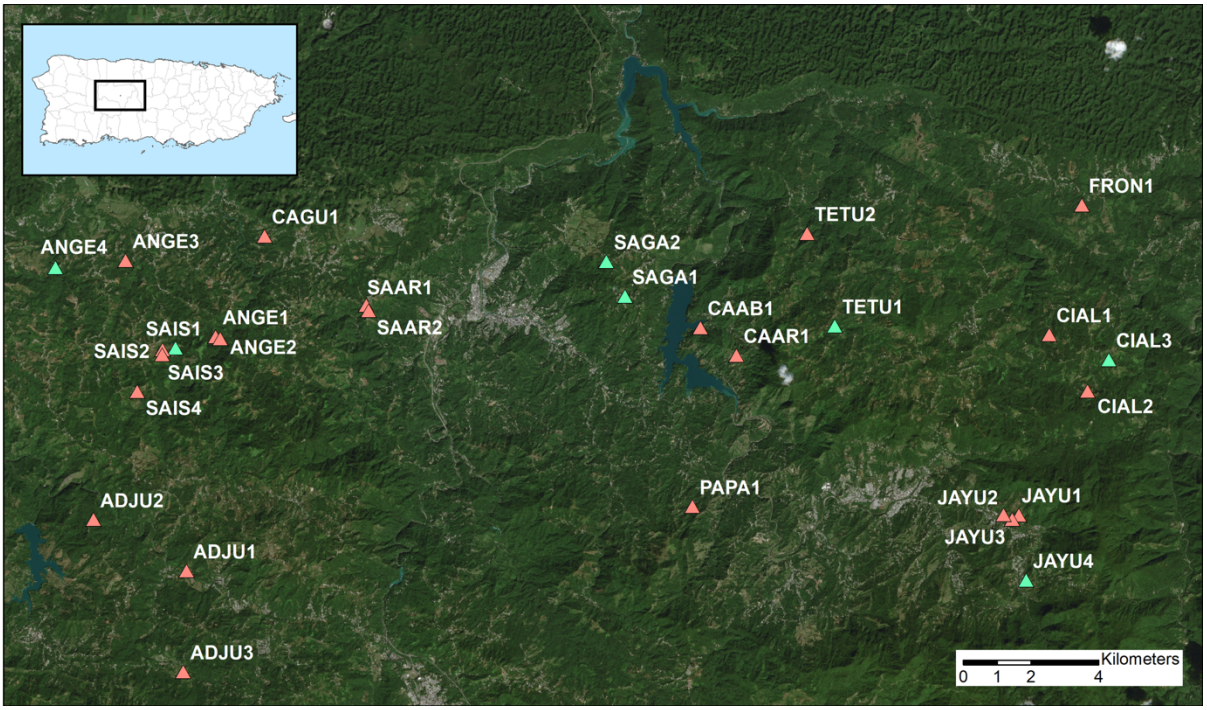

FIGURE 1 Study area and farm sites in the Cordillera Central of Puerto Rico. Farms at which coqui were tracked are marked in light green.

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 points were selected from points at which coquís had been observed (methods described below) while the remaining 10 points were generated randomly using ArcMap (ESRI, 2017) in order 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 plot boundaries. Vegetation data collected within each plot 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; whether dry/dead plantain leaves had been removed from stalks; and whether herbicide had been applied. 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. Herbicide application was determined by observing the state of herbaceous vegetation within a plot. If vegetation was present but dead and had not been replaced by new growth of 0.5 m or more, the plot was marked as having herbicide applied. Crop stems were summed and variables were averaged across points for each farm. Plantain management within a plot was assessed as either untrimmed (dead/dry leaves still attached to stalk), trimmed (dead/dry leaves removed), or NA (management not applicable due to lack of plantain or plants too young to have had full-sized leaves senesce).

2.3 | *Eleutherodactylus coqui* Surveys

Visual encounter surveys of *Eleutherodactylus coqui* were conducted on the first night of work at each farm. Surveys involved walking on farm trails and between rows of coffee after sunset when coquís activity begins. Individuals were spotted with the aid of a headlamp and singing males were located by following their calls. Search efforts were contained within and spread across the same 75 m radius used in vegetation surveys. If no coquí were located during the initial survey a second survey was conducted the following evening. Surveys were completed once 10 individuals had been located, each at a minimum distance of 10 m from other individuals to avoid overlapping vegetation survey points. Coquís were also recorded opportunistically during chance encounters while conducting fieldwork. Points at which coquí were observed were marked with flagging and their locations were recorded with a handheld GPS receiver (Garmin GPSmap 62st). During vegetation surveys, points were searched for coqui. Coffee, plantain, and root crops within the points were visually inspected for frogs hiding in foliage or in leaf axils. For all coquí observations, substrate or vegetation on which frogs were found, their height above ground and behavior, and the presence of eggs or newly hatched juveniles were recorded. Other *Eleutherodactylus* species were also recorded when observed.

2.4 | *Eleutherodactylus coqui* Telemetry

Twenty *E. coqui* were fitted with Holohil Bd-2x (0.35g and 0.31g) radio transmitters (Holohil Systems Ltd.; Carp, Ontario, Canada) and tracked for up to four days for a total of up to seven resightings (fixes). Transmitters were attached using Teflon tubing and cotton thread (Waye, 2001). Tubing was passed through a mounting hole in the front of the transmitter, then cotton thread was passed through the tubing and knotted, forming a padded waistband. The combined weight of the transmitter and waistband was less than 10% of the weight of each frog. The operational lifespan of the transmitters was approximately 12 (0.31g model) to 21 days (0.35g model). While wearing transmitters coquís were resighted twice daily: once during the day, while they sheltered, and once after dark, while they were

active. Evening telemetry began one hour after sunset to give individuals time to disperse from retreat sites (Woolbright, 1985). After four days individuals were recaptured and transmitters were removed. In the event that a transmitter could not be recovered, the cotton thread would deteriorate due to moisture and humidity and eventually break. Telemetry methods were approved by IACUC under permit number PRO00007690.

2.5 | Data Analysis

Analyses were conducted in R (R Core Team, 2019). Coquí vegetation use was compared to crop proportions in points at which coquís were observed and farm crop totals using Mann-Whitney-Wilcoxon tests. Coffee and plantain microhabitat use by *E. coqui*, *E. coqui* presence, and *E. coqui* abundance were also compared among survey points in which plantain were untrimmed, trimmed, or management was not applicable (NA) using Mann-Whitney-Wilcoxon tests. NA points without plantain present (n = 5) were not included in plantain use analyses. Points without coffee (n = 2) were not included in coffee use analyses.

Eleutherodactylus coqui coffee, plantain, and root crop use data were separated into activity periods for analysis and modeled using generalized linear models. Citrus use was not modeled due to its low planting density on farms (see vegetation survey results below). Possible covariates in models included the total number of stems of coffee, plantain, root crops, and citrus, and the management status of plantain (untrimmed, trimmed). Trimmed and NA points were combined in these analyses since both result in the absence of usable plantain leaves. Data was fit to a binomial distribution with a logit function. Models were selected from a list of candidate models which included a null intercept-only model, a full model with all terms, and all combinations of covariates. The best model was determined using backward model selection whereby terms were removed systematically from the full model. Models with Δ AIC > +2 were considered significantly better than the full and null models. Where no models had Δ AIC > +2 the full or null models was selected. Where Δ AIC values for models were within 2, candidate models were averaged; otherwise a single model was selected as the best fit. Significance of covariates was assessed at $p \leq 0.5$.

3 | RESULTS

3.1 | Vegetation Surveys

Farms contained between three and six crops, with four crops on average. Coffee was most common and accounted for 56.2% of crop stems overall (Figure 2). The relative density of coffee varied from 17% of crop stems on a farm to 95%. Plantain was the second most abundant crop, making up 28.9% of total crop stems and reaching a peak relative density of 62%. All 29 farms surveyed grew coffee and plantain, although one farm had a relative density of plantain of only 1%. Root crops and citrus trees constituted 12.2% and 2.3% of overall crop stems respectively. All other crops, which included avocado, papaya, guava, pineapple, breadfruit (*Artocarpus altilis*), and mango (*Mangifera indica*) together made up less than 0.5% of the 15,890 crop stems counted.

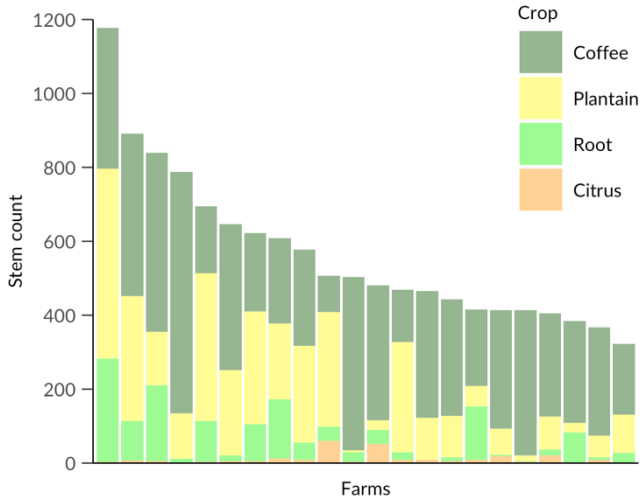

FIGURE 2 Total stem counts of coffee, plantain, root crops, and citrus at farms where *E. coqui* were observed.

3.2 | Coquí Surveys

A total of 182 individual *E. coqui* were observed. Ninety-two of these sightings occurred during coquí surveys, 63 occurred during vegetation surveys, and 27 resulted from chance encounters. Signs of *E. coqui* reproduction (eggs or offspring) were observed nine times. Although *E. antillensis* was not a focal species in this study, the number of observations was sufficient to warrant reporting the data. Twenty-eight *Eleutherodactylus antillensis* were observed during coquí surveys (n = 12), vegetation surveys (n = 12), or chance encounters (n = 4). One clutch of *E. antillensis* eggs was observed.

3.3 | Coquí Telemetry

Twenty *E. coqui* (19 female, 1 male) were tracked using radio telemetry, resulting in 87 total resightings (fixes). Of these, 43 fixes were recorded at night when coquí were active and 44 fixes were recorded during the day while coquí were in retreat sites. Coquí nightly movements and total movement distance each ranged from 0 to 34.5 m (Table 1). Average movement distance was 2.9 m across all intervals and

6.8 m when only intervals in which coqui changed location were included. Eighty-four percent of fixes occurred within 5 m of the previous sighting. For the seven coquís with three or more unique locations recorded, the area within the polygon formed by these locations was calculated. These seven coquís covered farm areas between four and 23 m^2 over a four-day period.

TABLE 1 *Eleutherodactylus coqui* telemetry survey results, including the number of fixes for each individual, the distances moved between sightings, and total linear distance travelled between all sightings. Area covered is provided where fixes occurred at three or more unique points.

		Interval Distance (m)							
Coqui ID	Sightings (no.)	1 - 2	2 - 3	3 - 4	4 – 5	5 - 6	6 - 7	Total distance (m)	Area (m^2)
*CC1	3	4.59	4.37					8.96	5.27
CC2	7	3.48	0	0	0	3.06	6.24	12.79	10.53
CC3	5	4.91	7.74	4.37	0			17.01	22.24
*CC4	2	13.32						13.32	
CC5	7	0	6.97	4.43	0	0	0	11.40	4.68
CC6	7	0	7.16	7.16	0	7.16	0	21.48	
CC7	7	15.53	0	0	0	0	0	15.53	
CC8	6	4.43	0	0	0	0		4.43	
CC9	5	2.11	0	0	2.11			4.23	
CC10	6	4.59	10.31	6.72	0	0		21.63	23.41
CC11	6	0	3.48	0	0	1.53		5.02	
CC12	5	12.74	0	5.74	0			18.48	
CC13	4	0	11.63	1.53				13.16	
CC14	6	0	34.49	0	0	0		34.49	
*CC15	3	0	6.34					6.34	
CC16	5	3.06	7.48	0	0			10.55	
CC17	6	0	0	0	0	0		0	
CC18	6	4.55	0	4.55	6.90	0		16.00	14.05
CC19	6	1.53	0	5.45	0	5.45		12.42	4.10
*CC20	6	0	0	0	0	0		0	

Notes: * CC1 and CC20 showed signs of possible encumberment or discomfort caused by transmitter attachment; CC4 dislodged the transmitter before the first resighting; CC15 was not detected after the second fix.

Two individuals exhibited erratic behavior likely related to the transmitters; the seven resightings of those individuals were excluded from analysis. The first coquí to be fitted with a transmitter (CC1) showed signs of abrasion from the waistband and was found resting on the ground at the same location during two consecutive fixes. The transmitter was removed after the third resighting and the individual was not observed again. The second individual excluded from analysis was the only male tracked (CC20). In all resightings this male was found in the same coffee bush in which it was

originally caught. While it moved proximally and distally within the bush between active and retreat period fixes, it was no longer heard singing during peak vocalizing hours. This change in vocalization behavior may have been caused by discomfort related to the transmitter, although no signs of skin abrasion were found. Townsend (1989) noted that captured males typically resume calling within 5 minutes of release. Two other individuals had transmitter-related issues including one whose waistband slipped off (CC4) and another whose transmitter could not be relocated after the third sighting (CC15).

3.4 | Vegetation Use

As predicted, rates of crop vegetation use by *E. coqui* differed significantly from the relative crop densities found within farms, indicating a preference for some crops over others. Of 270 total *E. coqui* sightings, 52.4% occurred on plantain, 24.3% on coffee bushes, 7.2% on root crops, and 1.7% on citrus. Diurnal habitat selection drove the observed differences in crop use. Coquí exhibited a preference for plantain as diurnal retreat sites at observation points ($p = 0.004$) and on farms ($p = 0.002$), while coffee was underutilized as a retreat ($p < 0.001$, $p < 0.001$) (Figure 3). The relative density of plantain was higher, and the relative density of coffee was lower in coqui observation points compared with farm densities. Root crops alone were significantly underutilized at night, with a rate of use 81% below the relative density.

Eighty-seven untracked coqui were found during the day; 82.8% were found on plantain, 6.9% on coffee, and 9.2% on root crops. No coquí were found using citrus as a diurnal retreat (Figure 4, Table 2). At night, observations of untracked *E. coqui* on plantain and root crops dropped to 34.7% and 3.2% of 95 sightings, while the proportion of sightings on coffee and citrus increased to 36.8% and 5.3%. Similar patterns were exhibited by the tracked individuals (n = 80 fixes). Plantain and coffee plants again harbored coqui most frequently, accounting for 55% and 22.5% of sightings during the day (n = 40 fixes). As with untracked *E. coqui*, plantain use dropped in the evening to 45% of 40 fixes while coffee use rose to 25%. All subsequent analyses for *E. coqui* combine unique sightings and telemetry fix data because tracked and untracked coquí vegetation use did not differ significantly between crops or activity periods (Table 2).

TABLE 2 Tracked and untracked *E. coqui* micro-habitat selections and Mann-Whitney-Wilcoxon test p-values for all observations, shelter period observations, and active period observations.

Period	Crop	*E. coqui*	*E. c.* tracked	P-value
All	Coffee	32.10	28.92	0.38
	Plantain	51.24	37.60	0.43
	Root	7.05	5.00	0.74
	Citrus	1.66	0	0.35
Day	Coffee	13.73	24.61	0.26
	Plantain	73.14	44.55	0.06
	Root	12.75	3.33	0.87
	Citrus	0	0	
Night	Coffee	53.29	32.78	0.21
	Plantain	27.47	30.77	1
	Root	2.24	6.67	1
	Citrus	3.74	0	0.28

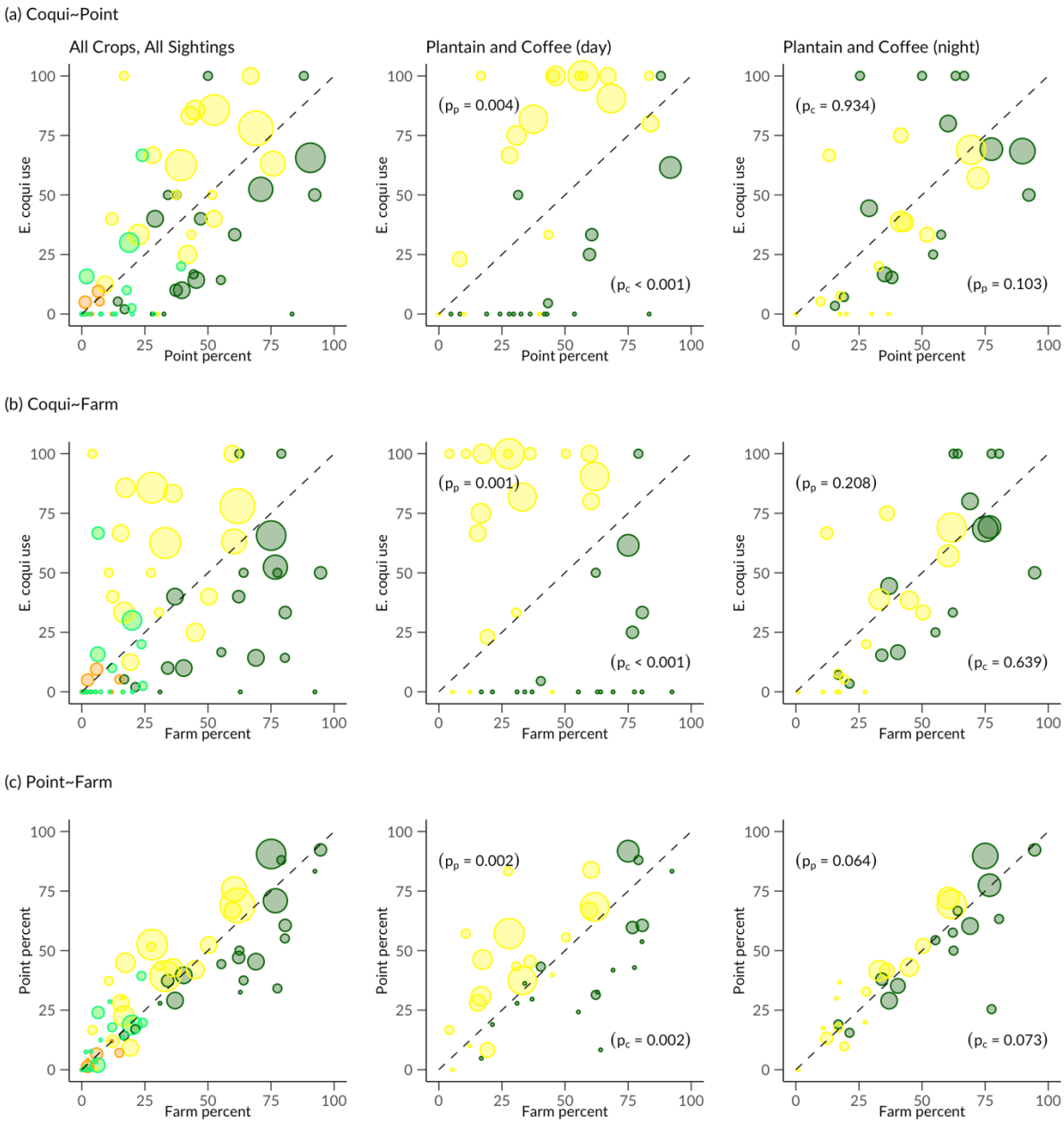

FIGURE 3 Proportion of *Eleutherodactylus coqui* vegetation use compared to: (a) the proportion of stems of each crop at the points where individuals were found, (b) the proportion of each crop at the farm level. Crop proportions between points with coquí and farm level totals are also compared (c). Plantain and coffee use are separated into day (retreat) and night (active) observations. P-values from Mann-Whitney tests are provided; values for plantain are noted with $_p$ and for coffee with $_c$.

E. antillensis also used plantain most frequently during the day (7 of 15 observations), and coffee most frequently at night (10 of 13 observations). Notably, root crop use was substantially higher for *E. antillensis* (40% of observations) during the day compared to *E. coqui* (9%) (Figure 4).

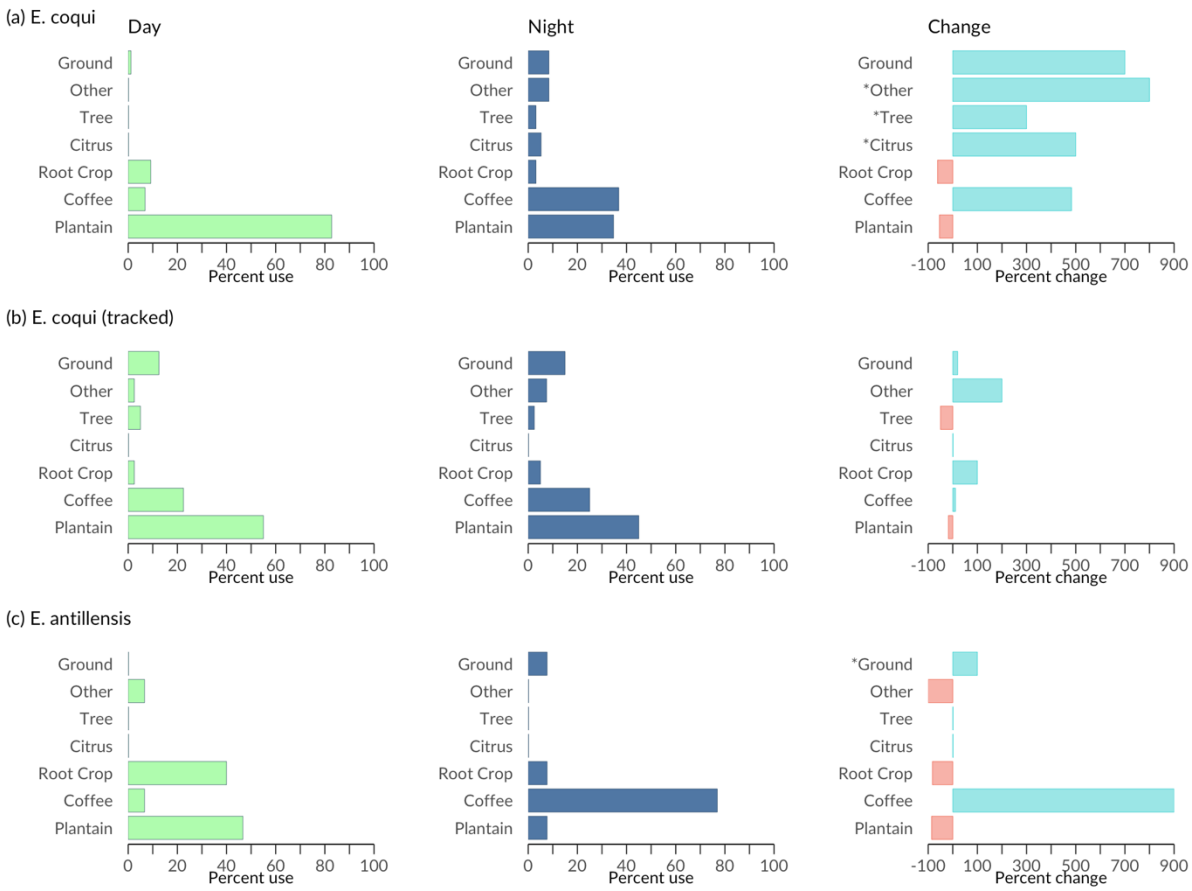

FIGURE 4. Coqui vegetation use by separated by time of day, and percent change in microhabitat used between diurnal retreat sites and active period for untracked *E. coqui* (a), tracked *E. coqui* (b), and *E. antillensis* (c). Microhabitat changes marked with an asterisk (*) required division by zero. These were adjusted by adding a constant of one to both day and night values.

3.5 | Plantain Management

Out of 580 vegetation survey points, 358 (61.7%) contained plantain plants mature enough to be managed. Of those 358 points, 181 encompassed untrimmed plantain (50.5%) and 177 contained plantain with dead leaves removed (49.4%); 222 points had no plantain management (NA) either because they did not contain plantain stems (n = 213) or contained plantain that were too small to have had leaves senesce (n = 9) (Figure 5). As predicted, use of plantain microhabitats by *E. coqui* was significantly higher at points in which plantain were untrimmed compared to trimmed points (p = 0.0059) (Figure 6a). Use of plantain by coquí at NA points was not significantly different than use at untrimmed points

(p = 0.13), though the small sample size of NA points that contained plantain likely influenced this result. Conversely, coffee microhabitat use at both trimmed and NA points was significantly higher than at untrimmed points (p = 0.046, p = 0.0042) (Figure 6b). Points in which plantain were trimmed or plantain was immature did not differ significantly in either plantain (p = 1) or coffee use (p = 0.15) by coquí.

Contrary to our expectation, the abundance of coquí did not differ significantly between untrimmed points and trimmed points (p = 0.08) despite a reduction of almost 60% in the number of individuals (Figure 7a). At untrimmed points coquís were observed 166 times (91 day, 75 night), while at trimmed points coquís were found 71 times (32 day, 39 night).

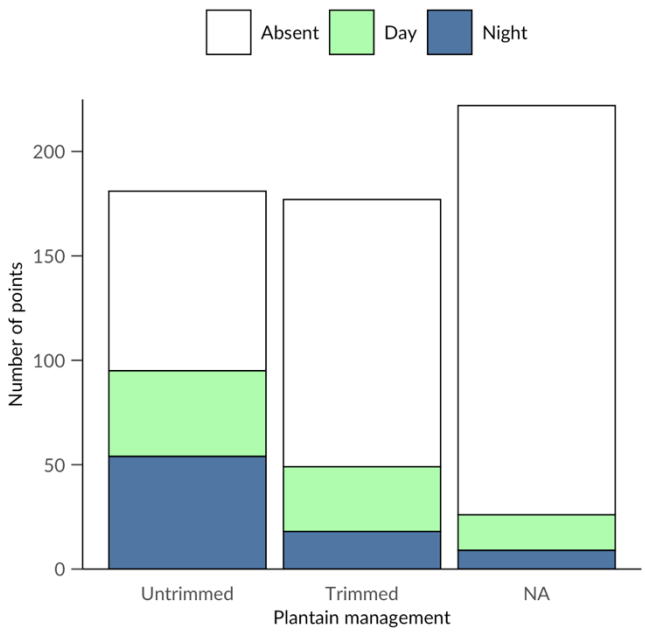

FIGURE 5 The number of vegetation survey points at which plantain were untrimmed, trimmed, or where plantain were either absent or too immature to have been maintained (NA). Points with coquí present are shaded depending on the activity period during which individuals were observed.

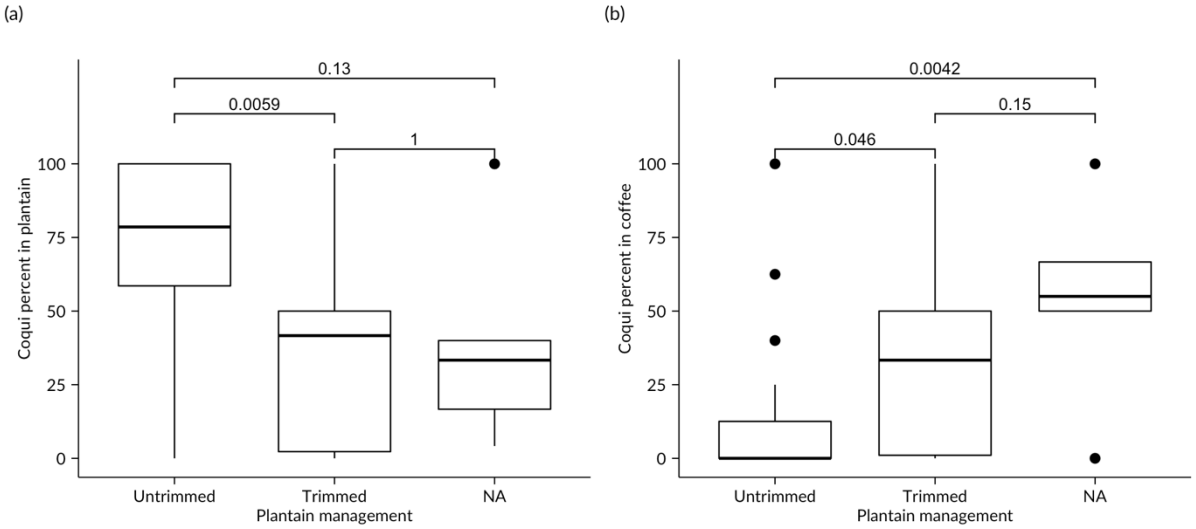

FIGURE 6 Plantain (a) and coffee (b) use by *E. coqui* compared across points with varying plantain management. Untrimmed points contained plantain that had senesced leaves still attached, senesced leaves had been removed at trimmed points. Plantain was either absent or not mature enough to have had leaves senesce at NA points. P-values are provided from pairwise comparisons using Mann-Whitney-Wilcoxon tests.

Coquís were found at points in which plantain was absent or immature 44 times (16 day, 28 night). Neither untrimmed and NA point (p = 0.58), nor trimmed and NA point (p = 1) comparisons were significantly different.

The number of points at which coquí were found only differed significantly between untrimmed and NA point totals (p = 0.025) (Figure 7b). Fifty-two percent of untrimmed points contained coquís (41 day, 54 night) compared to 28% of trimmed points (31 day, 18 night) (Figure 5). Coquís were detected in only 12% of sites without mature plantain (17 day, 9 night). Again, the small sample size for NA points may have influenced results, as there were few points (n = 4) that had both immature plantain and coquís present.

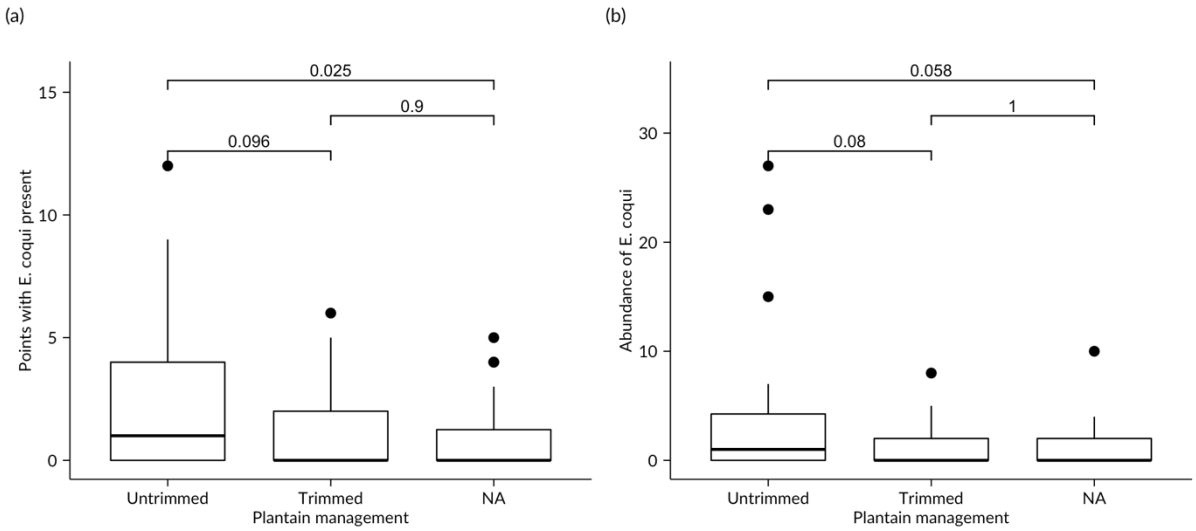

FIGURE 7 Presence (a) and abundance (b) of *E. coqui* compared across points with varying plantain management. Untrimmed points had plantain with senesced leaves still attached, NA points either had no plantain or plantain that were not mature enough to have had leaves senesce, and trimmed points had plantain stalks with dead leaves removed. P-values are provided from pairwise comparisons using Mann-Whitney-Wilcoxon tests.

3.6 | Crop Vegetation Model Selection

3.6.1 | Coffee

Crop microhabitat use by *E. coqui* was separated into active and shelter periods before analysis. For coffee, both activity periods had three candidate models with Δ AIC > +2 over the null and full models, and AIC values within +/-2 of each other (Table 3, Table 4). In each case the averaged final model included all full model covariates (quantity of coffee, plantain and root crops and plantain management (untrimmed, trimmed)) with model weights added. The shelter period model showed a significant

negative effect of plantain, which varied from 0-53 stems, on the probability of *E. coqui* using coffee as a retreat site (β_p = 0.64, p = 0.001). Plantain management had the opposite effect, with an eightfold increase in probability of finding coquís in coffee when dead leaves were removed from plantain (p = 0.032). In the active period averaged model, the effect of plantain quantity remained significant, though reduced (β_p = 0.91, p < 0.001). However, the effect of plantain management was no longer significant. In its place the quantity of coffee planted, which ranged from 0 to 56 stems, gained significance. As the number of coffee stems increased the probability of coqui using coffee increased (β_c = 1.1, p < 0.001).

TABLE 3 Coffee use as a diurnal retreat by *E. coqui*. The three models with the highest AIC score were averaged (avg).

Model selection		df	AIC	Δ AIC	Weight
	~ 1	1	93.47	-50.04	
(full)	~ C + P + R + T	5	45.75	-2.31	
(a)	~ P + T	3	43.44	0	0.44
(b)	~ R + P + T	4	43.8	-0.36	0.37
(c)	~ C + P + T	4	45.13	-1.69	0.19

Models		Estimate (±SE)	z value	Pr(>|z|)
(a)	(Intercept)	0.516 ± 2.347	-0.776	0.438
	Plantain	0.634 ± 1.136	-3.564	< 0.001
	Trimmed	7.029 ± 2.515	2.115	0.034
	Deviance	37.44		
(b)	(Intercept)	0.538 ± 2.355	-0.724	0.469
	Root crop	0.913 ± 1.081	-1.165	0.244
	Plantain	0.630 ± 1.141	-3.489	< 0.001
	Trimmed	8.996 ± 2.600	2.299	0.021
	Deviance	35.80		
(c)	(Intercept)	0.213 ± 5.756	-0.884	0.377
	Coffee	1.042 ± 1.070	0.607	0.544
	Plantain	0.661 ± 1.151	-2.946	0.003
	Trimmed	8.706 ± 2.793	2.107	0.035
	Deviance	37.13		
(avg)	(Intercept)	0.443 ± 3.159	-0.708	0.479
	Plantain	**0.638 ± 1.144**	**-3.346**	**0.001**
	Trimmed	**8.017 ± 2.643**	**2.142**	**0.032**
	Root crop	0.967 ± 1.067	-0.516	0.606
	Coffee	1.008 ± 1.035	0.230	0.818

Notes: The selected model and significant terms are shown in bold.

TABLE 4 Coffee use by *E. coqui* while hunting or calling at night. The three models with the highest AIC score were averaged (avg).

Model selection		df	AIC	Δ AIC	Weight
	~ 1	1	167.57	-40.36	
(full)	~ C + P + R + T	5	130.96	-3.75	
(a)	~ C + P	3	127.21	0.00	0.56
(b)	~ C + P + R	4	129.09	-1.88	0.22
(c)	~ C + P + T	4	129.10	-1.89	0.22

Models		Estimate (±SE)	z value	Pr(>|z|)
(a)	(Intercept)	0.414 ± 1.664	-1.733	0.083
	Coffee	1.104 ± 1.028	3.532	< 0.001
	Plantain	0.905 ± 1.024	-4.293	< 0.001
	Deviance	121.21		
(b)	(Intercept)	0.396 ± 1.690	-1.764	0.078
	Coffee	1.105 ± 1.029	3.542	< 0.001
	Plantain	0.904 ± 1.024	-4.280	< 0.001
	Root crop	1.009 ± 1.025	0.353	0.724
	Deviance	121.09		
(c)	(Intercept)	0.369 ± 1.850	-1.622	0.105
	Coffee	1.103 ± 1.028	3.508	< 0.001
	Plantain	0.908 ± 1.026	-3.834	< 0.001
	Trimmed	1.181 ± 1.631	0.339	0.734
	Deviance	121.10		
(avg)	(Intercept)	0.400 ± 1.724	-1.684	0.092
	Coffee	**1.104 ± 1.029**	**3.494**	**< 0.001**
	Plantain	**0.905 ± 1.024**	**-4.133**	**< 0.001**
	Root crop	1.002 ± 1.012	0.157	0.875
	Trimmed	1.037 ± 1.273	0.151	0.880

Notes: The selected model and significant terms are shown in bold.

3.6.2 | Plantain

The best model for diurnal plantain use by coquí was the full model, in which each covariate (coffee, plantain, and root crop stem counts, plantain management) had a significant effect (Table 5). Plantain abundance was the only predictor with a positive effect; the probability of encountering an *E. coqui* on plantain increased by 16% with each additional plantain stem (p = 0.003). Coffee (β_c = 0.93, p = 0.043), root crop (β_r = 0.89, p = 0.016) and plantain management (β_m = 0.12, p = 0.001) each had a negative impact on the probability of coquí use of plantain as shelter.

TABLE 5 Plantain use as a diurnal retreat by *E. coqui*.

	Model selection	df	AIC	Δ AIC	Weight
	~ 1	1	145.68	-54.23	
(full)	**~ C + P + R + T**	**5**	**91.46**	**0**	**1**
	~ P + R + T	4	94.49	-3.03	
	Models	Estimate (±SE)		z value	Pr(>|z|)
(full)	(Intercept)	5.281 ± 2.274		2.026	0.043
	Coffee	**0.934 ± 1.033**		**-2.121**	**0.034**
	Plantain	**1.162 ± 1.052**		**2.988**	**0.003**
	Root crop	**0.892 ± 1.049**		**-2.415**	**0.016**
	Trimmed	**0.117 ± 1.858**		**-3.468**	**0.001**
	Deviance	81.46			

Notes: The selected model and significant terms are shown in bold.

As with coffee, three models for plantain habitat use at night had Δ AIC > +2 over the null and full model and AIC values within +/- 2 of the candidate model with the lowest AIC score (Table 6). The averaged final model for coffee contained the same parameters as the full model but with model weights added. In the averaged full model, the quantity of coffee negatively impacted plantain use (β_c = 0.93, p = 0.005), while each additional stem of plantain increased the odds of observing *E. coqui* by 8% (β_c = 1.08, p < 0.001).

TABLE 6 Plantain use by *E. coqui* while hunting or calling at night. The three models with the highest AIC score were averaged (avg).

	Model selection	df	AIC	Δ AIC	Weight
	~ 1	1	172.33	-24.94	
(full)	~ C + P + R + T	5	149.56	-2.17	
(a)	~ C + P	3	147.39	0	0.47
(b)	~ C + P + T	4	148.18	-0.79	0.31
(c)	~ C + P + R	4	148.86	-1.47	0.22
	Models	Estimate (±SE)		z value	Pr(>|z|)
(a)	(Intercept)	0.428 ± 1.508		-2.067	0.039
	Coffee	0.936 ± 1.024		-2.796	0.005
	Plantain	1.079 ± 1.018		4.244	< 0.001
	Deviance	141.20			
(b)	(Intercept)	0.295 ± 1.699		-2.304	0.021
	Coffee	0.931 ± 1.025		-2.928	0.003
	Plantain	1.092 ± 1.021		4.136	< 0.001
	Trimmed	1.758 ± 1.638		1.143	0.253
	Deviance	139.85			
(c)	(Intercept)	0.384 ± 1.541		-2.210	0.027
	Coffee	0.937 ± 1.024		-2.729	0.006
	Plantain	1.079 ± 1.018		4.250	< 0.001
	Root crop	1.019 ± 1.023		0.823	0.411
	Deviance	140.54			
(avg)	(Intercept)	0.372 ± 1.629		2.027	0.043
	Coffee	**0.934 ± 1.025**		**2.781**	**0.005**
	Plantain	**1.083 ± 1.020**		**3.982**	**< 0.001**
	Trimmed	1.193 ± 1.466		0.462	0.644
	Root crop	1.004 ± 1.014		0.312	0.755

Notes: The selected model and significant terms are shown in bold.

3.6.3 | Root Crop

The best model for the use of root crops as shelter by coquí was the full model (Table 7). Two predictors had significant effects in this model: root crop stem quantity (p = 0.015) and plantain management (p = 0.023). Root crop stems, which varied between 0 and 47, increased the probability of finding *E. coqui* sheltering in root crops by 21%. Removing dead plantain leaves also had a positive effect on root crop use during the day. When dry leaves were removed the probability of finding coquís in root crops rose more than thirteen-fold, constituting the largest effect size of any variable in any crop model.

Root crop use at night was the only analysis in which no model improved sufficiently upon the null model, although there were four candidate models with Δ AIC ≤ 2 (Table 8).

TABLE 7 Root crop use as a diurnal retreat site by *E. coqui*.

Model selection		df	AIC	Δ AIC	Weight
	~ 1	1	66.55	-23.84	
(full)	**~ C + P + R + T**	**5**	**44.41**	**0**	**1**
	~ P + R + T	4	42.71	1.70	

Models		Estimate (±SE)	z value	Pr(>|z|)
(full)	(Intercept)	0.013 ± 5.715	-2.436	0.015
	Coffee	0.959 ± 1.081	-0.010	0.992
	Plantain	0.938 ± 1.093	-1.049	0.294
	Root crop	**1.205 ± 1.077**	**2.434**	**0.015**
	Trimmed	**13.212 ± 3.812**	**2.280**	**0.023**
	Deviance	0.013 ± 5.715		

Notes: The selected model and significant terms are shown in bold.

TABLE 8 Root crop use by *E. coqui* while hunting or calling at night. No model outperformed the null model during model selection.

Model selection		df	AIC	Δ AIC	Weight
	~ 1	**1**	**37.66**	**0.00**	**1**
(full)	~ C + P + R + T	5	43.59	5.93	
	~ P	2	37.80	0.14	
	~ C + P	3	39.61	1.94	
	~ C	2	39.62	1.96	
	~ R	2	39.66	2.00	

Notes: The selected model is shown in bold.

4 | DISCUSSION

4.1 | Farm Vegetation Use

Our study provides evidence that *E. coqui* exhibits preferential microhabitat use among crops when selecting diurnal retreat sites in coffee agroecosystems. This finding is line with studies of coqui natural history documenting associations with the leaves or leaf axils of specific forest vegetation (e.g. sierra palms, *Cecropia*, *Heliconia*, bromeliads) (Joglar, 1998; Stewart & Pough, 1983; Townsend, 1989; Woolbright, 1996; Woolbright & Stewart, 2008). During the day we found farm-dwelling coquí to be positively associated with plantain, and negatively associated with coffee and citrus. Coquí were found on plantain far more frequently than would be expected based on either the proportion of plantain stems available in their immediate vicinity (Figure 3a) or the total proportion planted on farms (Figure 3b). Additionally, the points where coquí were found during the day contained high relative densities of plantain compared to corresponding

farm-level densities (Figure 3c). Contrary to our prediction, root crops were not an important component of coquí retreat sites. Coquí were found on root crops (malanga, yautia) more frequently than baseline levels at point and farm scales, suggesting some preference, but this trend was not significant. We had predicted a higher utilization of root crops based on their structural similarity to bromeliads, which coquí commonly shelter in within forests (Woolbright & Stewart, 2008). Possible reasons for the low rate of use of root crop habitat include the generally low proportion of root crops available on farms and the abundance of retreat sites provided by plantain. The selection of plantain over other farm vegetation is similar to the positive association noted by Townsend (1989) between coquí and both *Cecropia* and sierra palm in forested areas. It is worth noting that *E. antillensis* was much more common in root crops than was *E. coqui* (Figure 4), and that during the day *E. antillensis* was found to use both root crops and plantain at comparable rates. Intraspecies niche partitioning between *Eleutherodactylus* may be occurring on coffee farms in Puerto Rico, but further studies are needed to appropriately demonstrate this.

GLM results identified plantain density as the main driver of both plantain and coffee diurnal microhabitat use. Coffee, the dominant crop across farms, was underutilized as a retreat as a direct result of the availability of preferred plantain habitat. Plantain density also appeared in the final model of root crop microhabitat use, but had no significant effect. In contrast to coffee, increases in the quantity of root crop stems enhanced the use of root crops as a retreat site, suggesting that even where plantain are abundant, higher planting densities of malanga and yautia would lead to a corresponding increase in their use by coquí.

Coquí clearly avoided citrus. As a diurnal retreat citrus was used dramatically below its availability. At night, points at which coquí were found contained low densities of citrus compared to farm levels. This negative association could be the result of the toxicity of citric acid to amphibians, as demonstrated by the use of citric acid in the control of introduced populations of *E. coqui* in Hawaii (Beachy et al., 2011; Ohashi, 2004). Though no coquí were found in citrus during the day, a small number were found on citrus trees at night. It may be that coquí are more vulnerable to citric acid during the day because coquí absorb moisture from retreat site substrates to maintain water balance while in diurnal retreats (Van Berkum et al., 1982).

The associations between coquí and both plantain and coffee were limited to retreat site selection. No preference for either crop was detected at night, in accordance with recorded coquí behavior in natural systems (Beard et al., 2003b). However, we did find a low nocturnal rate of use of root crops, perhaps due to limited feeding opportunities on these crops; while conducting fieldwork we observed fewer insects on root crops than on other vegetation.

One subgroup of coquí on farms, calling males, was encountered on plantain more frequently than other vegetation types. Thirty-eight of the 79 coquís observed calling were found on plantain while 32 were found on coffee. This is surprising given that the number of coffee stems across farms was

twice the number of plantain stems. Coquí were found calling from plantain trunks, leaves, and axils. Townsend (1989) demonstrated that coquís prefer open, elevated calling sites, including shallow depressions, the surface of leaves, and the axils of sierra palms. Previous studies of other amphibian species have found that males have higher mating success when calling from elevated perches unobstructed by surrounding vegetation (Fellers, 1979; Greer & Wells, 1980; Wells & Schwartz, 1982). Within farms coffee and plantain each provide elevated perches, but coquí calling from plantain were positioned 30 cm higher on average than those calling from coffee plants. We observed a median calling height of 200 cm, higher than the median of 79 cm reported by Townsend. The tall robust stalk, wide sturdy leaves clustered at the top, and open axils of plantain may provide enhanced sound amplification compared to coffee, where dense foliage may muffle calls.

Coquí movement distances between resightings on farms varied, averaging approximately 5 m per night. Though similar to the 3-4.5 m averages observed by Woolbright (1985) in El Yunque National Forest, our distance is based on single point-to-point measurements between retreat sites and thus captures only a portion of the total nightly measurements taken by Woolbright, suggesting coqui move farther on farms than in forests. The greater movement on farms may result from a reduction in the site fidelity observed in natural settings (Joglar, 1998; Woolbright, 1985) due to a higher availability of retreat sites from which to choose. Coquí were regularly found within 5 m of their last sighting; however, they were only occasionally found on the same crop stem more than once, and rarely in the same retreat.

4.2 | Plantain Management

Farmers in Puerto Rico commonly “clean” dead, hanging leaves from plantain stalks and bromeliads and orchids, often mistaken for parasites, from citrus and shade trees. Removing senesced leaves from plantain stalks occurred to varying extents on 27 of 29 farms surveyed. Our results show that trimming these leaves dramatically affects coquí microhabitat selection, causing a sharp decline in their preference for plantain over other crops (Figure 8). Plantain leaves are removed for purely aesthetic purposes, giving farms a more manicured appearance (personal communication). GLM results demonstrate that trimming leaves decreased plantain use and increased coffee and root crop use by coquí (Table 3, Table 7). Sampling points with plantain leaves left attached contained a greater number of coquí than those with trimmed leaves, suggesting a positive relationship between management type and coquí abundance, but this difference was not significant (Figure 7a). Points without plantain or where plantain stems were too small for leaves to have senesced were significantly less likely to harbor coquí than sites with untrimmed plantain (Figure 7b).

Vegetation structure among coffee farms in Puerto Rico encompasses only a portion of the spectrum of structures that can be found in coffee-growing regions. Farms in this study predominantly resembled the descriptions of commercial polycultures and shaded monocultures provided by Moguel

and Toledo (1999), but also included several unshaded monocultures and one “rustic” farm. In all of the farms in this study, vertical structure has been simplified to include only crops and shade trees, reducing habitat complexity compared to surrounding forest (Moguel & Toledo, 1999; Murrieta-Galindo et al., 2013b; Pineda & Halffter, 2004; Santos-Barrera & Urbina-Cardona, 2011) and limiting the variety of microhabitats available to coquí and other species. In these simplified agroecosystems, plantain provides important structural complexity that is absent from other understory farm vegetation, and the retention of senesced leaves dramatically increases available microhabitats in coffee farms.

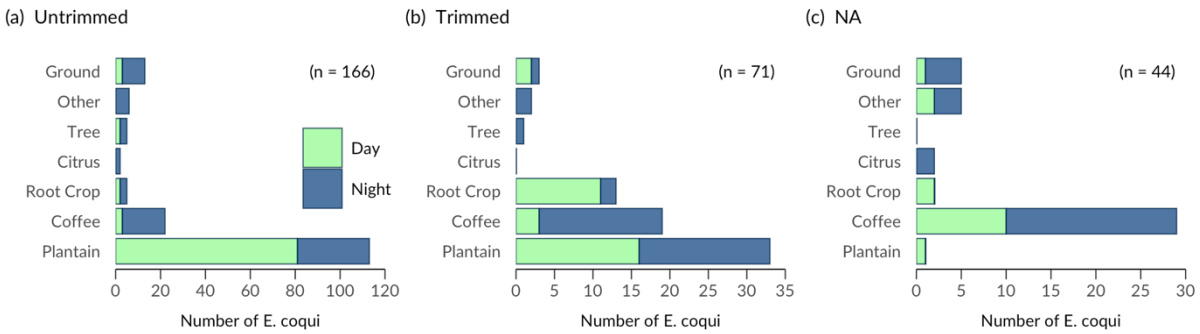

FIGURE 8 All *E. coqui* vegetation use at points at which dry/dead leaves were still attached (a), points at which dead leaves had been removed (b), and points at which plantain were either absent or not mature enough to have had leaves senesce (c). Sightings are separated into diurnal retreat sites (Day) and active hunting or calling locations (Night). The number of frogs observed is listed in the top right of each panel.

Because *Eleutherodactylus* lay their eggs on land, nest site quality, availability and selection are critical components of reproduction. Coquí eggs lack shells and are unable to limit the exchange of water with surrounding air and surfaces; as a result they are dependent on microclimate conditions, male parental care, and nest structure (Taigen et al., 1984; Townsend et al., 1984). In El Yunque National Forest, Townsend (1989) found that coquís predominantly nested in enclosed cavities and curled leaves, with fallen *Cecropia* leaves and sierra palm leaf petioles accounting for 70% of nest sites. When dry, these leaves form cavities with stable microclimates that reduce evaporative water loss to eggs and tending males, and conceal eggs from predators, including conspecifics (Townsend, 1989; Townsend et al., 1984). Sierra palm leaves are durable and decompose more slowly than other vegetation, providing long-term nest sites and lowering the chance of nest collapse or flooding during heavy rain events. On farms, senesced plantain leaves provide similar structural characteristics. The leaves are fairly rigid and fold in half while drying, creating a thatched effect as each successive leaf folds and droops down on top of previous layers. When left untrimmed, these leaves create a maze of irregularly shaped cavities within and among layers that conceal coquí from predators and provide secure retreat and nesting sites. In our study, all nine observed nest sites of *E. coqui* were located in folded, untrimmed plantain leaves.

Plantain leaves may provide higher quality microhabitats than *Cecropia* and sierra palm leaves because they remain attached to the stalk after drying, providing nest and retreat sites raised above the ground. In the study by Townsend (1989), senesced *Cecropia* and palm leaves that settled in elevated locations had a higher rate of nesting by coqui, and those nests had higher hatching success and an increased incidence of multiple clutches, compared with those on the forest floor. Enhanced reproduction in elevated nest sites was attributed to the capacity of males to call more frequently, from taller sites, and closer to their nests. The ability to tend nests while continuing to attract females affords males higher rates of mating and facilitates guarding multiple clutches.

The availability of high-quality nest sites can limit coquí populations in natural and human-altered habitats. Beachy et al. (2011) used nest and retreat site removal as an integrated part of the eradication of an invasive population of coquí in Hawaii. Conversely, Stewart and Pough (1983) recorded increased numbers of nests and coquís after artificially increasing the number of potential nest sites in a forest. Parallel findings from Dendrobatid frogs in Colombia lend support to the role of conserved forest habitat structures in enhancing amphibian breeding in farm settings. Meza-Joya et al. (2015) found that higher numbers of *Andinobates virolinensis* in a shaded coffee and plantain farm compared to a nearby plantain monoculture were driven by the number of available bromeliads on remnant trees in each farm. No frogs were found in areas without trees or where trees lacked large bromeliads. Studies of other *Dendrobatid* frogs in natural settings have found similar associations with bromeliad density (Pröhl, 2002; Vargas-Salinas & Amézquita, 2013). As with coquí nest sites, experimental addition of bromeliads increased the density of both male and female adult *Oophaga pumilio* (Donnelly, 1989). The need for adequate nesting structures in agroecosystems extends beyond amphibians. Cruz-Angón and Greenberg (2005) found the abundance of resident bird species that used epiphytes as nesting material to be significantly lower in areas of coffee farms where epiphytes were experimentally removed. Cavity-nesting birds in managed forests and Western bluebirds in California vineyards increased in abundance when artificial nest sites were provided or snags were left intact (Jedlicka et al., 2011; Newton, 1994).

4.3 | Implications for Farm Management

Providing adequate microhabitats for coquí by intercropping coffee with plantain and refraining from trimming dead plantain leaves may benefit farmers by promoting biological control of coffee pests. *E. coqui* have been described as the most important consumer of nocturnal arthropods in Puerto Rico (Joglar, 1998). They can consume up to 114,000 prey/ha/night at normal densities (Stewart & Woolbright, 1996; Woolbright, 1991) and are capable of reducing aerial invertebrates by 28% and overall herbivory by 80% in secondary forests (Beard et al., 2003a). Coquí have also been shown to suppress insect abundance in Hawaii, a novel ecosystem for the species (Sin et al., 2008). These findings,

together with the high abundance and generalist tendencies of coquí in Puerto Rico, support a potentially important role for coquí in providing pest control in farming landscapes.

We suggest coquí may be particularly relevant to control of the coffee leaf miner (*Leucoptera coffeella*), an economically significant coffee pest. Although birds and lizards are known to suppress a variety of insect pests on coffee farms (Borkhataria et al., 2006; Monagan Jr. et al., 2017; Perfecto et al., 2004), research has shown that neither successfully controls the coffee leaf miner in Puerto Rico (Borkhataria et al., 2006). This pest is shielded from insecticides and predators during the larval stage, when it is enclosed within a coffee leaf, while its nocturnal habit as an adult moth protects it from diurnal predators. The nocturnal activity pattern and movement from plantain retreat sites to coffee vegetation at night make coquí a likely natural enemy, though predation on the coffee leaf miner has yet to be reported. It will be important for future studies to document and quantify leaf miner consumption by coquí, as well as to evaluate whether intercropping coffee with plantain can enhance leaf miner control.

4.4 | Conclusions

The results of this study show the presence of plantain affects coquís inhabiting coffee agroecosystems in several ways. Farms cultivating plantain provide preferred retreat habitat for coquí and preferred posts from which to call at night. Where plantain leaves are left untrimmed, retreat habitats and nesting sites are more plentiful and reproduction may be more successful. Male coquí in all habitats face a tradeoff between successfully tending nests and attracting new mates through calling. In farms, plantain provide an ideal microhabitat in which coquí may mitigate this tradeoff by advertising from tall perches with plentiful senesced leaves nearby in which females can deposit eggs.

Our results show that a species capable of occupying a wide range of habitats still exhibits a strong association with certain natural habitat characteristics in a human-altered system. While the specific vegetation on which coquí are commonly found in forests was missing from farms, a structurally similar substitute was able to fulfill the same needs. That *E. coqui* maintain the same behavioral traits in farms as in forest implies that the system is meeting habitat requirements rather than the species adapting to the system. This is important because it suggests that the needs of other amphibians species that are present in the landscape but absent from coffee farms are not being similarly met. This study adds to a growing body of evidence demonstrating that life history traits and the ecology of individual species interact with habitat structure in determining how species respond to habitat alteration. For tropical biodiversity conservation to be fully realized in coffee farms and other agroecosystems, the management of farms must address the habitat needs of species of concern, often forest specialists, along with crop production.

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CHAPTER 2

Farm management intensity and landcover effects on *Eleutherodactylus* presence and abundance in coffee agroecosystems in central Puerto Rico

ABSTRACT

Habitat loss across the tropics has prompted conservation efforts in human-modified landscapes. Shaded coffee farms are known to serve as habitat for many vertebrates requiring forest elements, but the extent to which they can support forest amphibian communities is poorly understood. Trends of coffee farm intensification in many tropical regions have resulted in a gradient of farm structure and management activities, with impacts on biodiversity varying by taxa and species. In this study we used bioacoustic monitoring and farm surveys to evaluate the richness and abundance of *Eleutherodactylus* frogs in 18 coffee farms and 6 secondary forest sites in Puerto Rico. We asked to what extent farm management intensity and surrounding landcover impact *Eleutherodactylus* community structure in coffee agroecosystems. Species richness was similar between farm and forest site types, however the only forest specialist detected (*E. wightmanae*) was not found on farms. While overall management intensity did not affect the species found on farms (*E. antillensis*, *E. brittoni*, *E. coqui*), each of which is common in disturbed habitats, individual aspects of farm management had negative impacts. The application of pesticides and high densities of root crops, which may concentrate pesticides, were associated with lower abundances of *Eleutherodactylus* species on farms. Surrounding landcover did not impact farm-level richness or abundance. This study demonstrates that while farms have the capacity to harbor similar levels of amphibian diversity to forest ecosystems, species composition may differ, and current management practices and farm structure may exclude forest species of conservation concern.

1 | INTRODUCTION

Unprecedented habitat loss across tropical regions is stimulating conservation approaches focused on the persistence of biodiversity in human-modified landscapes (Gardner et al., 2009; Harvey et al., 2008; Perfecto et al., 2007; Perfecto & Vandermeer, 2008, 2010; Perfecto et al., 2009; Pineda & Halffter, 2004; Tscharntke et al., 2012; Vandermeer & Perfecto, 2007). Shaded coffee and cacao farms have been recognized as promising habitats within agricultural landscapes because of their structural resemblance to a forest ecosystem and capacity to maintain high levels of avian, bat,

arthropod, and plant diversity (Frishkoff et al., 2014; Mas & Dietsch, 2003; Moguel & Toledo, 1999; Perfecto et al., 2007; Pineda et al., 2005). Amphibians, particularly vulnerable to land use change because of their temperature and moisture requirements and low vagility, are also known to occupy coffee agroecosystems (Mendenhall et al., 2014; Meza-Joya et al., 2015; Monroe et al., 2017; Murrieta-Galindo et al., 2013a). However, species-level persistence varies with local and landscape-level characteristics such as patch area and degree of canopy cover, which mediate microhabitat availability (Murrieta-Galindo et al., 2013b; Pineda & Halffter, 2004; Pineda et al., 2005). The extent to which coffee farms can support amphibian communities present in nearby forests remains in question and holds important implications for conservation efforts in working landscapes.

In Puerto Rico, seventeen of the nineteen amphibian species native to the archipelago belong to the emblematic, Neotropical genus of frogs *Eleutherodactylus*, known locally as coquí. *Eleutherodactylus* are small, nocturnal frogs that undergo direct development, however elevational ranges, habitat preferences and degrees of specialization vary by species (Joglar, 1998; Rivero, 1998). Population declines driven by habitat loss, climate warming and drying trends, and infection by the fungus *Batrachochytrium dendrobatidis* are affecting the majority of species (Burrowes et al., 2004). Of the sixteen *Eleutherodactylus* species native to the main island, three are presumed extinct, seven are listed as endangered or critically endangered by IUCN, and two are listed as vulnerable (IUCN Red List, http://www.iucnredlist.org [accessed 15 November 2019]). Several species appear to be experiencing range contractions (Barker & Ríos-Franceschi, 2014) or population declines even within large protected areas (Burrowes et al., 2004). The Central Mountains of Puerto Rico are home to ten *Eleutherodactylus* species and are an important region for coffee production on the island. Coffee farms occur within a largely forested landscape and are traditionally managed as shaded polycultures intercropped with other fruits and root vegetables, which provide retreat sites and hunting grounds for some *Eleutherodactylus* species (Harmon et al., 2019, unpublished manuscript).

The ability of coffee landscapes to ameliorate the loss of natural habitats depends on the suitability of individual farms and of surrounding landscapes, which may function as habitat or as corridors for migration (Perfecto & Vandermeer, 2010; Perfecto et al., 2009). Shaded coffee farms in this region are thought to have served as refugia for forest-dependent biodiversity during a period of extensive clearing for agriculture in the nineteenth and early twentieth centuries, providing sources for recolonization of former habitats as forest cover returned following mid-century economic shifts in Puerto Rico (Brash, 1987; Nir, 1988; Weaver & Birdsey, 1986). In recent decades however, coffee farms have become increasingly varied in their management, resulting in a gradient of structure and composition among farms including canopy cover and shade tree diversity. A trend of production intensification prompted by government promotion of sun-grown coffee beginning in the 1960s has led to the structural simplification of many farms, with consequences for forest biodiversity (Borkhataria et al., 2012b; Perfecto et al., 1996; Perfecto et al., 2005). One study demonstrated that a forest-dependent

Eleutherodactylus species reached high occupancies in shade-grown but not sun-grown coffee in the Central Mountains, while species known to prefer open habitats occurred in high abundances in sun-grown farms (Monroe et al., 2017). Understanding how fine-scale differences in farm structure and composition affect their capacity to harbor *Eleutherodactylus* species is key to evaluating the conservation potential of coffee farms and identifying favorable scenarios of farm management.

In this study we ask whether coffee agroecosystems in the central mountains of Puerto Rico harbor similar richness and abundance of *Eleutherodactylus* species as surrounding forest habitats, and to what extent these metrics vary among coffee farms. Further, we evaluate the impacts of farm management and surrounding landscape composition on *Eleutherodactylus* species in coffee farms. We expand upon the findings of Monroe et al. (2017) of coqui occupancy of sun or shade farms by quantifying *Eleutherodactylus* species responses to a gradient in farm management and to landscape composition at multiple scales. We hypothesize that farm management characteristics and overall intensity will impact *Eleutherodactylus* communities, with (a) species richness and abundance declining as farm management intensity increases, (b) species abundances declining with increased herbicide application, (c) species abundances increasing with plantain and root crop densities as these may provide important microhabitats and (d) decreasing abundances of open-habitat species and increasing abundances of forest-dependent species with higher levels of shade cover. Farms with greater areas of secondary forest in the surrounding landscape are expected to have higher *Eleutherodactylus* species richness. We predict surrounding land cover to have guild-specific impacts on species abundances within farms, including higher abundances of forest species in landscapes with a greater area of secondary forest cover, and higher abundances of open-habitat species in landscapes with greater areas of agriculture and non-forest cover. No response to surrounding landcover is expected for the widespread generalist species *Eleutherodactylus coqui*, which is abundant across the island.

2 | METHODS

2.1 | Study Site

We conducted this study on 18 coffee farms and six secondary forest sites in the Cordillera Central of Puerto Rico between June and September of 2017. Sites were located within the municipalities of Adjuntas, Ciales, Jayuya and Utuado (Figure 1). The central mountains comprise the primary coffee-producing region on the island and the landscape is composed of a matrix of secondary forest, agriculture, and low-intensity development. Farms in the region typically cultivate coffee (*Coffea spp.*) intercropped with a combination of plantain/banana (*Musa spp.*) (herein plantain), citrus (*Citrus spp.*), and

malanga and yautia (*Colocasia esculenta* and *Xanthosoma sagittifolium*) (herein root crops) under varying levels of shade. 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.

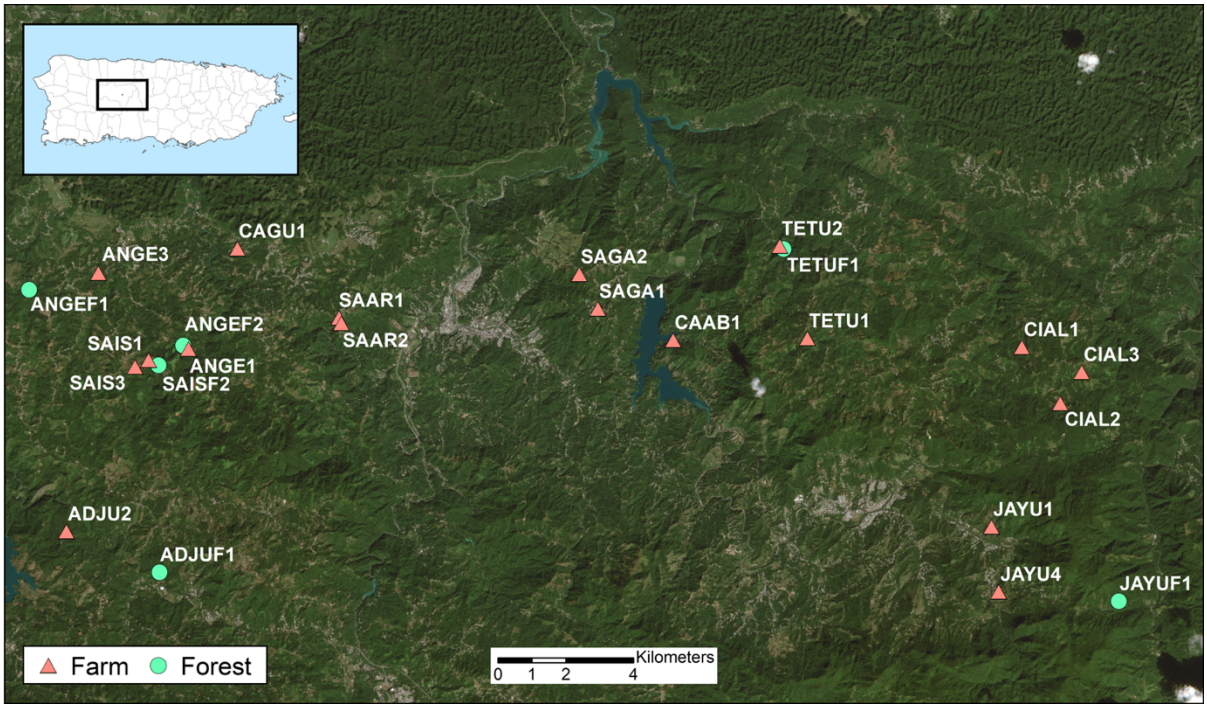

FIGURE 1 Study area in the Cordillera Central of Puerto Rico (inset). Recorder locations are marked with orange triangles at farm sites and green circles at forest sites. Sites were within the municipalities of Adjuntas, Ciales, Jayuya, and Utuado.

2.2 | *Eleutherodactylus* Surveys

2.2.1 | Visual Survey

Eleutherodactylus spp. were surveyed visually on farms following the methods used in Harmon et al. (2019, unpublished manuscript) to inform the placement of up to ten vegetation survey plots per farm and to evaluate the relationship between bioacoustic and visual detection. Frog surveys were conducted inside farm boundaries within 75 m of bioacoustic recorder locations. Surveys began at least one hour after sunset and consisted of walking along farm trails and between rows of coffee, locating individuals using a headlamp or by following the songs of males. Surveys were considered complete when 10 frogs

had been located at least 10 m from one another. Additionally, crop plants within vegetation survey plots were visually inspected for frogs, and opportunistic sightings outside of frog and vegetation surveys were recorded.

2.2.2 | Bioacoustic Survey

We employed ARBIMON portable acoustic recorders, described by Campos-Cerqueira et al. (2017), 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* (Joglar, 1998) 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) (Hilje & Aide, 2012).

The microphones on the recorders have an operational distance of approximately 50 m (Campos-Cerqueira & Aide, 2017). 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 coqui*, the amphibian with the loudest known call, calls at a frequency of approximately 2.5 khz (Drewry & Rand, 1983) at a volume of up to 90 dB (Beard & Pitt, 2005). 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.

2.3 | Vegetation and Site Survey

Vegetation surveys encompassed twenty 10 m-diameter plots at each of the 18 farm sites and followed the methods outlined in Harmon et al. (2019, unpublished manuscript). Plot locations were constrained within farm boundaries and were no more than 75 m from bioacoustic recorder locations. Vegetation

data collected within each point included: percent shade cover; number of shade trees; diameter at breast height (DBH) of shade trees; number of stems of coffee, plantain, citrus, root vegetable, and other crops; whether dry/dead plantain leaves had been removed from plantain stalks (a common management practice); leaf litter depth (deepest area within 0.25 m of point center); herbaceous vegetation height (tallest representative height within 0.25 m of point center); percentage of exposed soil (estimated within 0.25 m radius of point center); and whether herbicide had been applied. Data were summed or averaged across vegetation points to obtain farm-level values. Shade cover was calculated using an iOS device with CanopyApp installed (University of New Hampshire, 2018) . The phone was held level approximately 2 m above the ground when capturing images. Images were analyzed within CanopyApp to identify the percentage of the image in which the sky was visible. The inverse of that value was used as percent shade cover. Shade trees were defined as any tree tall enough for the lowest branches to extend above the height of surrounding coffee. Shade trees were not identified with the exception of crop species (i.e. citrus, avocado). Coffee and plantain stems too small (<0.5 m in height) to provide shelter to *Eleutherodactylus* were not included in stem counts. Herbicide application was determined by evaluating the state of herbaceous vegetation, though it was likely underestimated given that vegetation recovers rapidly in the tropics. We collected data on time since last herbicide, insecticide, and fungicide application from farmer surveys, however we found high uncertainty in farmer estimates due to a lack of written records and continuous nature of spraying on large farms. Because traces of insecticides and fungicides are difficult to detect visually we were unable to include these variables in our site surveys.

2.4 | Landscape Variables

ArcGIS (ESRI, 2017) was used to generate geophysical variables for use in *Eleutherodactylus* abundance analyses. Slope and elevation were determined for the center of each site using a digital elevation model with 30 m resolution from the ASTER II satellite platform. To explore the effects of spatial variables at multiple distances from farms, four ring buffers (75 m, 150 m, 300 m, 500m) were created around each farm site (Figure 2). Landcover within the 500 m buffer was digitized using imagery from DigitalGlobe within Google Earth Pro (Google LLC, 2019) and imported into ArcGIS. Images were georectified by marking sets of five coordinates in the source image as ground control points and pairing them with identical coordinates mapped within ArcGIS. Digitization was done at a scale of 1:1,000. Landcover was classified into 7 categories: secondary forest (SF), non-forest vegetation (grass, shrub) (NF), agriculture (AG), exposed soil (ES), water (WA), paved roads (RD), and structures or concrete (ST). To digitize the roads class an OpenStreetMap (www.opendatacommons.org/licenses/odbl) roads layer for Puerto Rico was downloaded and edited for accuracy using satellite imagery.

2.5 | Indices

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. 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. We calculated the Shannon Diversity Index (SDI) for forest and farm sites using data from the bioacoustic surveys. The ratio of recordings with a species present to total recordings was used as the number of observations for species.

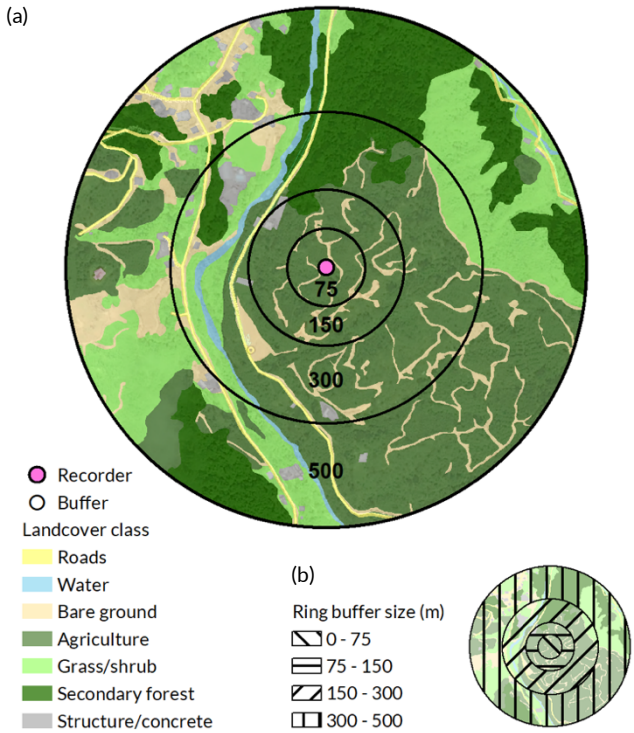

FIGURE 2 (a) Landcover classification example (JAYU4), including ring buffers used in spatial analyses. (b) Ring buffer extent diagram. Buffers are not additive and do not include the area enclosed in the previous buffer. The initial buffer is a 75m radius around recorder locations.

2.6 | Data Analysis

2.6.1 | Bioacoustics 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 (Francisco & Achim, 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 (Smithson & Verkuilen, 2006).

2.6.2 | Site Analyses

Wilcoxon signed-rank tests were used to determine whether species richness, individual *Eleutherodactylus* species abundances, and SHDI differed significantly between farm and forest sites, among farm sites, and among forest sites. All statistical analyses were conducted in program R (R Core Team, 2019). Significance for all analyses was assessed at $p \leq 0.05$.

2.6.3 | Farm-Level Analysis

To test for relationships between farm management variables and the abundance of each species on farms we fit the bioacoustic data to beta regression models with a logit link. Optimal models for each outcome variable (*Eleutherodactylus* species abundance) were selected from a set of candidate models generated from biologically relevant covariates using the model selection package glmulti (Calcagno, 2019). We included the abundance of each non-outcome *Eleutherodactylus* species, all vegetation survey variables, FMI, site size, mean slope, and recorder elevation. While site size, slope, and elevation are physical, not management variables they were included in the farm level models to control for possible effects of site characteristics. We also included interactions between *E. antillensis* and root crop quantity; *E. coqui* and root crop quantity; *E. antillensis* and plantain quantity; *E. coqui* and plantain quantity; herbicide application and slope; and herbicide application and: coffee, plantain, root crop, total crop stems. Candidate models included a full model with all terms, a null intercept only model, and all combinations of covariates. The best model was determined using backwards model selection in which terms were removed systematically from the full model. The maximum number of covariates was

constrained to five to minimize potential model over-fitting, and the number of interaction terms was limited to one to facilitate clearer model interpretation. Models were selected using Akaike information criterion (AIC); models with Δ AIC ≤ -2 were considered significantly better than the full and null models. When no model had Δ AIC ≤ -2 the full or null model was selected. In instances in which the top model AIC values were within 2 points of the closest candidate models, the model with the highest adjusted r^2 value was selected.

Multivariate analysis of variance (MANOVA) was used in the farm-level analysis of species richness and the coquí abundance index. Model selection methods for species richness and SHDI were identical to those used in modeling individual *Eleutherodactylus* species abundances.

2.6.4 | Landscape Level Analysis

To test for significant relationships between *Eleutherodactylus* and landscape-level spatial variability we conducted a second round of model selection using bioacoustic and landcover class data. The seven landcover classes (secondary forest [SF], non-forest vegetation [NF], agriculture [AG], exposed soil [ES], water [WA], roads [RD], structures / concrete [ST]) along with total impervious area (IM) (RD + ST) were modeled with the abundances of each species found in farms, species richness, and SHDI. Model selection at the 75 m, 150 m, 300 m, and 500 m buffer levels were evaluated using identical methods as the farm-level analysis. Beta regressions were used to fit the abundance data for each species, while MANOVA was used with species richness and SHDI.

3 | RESULTS

3.1 | Visual Counts & Bioacoustic Detections of *Eleutherodactylus* Frogs

A total of 159 individual frogs were found across the 18 farm sites. Of those, 100 were seen during visual encounter surveys (82 *E. coqui*, 18 *E. antillensis*), while another 59 were found within survey plots during vegetation surveys (49 *E. coqui*, 10 *E. antillensis*). When we evaluated the relationship between the number of frogs observed and the number of detections in acoustic analyses, we found a significant positive effect of sightings on bioacoustic detections ($z = 2.356$, $p = 0.0185$), with each additional frog observed increasing the likelihood of acoustic detection by 1.1% (Figure 3).

Each site had 288 viable recordings collected while recorders were deployed, with the exceptions of one farm (ANGE3) which had 287, and one forest (ANGEF2) which had 280. Of the 6,903 recordings analyzed, 5,634 (82%) contained one or more species of *Eleutherodactylus*. While there are

ten species of *Eleuthero-dactylus* with ranges that historically overlap our study area (*E. antillensis*, *E. brittoni*, *E. eneidae*, *E. cochranae*, *E. coqui*, *E. gryllus*, *E. hedricki*, *E. portoricensis*, *E. richmondi*, *E. wightmanae*), only four were detected in recordings (Figure 4, Figure 5). Farm sites harbored two to three species while one to three species of *Eleutherodactylus* were detected in forest sites. No site contained all four species. *Eleutherodactylus coqui*, the most commonly detected species, was present in all 24 sites (18 farms, 6 forests). Over one third of farm sites had *E. coqui* in 95% or more of recordings and all forest sites had *E. coqui* in 98% or more of recordings. All farm sites contained *E. antillensis*, which occurred in 3-88% of recordings, but this species only occurred in one forest site. *Eleutherodactylus brittoni* was equally uncommon between farms (28% of sites) and forests (33% of sites). The endangered *E. wightmanae* was the least commonly detected species. It was found in three sites, all of them forests, but was locally abundant where detected, with rates between 60-100%.

3.2 | Vegetation Surveys

Farms cultivated four to six crops, and 55% of farms grew five or more crops. Coffee was the most common crop on farms and accounted for 58% of crop stems on average. Plantain was the second most common crop, with a mean farm value of 29% of stems. Root crops (9%) and citrus

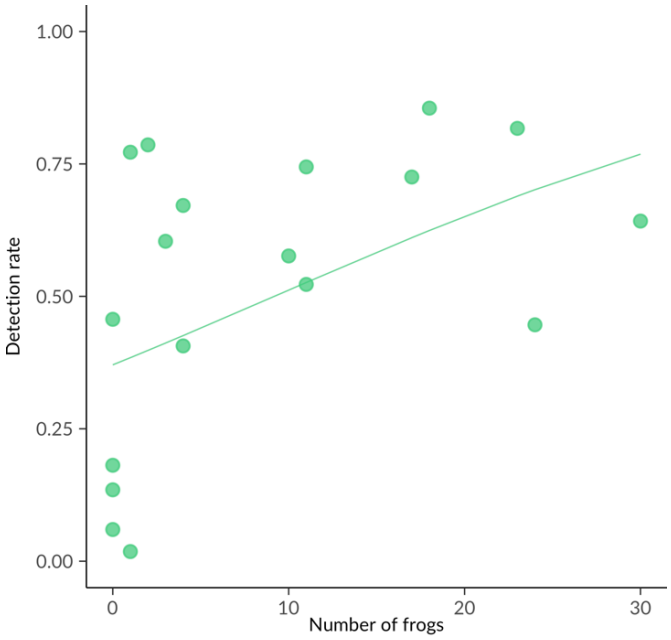

FIGURE 3 The proportion of recordings in which *E. coqui* and *E. antillensis* were detected modelled with the number of individuals of those species observed during coqui surveys using a beta regression (p = 0.0185).

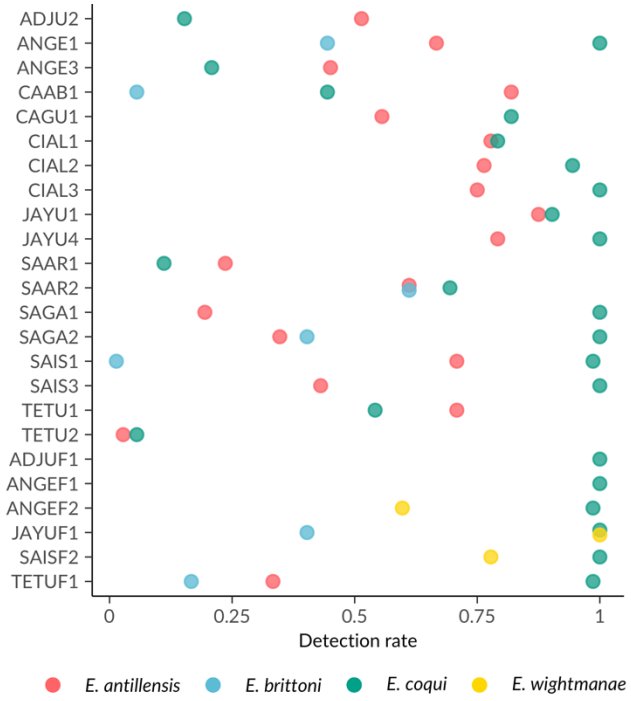

FIGURE 4 Detection rates of *Eleutherodactylus* species in coffee farm (ADJU2:TETU2) and secondary forest sites (ADJUF1:TETUF1) in the central mountains of Puerto Rico.

trees (4%) were the third and fourth most abundant crops planted on farms. All other crops surveyed (avocado [*Persea americana*], papaya [*Carica papaya*], guava [*Psidium guajava*], pineapple [*Ananas comosus*], mango [*Mangifera indica*], and breadfruit [*Artocarpus altilis*]) accounted for less than 1% of total stems combined. The planting density on farms, and thus the vegetative density in cultivated areas, varied widely, with a threefold increase between the lowest (394 stems) and highest (1,182 stems) farm totals (Table 1). The mean planting density on farms was approximately 376 stems/ha.

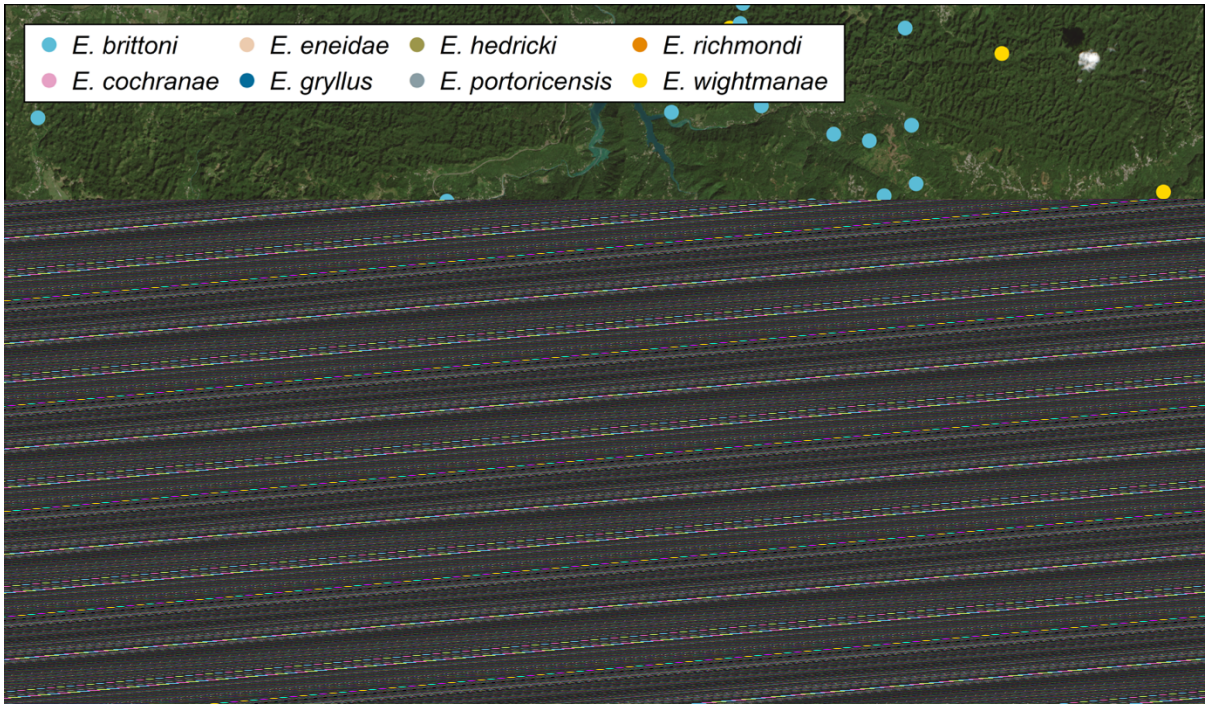

FIGURE 5 Documented observations of the *Eleutherodactylus* species known from the Cordillera Central of Puerto Rico. *Eleutherodactylus antillensis* and *E. coqui* are not included as they are abundant and widespread. *Eleutherodactylus eneidae* and *E. hedricki* are potentially extinct. Farm and forest recorders are designated with triangles. Points are adapted from Joglar 1998, Campos-Cerquiera et al. 2019, and Barker & Rios-Franceschi 2014.

The amount of shade cover and the number and size of shade trees were also highly variable among farms. Shade cover averaged 44% and all farms contained shade trees within cultivated areas, though three farms had only one tree. The farm with the greatest number of shade trees (CAAB1, n = 42) also had the highest shade cover of 89%. Only six farms had more than 50% shade, and no farms had less than 22% (Table 1).

FIGURE 6 (Previous page). Boxplots of detection rates for *Eleutherodactylus* species (a, b, c, d), *Eleutherodactylus* species richness (e), and Shannon Diversity Index (SHDI) values (f) for all sites. Site types and means are differentiated using differing shades (black, grey) and line types (dot-dash, dot, dash). Asterisks denote sites that differed statistically ($p < 0.05$) from the mean for their group (farm, forest). P-values and corresponding bars at the top of plots (a), (c), (d) note where the mean species detection rates were statistically different between farm and forest site types.

TABLE 3 Bioacoustic survey results including site elevation, the number of species detected at each site, percentage of recordings in which each species was detected, and the Shannon Diversity Index (SHDI) values.

	Elevation	Species (no.)	*E. antillensis* (%)	*E. brittoni* (%)	*E. coqui* (%)	*E. wightmanae* (%)	SHDI (val.)
Farm sites							
ADJU2	612	2	51.39	0	15.28	0	0.509
ANGE1	497	3	66.67	44.44	100	0	1.088
ANGE3	419	2	45.07	0	20.83	0	0.600
CAAB1	272	3	81.94	5.56	44.44	0	0.821
CAGU1	389	2	55.56	0	81.94	0	0.685
CIAL1	639	2	77.78	0	79.17	0	0.691
CIAL2	704	2	76.39	0	94.44	0	0.692
CIAL3	704	2	75	0	100	0	0.690
JAYU1	593	2	87.5	0	90.28	0	0.692
JAYU4	639	2	79.17	0	100	0	0.692
SAAR1	499	2	23.61	0	11.11	0	0.604
SAAR2	460	3	61.11	61.11	69.44	0	1.083
SAGA1	521	2	19.44	0	100	0	0.474
SAGA2	520	3	34.72	40.28	100	0	1.033
SAIS1	552	3	70.83	1.39	98.61	0	0.747
SAIS3	606	2	43.06	0	100	0	0.634
TETU1	655	2	70.83	0	54.17	0	0.673
TETU2	376	2	2.78	0	5.56	0	0.655
Average	537	2	56.83	8.49	70.29	0	0.726
Forest sites							
ADJUF1	578	1	0	0	100	0	0.000
ANGEF1	392	1	0	0	100	0	0.000
ANGEF2	530	2	0	0	98.61	59.72	0.663
JAYUF1	364	3	0	40.28	100	100	1.081
SAISF2	764	2	0	0	100	77.78	0.685
TETUF1	566	3	33.33	16.67	98.61	0	0.943
Average	509	2	5.56	9.49	99.54	39.58	0.562

3.4 | Farm Management and Site Characteristics Analysis

Contrary to our expectations plantain stem quantity was not a strong predictor of species abundances and root crop stem quantity had a strong negative impact in each of the six final farm management models. Increasing root crop abundance led to significant decreases in the probabilities of detecting *E. antillensis* ($z = -2.97$, $p < 0.01$), *E. brittoni* ($z = -2.74$, $p = 0.01$), and *E. coqui* ($z = -4.7$, $p < 0.01$) on farms, as well decreases in SHDI ($z = -4.57$, $p < 0.01$) and species richness ($z = 4.1$, $p < 0.01$) (Table 4). Interestingly, interactions between root crop quantity and the abundances of other *Eleutherodactylus* species increased the odds of detecting both *E. antillensis* ($z = 3.65$, $p < 0.01$) and *E. coqui* ($z = 3.43$, $p < 0.01$). Farms with steeper slopes had higher species richness ($z = 4.1$, $p < 0.01$), higher abundance of *E. brittoni* ($z = 5.78$, $p < 0.01$), and higher SHDI than flatter farms. Herbicide application followed our predictions for *E. coqui* but not the remaining species. Farms with herbicide applied to a greater number of vegetation survey plots had lower species richness ($z = -3.33$, $p = 0.01$) and lower abundance of *E. coqui* ($z = -5.66$, $p < 0.01$) (Figure 7, Table 4). Herbicide application did not appear in the final models of *E. antillensis*, *E. brittoni*, or SHDI. Because no forest specialist species of *Eleutherodactylus* were found in farms we were unable to evaluate the impacts of shade cover on their abundance. Shade cover had opposing

TABLE 4 Results of farm level models for each species of *Eleutherodactylus* detected in farms (a, b, c), species richness (d), and the Shannon Diversity Index (SHDI) (e).

	Model	Estimate (±SE)	z value	Pr(>|z|)
(a)	*E. antillensis* †			
	(Intercept)	1.263 ± 1.447	0.631	0.5283
	Shade cover	1.029 ± 1.010	**2.861**	**0.0042**
	Vegetation height	0.944 ± 1.017	**-3.370**	**0.0008**
	Root crop	0.988 ± 1.004	**-3.359**	**0.0008**
	E. coqui * Root	1.018 ± 1.004	**4.495**	**< 0.0001**
	Adjusted r2	0.647		
(b)	*E. brittoni* †			
	(Intercept)	0.546 ± 4.797	-0.386	0.6992
	Recorder elevation	0.992 ± 1.002	**-3.405**	**0.0007**
	Shade cover	0.972 ± 1.013	**-2.224**	**0.0262**
	Root crop	0.991 ± 1.003	**-2.744**	**0.0061**
	Slope	1.296 ± 1.046	**5.781**	**< 0.0001**
	Adjusted r2	0.649		
(c)	*E. coqui* †			
	(Intercept)	5.071 ± 2.815	1.569	0.1167
	Root crop	0.979 ± 1.005	**-4.695**	**< 0.0001**
	Litter depth	0.619 ± 1.116	**-4.375**	**< 0.0001**
	Herbicide	0.951 ± 1.009	**-5.664**	**< 0.0001**
	Farm area	1 ± 1	**6.300**	**< 0.0001**
	E. antillensis * Root	1.022 ± 1.006	**3.425**	**0.0006**
	Adjusted r2	0.733		
(d)	Species Richness ‡			
	(Intercept)	1.509 ± 0.277	5.446	0.0001
	Coffee	**0.002 ± 0.001**	**3.216**	**0.0068**
	Root crop	**-0.006 ± 0.001**	**-5.865**	**0.0001**
	Herbicide	**-0.009 ± 0.003**	**-3.325**	**0.0055**
	Slope	**0.057 ± 0.014**	**4.103**	**0.0012**
	Adjusted r2	0.692		
(e)	SHDI ‡			
	(Intercept)	0.7126 ± 0.1581	4.509	0.0007
	Coffee	**0.0006 ± 0.0002**	**2.982**	**0.0114**
	Root crop	**-0.0015 ± 0.0003**	**-4.574**	**0.0006**
	Litter depth	**-0.0379 ± 0.0154**	**-2.461**	**0.03**
	Slope	**0.0332 ± 0.0053**	**6.298**	**< 0.0001**
	DBH	**-0.0106 ± 0.0027**	**-3.907**	**0.0021**
	Adjusted r2	0.73		

Notes: Significant terms (p<0.05) are in bold.
DBH = diameter at breast height.
† Estimates (odds ratios) from beta regressions.
‡ Estimates from linear models.

effects on the two open-habitat species, with greater shade cover related to higher *E. antillensis* abundance (z = 2.86, p = 0.004) but lower *E. brittoni* abundance (z = -2.22, p = 0.026). Shade cover did not appear in any other models. The number of shade trees did not appear in any of the final models, however trees with larger diameters were negatively associated with SHDI (z = -3.91, p < 0.01). Where leaf litter depth was greater, the abundance of *E. coqui* (z = -4.38, p < 0.01) and the SHDI (z = -5.02, p < 0.01) both decreased.

Farm management intensity did not hold to our prediction. The farm management index (FMI), which had a low of 1.61 and high of 6.82, did not have a significant effect as a sole predictor for any species of *Eleutherodactylus*, or for species richness or SHDI. There was a small positive association between FMI and each species and between FMI and SDHI (Figure 8), but p-values did not approach even marginal levels of significance and FMI explained less than one percent of the variance in all models.

3.5 | Landscape Level Analyses

Surrounding land cover composition was not an important determinant of *Eleutherodactylus* presence and abundance on farms. Model selection found no improvement using landcover data in predicting the abundances of *E. antillensis*, *E. brittoni*, species richness, and SHDI over the null models at any distance. We predicted the abundances

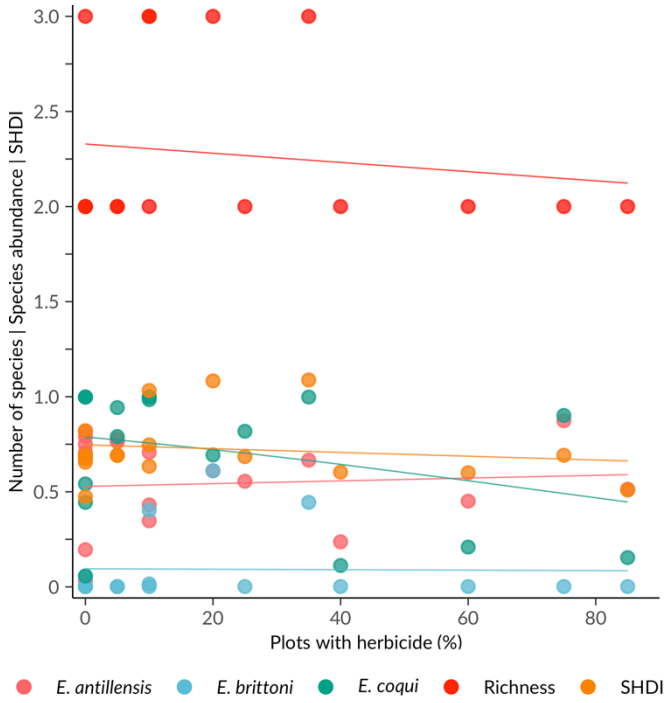

FIGURE 7 Responses of *Eleutherodactylus* species abundances, species richness, and Shannon Diversity Index (SHDI) to changes in herbicide application. The vertical axis represents all variables as the unit intervals are the same for each measure.

TABLE 5 Landscape level beta regression model comparisons for *E. coqui* at the 75 m, 150 m, and 300 m ring buffer sizes.

Model	Parameter	Estimate ± (SE)	z value	Pr(>|z|)
E. coqui				
75 m	**(Intercept)**	**8.016 ± 1.624**	**4.291**	**< 0.01**
	Non-forested	**0.715 ± 1.144**	**-2.489**	**0.01**
	Secondary forest	**0.840 ± 1.074**	**-2.450**	**0.01**
	Adjusted r2	0.416		
150 m	**(Intercept)**	**16.259 ± 2.075**	**3.820**	**< 0.01**
	Impervious	**0.778 ± 1.132**	**-2.032**	**0.04**
	Secondary forest	**0.942 ± 1.025**	**-2.389**	**0.02**
	Adjusted r2	0.334		
300 m	**(Intercept)**	**8.871 ± 2.446**	**2.440**	**0.02**
	Secondary forest	0.990 ± 1.007	-1.556	0.12
	Adjusted r2	0.281		

Notes: Significant terms (p<0.05) are shown in bold.

of open-habitat species on farms would not be impacted by nearby secondary forest cover but found a negative impact on *E. coqui* abundance at multiple distances from farm sites recorders (Table 5). The percentage of forest area, with average values of 16% at 75 m and 40% at 150 m (Appendix A), had a negative relationship with *E. coqui* abundance at both 75 m (z = -2.45, p = 0.01) and 150 m (z = -2.39, p = 0.01). At 300 m, where average forest cover rose to 58% of total area, a trend remained between forest cover and *E. coqui* (p = 0.12) but the relationship was not significant. The percentage of surrounding area covered by grass and shrubs and by development (structures, concrete, asphalt) also negatively impacted *E. coqui* abundance inside of farms. Though landscape effects on forest habitats were outside the scope of our research questions, we noted surrounding forest cover had a positive influence on *E. wightmanae* up to, but not past, 150 m (Table 6).

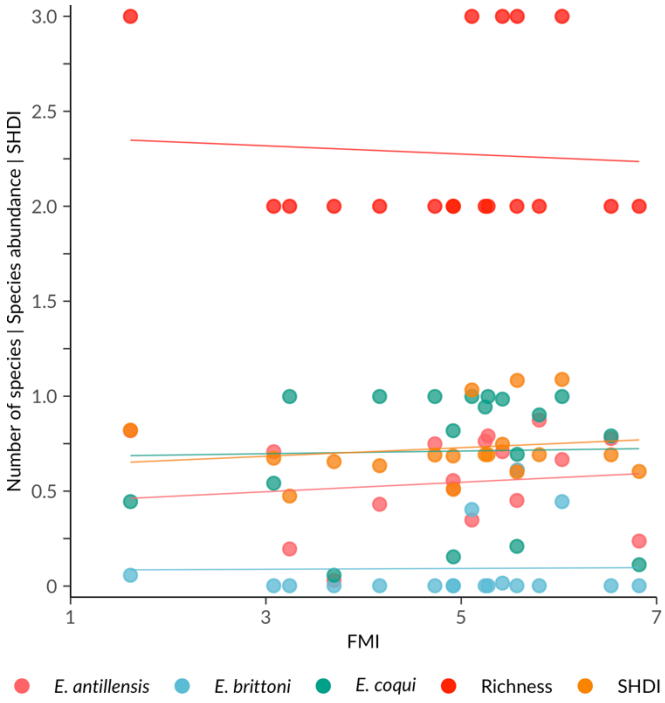

FIGURE 8 Responses of *Eleutherodactylus* species abundances, species richness, and Shannon Diversity Index (SHDI) to changes in farm management intensity index (FMI). The vertical axis represents all variables as the unit intervals are the same for each measure.

TABLE 6 Landscape level beta regression model comparisons for *Eleutherodactylus wightmanae* at the 75 m, 150 m, and 300 m ring buffer sizes.

	Model	Estimate (±SE)	z value	Pr(>|z|)	Adjusted r2
E. wightmanae					
75 m	~ SF	1.055 ± 1.035	1.572	0.116	0.276
150 m	~ SF	1.022 ± 1.016	1.393	0.164	0.209
300 m	~ 1				
500 m	~ 1				

4 | DISCUSSION

4.1 | *Eleutherodactylus* Diversity and Abundance Variability in Farms and Forests

We compared the species richness and abundances of *Eleutherodactylus* frogs between and among coffee agroecosystems and secondary forests in Puerto Rico to evaluate the potential for amphibian conservation in a common agricultural land use in the tropics. We found significant variability among coffee farms in *Eleutherodactylus* species richness, individual species abundances, and the Shannon Diversity Index (SHDI). Among forest sites, species richness was consistent but diversity and species abundances showed variation.

Comparison of coffee farm sites with secondary forest sites revealed equal richness and diversity, with each containing an average of two species of *Eleutherodactylus*. Similar species richness between farms and forests has also been reported for the western central mountains in Puerto Rico (Monroe et al., 2017) and for avian (Frishkoff et al., 2014), arthropod (Mas & Dietsch, 2004), and herpetofaunal (Lenart et al., 1997; Murrieta-Galindo et al., 2013b) diversity in other coffee growing regions in Latin America. Although farms supported the same species numbers as secondary forests in our study, species communities differed**.** The endangered *E. wightmanae* (Angulo, 2008) occurred solely in forest sites while *E. antillensis*, widely considered an open-habitat species (Joglar, 1998), occurred almost exclusively in farm habitats. The three species we detected on farms (*E. antillensis*, *E. brittoni*, and *E. coqui*) are widespread and listed as species of least concern by IUCN (Angulo, 2010; Hedges et al., 2008; Ríos-López, 2008). In contrast *E. wightmanae*, like the majority of *Eleutherodactylus* species in Puerto Rico, is dependent upon forest habitats (Joglar, 1998) and more restricted in range. Of the four species of *Eleutherodactylus* previously observed in the central mountains but not detected in this study, three (*E. gryllus*, *E. portoricensis*, *E. richmondi*) are also forest specialists (Joglar, 1998). Had a greater number of forest specialists been found, differences in species richness and composition may have been more pronounced.

In the only other study of *Eleutherodactylus* occurrence within coffee farms in Puerto Rico, Monroe et al. (2017) found equal probability of occupancy of *E. antillensis* and increasing probability of occupancy of *E. wightmanae* across sun coffee, shade coffee and forest sites. Although their study was conducted in a more western part of the central mountains than our study area, the agricultural landscapes and regional species pools are the same. Discrepancies in bioacoustic detection of the aforementioned species may be related to differences in sampling protocol. To reduce edge effects Monroe et al. placed recorders in forest sites at least 50 m from major roads, the effective range of the recorders used. However, movement of roadside species into forest edges can result in their detection at that distance. Previous research indicates *E. antillensis* is commonly found in vegetation along roads

(Henderson & Powell, 2009) and frequently occupies forest borders, but not closed-canopy forest (Joglar, 1998). In our study the only forest site in which *E. antillensis* was found (TETUF1) contained a semi-paved private road leading to a nearby farm, while all other forest sites were 75 m from any road. It is plausible that in both studies the detection of *E. antillensis* in forests was driven by their presence in forest edges rather than in core forest habitat. Sampling beyond the intended survey area, i.e. farm or forest boundaries, could also be the source of discrepancies in *E. wightmanae* detection. While Monroe et al. found this species in sun and shade coffee farms we did not detect *E. wightmanae* outside of forests. A complicating factor in bioacoustic surveys on farms in Puerto Rico is that many have smaller dimensions (< 100 m) than the detection range of the recorders. In our study the addition of white noise to recordings from small farms to limit detection distance reduced the number of species detected at two farm sites (ANGE3, CAGU1), implying the calls of some species originated outside of the farms. It is possible that the occupancy of farms by *E. wightmanae* reported by Monroe et al. was the result of individuals calling from surrounding forest rather than from within farms.

Eleutherodactylus brittoni proved to be uncommon in our study irrespective of land use. Despite a known preference for open and disturbed sites (Joglar, 1998) this species was detected in less than 10% of farm site recordings. The reasons for such low detection rates are unclear and may warrant further attention. In contrast the detection of *E. coqui* in all farm and forest sites is unsurprising given its presence in all ecotypes across Puerto Rico (Joglar, 1998; Stewart & Woolbright, 1996). Unexpectedly, however, *E. coqui* detection rates in forest sites were nearly 1.5 times those of farms (Figure 6, Table 4) and within farms rates varied from only 5% to 100% of recordings. This suggests that many but not all coffee farms serve as high-quality habitat for *E. coqui*.

Overall, the observed variation in *Eleutherodactylus* species abundances among sites is in line with other studies in agroecosystems which have demonstrated that effects of habitat alteration and intensification are species-specific (Borkhataria et al., 2012a; Greenberg et al., 1997; Lenart et al., 1997; Murrieta-Galindo et al., 2013b; Perfecto et al., 2003).

4.2 | Farm Management Impacts on *Eleutherodactylus* Diversity and Abundance

We found large differences across farms in shade and ground cover, crop composition, and management activities. Each of the 14 variables related to vegetation and site characteristics surveyed on farms (Table 1) showed wide swings (threefold or greater) in the data. Our farm management models aimed to link differing *Eleutherodactylus* abundances among sites to the high site variability we observed qualitatively among farms and quantitatively in the management variables. The farm management intensity index generally agreed with the visible gradient in structure and habitat complexity among farms and we expected to see strong responses of *Eleutherodactylus* to changes in coffee farm management, as amphibians in both aquatic and terrestrial habitats are highly sensitive to environmental change. Yet

when we attempted to correlate measures of species abundance and richness to the management intensity index, we found no predictable response or significant correlation (Figure 8). While forest species may depend on structurally complex farms that resemble forest habitats, the disturbance-adapted species present in our farm sites were abundant in many simplified farms and did not respond uniformly to changes in management intensity. Mas and Dietsch (2003) found that a management intensity index successfully predicted butterfly species richness and proved a useful tool for evaluating the conservation potential of coffee agroecosystems under varying management practices. However, Mas and Dietsch detected many forest-dependent butterflies highly sensitive to changes in vegetation structure and diversity. Further, their study took place within a landscape of large farms with only patches of remnant forest remaining. In this setting, habitat loss caused by intensification of shaded farms can have considerable impacts on biodiversity in agroecosystems (Tscharntke et al., 2005). The farm sites in our study were small and surrounded by a mosaic of secondary forests and agriculture, where suitable habitats for the species occupying farms are abundant. As a result, migration from surrounding landscapes may dampen the effects of management intensity on species abundances.

Although the management intensity index did not predict *Eleutherodactylus* species richness or abundances, important predictors within the farm survey variables were identified by models of farm-level richness, SHDI, and species abundances. We expected the root crops malanga and yautia to be important retreat sites because of their structural similarity to bromeliads, which many *Eleutherodactylus* species are known to use as retreat sites in forests (Henderson & Powell, 2009; Joglar, 1998). Instead we found a negative effect of root crop quantity in all five models despite frequent observations of frogs on root crops. Forty percent of *E. antillensis* found during the day, and the only *E. antillensis* nest observed in our study, were located on root crops. We suggest two potential, non-exclusive explanations for this surprising relationship. The first is that root crop leaf axils, which pool water, may collect and concentrate herbicides and insecticides from overspray during application or from runoff dripping from overhanging coffee plants. Herbicide application had a negative impact on species richness and *E. coqui* abundance in our models. Prior research has highlighted the propensity of pesticides to move, accumulate and persist in agricultural settings (D. E. Robinson & Mansingh, 1999; D. E. Robinson et al., 1997) and has documented the detrimental effects of many farm chemicals on amphibians, including high mortality of juveniles (Caballero de Castro et al., 1997; Relyea, 2005; Storrs Méndez et al., 2009). A second potential driver of the negative relationship between root crops and *Eleutherodactylus* may be a vulnerability of sheltering frogs to terrestrial predators during the day. While most bromeliads are elevated in trees, root crops are located on the ground where frogs are more exposed to chickens, ducks, geese, cats and dogs. Both pesticides and predator exposure could make root crops an ecological trap on farms.

For two species, *E. antillensis* and *E. coqui*, the impact of root crops on abundance changes when the other species is found in high densities. The models for both species contain a positive interaction

between root crop quantity and abundance of the other species. *Eleutherodactylus antillensis* and *E. coqui* were the two most abundant species detected and overlap in their size and habitat use. When both species are abundant they may compete for retreat and reproduction sites on farms. Harmon et al. (2019, unpublished manuscript) found that *E. coqui* demonstrated a preference for plantain as a diurnal retreat in farms and that *E. antillensis* used plantain and root crops more frequently than other farm vegetation. When abundances are high and available plantain sites are occupied, these species likely shelter in root crop axils in greater numbers. Higher densities of root crops in this scenario might provide essential habitat and offset negative effects of root crop use on abundance. Furthermore, farms applying fewer or no pesticides are more likely to harbor high abundances of *E. antillensis* and *E. coqui*; in these farms root crops could provide important habitat without the harmful effects of accumulating pesticides.

Steeper farms were associated with higher species richness, diversity, and *E. brittoni* abundance. Previous studies have found a relationship between degree of slope and pesticide residence time, with higher runoff reducing pesticide levels on steep slopes (D. E. Robinson et al., 1997). In contrast pesticide accumulation could explain the negative impact of leaf litter depth on SHDI and *E. coqui* abundance. Pesticide breakdown through photolysis has been shown to occur at lower rates where access to light is limited (D. E. Robinson & Mansingh, 1999; D. E. Robinson et al., 1997). Deep leaf litter may slow decomposition of pesticides by trapping residue in small, shaded pools between leaf layers where degradation by photolysis and by soil microbes is likely inhibited. Juvenile frogs, which are often found on or near the ground (Joglar, 1998; K. Harmon, personal observation), may be disproportionately affected by prolonged residence times. Mortality may be further increased by predators such as chickens and ducks that forage in leaf litter in farms.

Shade cover was not associated with higher species richness or SHDI, and higher amounts of shade did not result in lower abundances of open-habitat species. Despite similarities in their natural histories including absence in closed-canopy forests, models showed opposing effects of shade on *E. antillensis* and *E. brittoni* abundances. While the negative impact of shade on *E. brittoni* is in line with known habitat preferences, the positive effect on *E. antillensis* is unexpected and seemingly driven by its high abundance on the farm with the most shade cover (CAAB1). Roughly half the extent of this small farm is bordered by a road, meaning the high density of *E. antillensis* could be due to the large proportion of forest edge habitat.

4.3 | Landscape Effects

Our landscape analyses found surrounding landcover did not impact species richness or diversity of *Eleutherodactylus* on farms. Secondary forest was the dominant landcover 150-500 m from farm recorders, followed by agriculture and non-forest vegetation. The amount of secondary forest in the landscape did not affect the abundances of the two open-habitat species, confirming our expectation

that these species can make use of open areas within highly forested landscapes. Contrary to our predictions, however, larger proportions of agriculture and non-forest cover did not lead to higher abundances of *E. antillensis* or *E. brittoni*, perhaps because even in lower proportions these landcovers, along with roads and forest edges provide ample connectivity and opportunity for colonization of already favorable farm habitats. The finding that only *E. coqui* was affected by surrounding landcover, despite being the least demanding species in its habitat requirements and most abundant species in this study, is perplexing. The negative effect of secondary forest cover on *E. coqui* abundance at multiple scales contrasts with higher detection rates in forests than farms and appears to be driven by a farm site with unusually low abundance of *E. coqui* and high proportions of surrounding forest cover (TETU2; Appendix B). High shade cover and shade tree density, an average FMI score for farms, and no detected herbicide application would suggest this farm is high-quality habitat for *E. coqui* (Appendix C); that TETU2 instead had the lowest *E. coqui* abundance of any site is surprising and may point to variability in habitat quality not captured in our farm survey. The only other species found on this farm, *E. antillensis*, was also found at its lowest farm-level density. Site TETU2 contained a remarkably high concentration of the invasive ant species *Wasmannia auropunctata* (K. Harmon, personal observation) which was being treated with insecticide by the farm owner (personal communication). Disturbance by this aggressive, stinging ant, and the insecticide used to combat it could represent unmeasured drivers of *Eleutherodactylus* abundance. When TETU2 was excluded from land cover analyses the secondary forest effect on *E. coqui* disappeared and no landcover model outperformed the null model.

4.4 | Implications for farm management and biodiversity conservation

Shade-grown coffee agroforestry systems have received a great deal of attention for their potential to maintain tropical biodiversity within working landscapes. In Puerto Rico, the presence of many threatened or endangered *Eleutherodactylus* species in coffee-growing regions begs the question of whether coffee farms function as suitable habitat. Although our study found comparable levels of species richness and evenness between farms and secondary forests, the absence of forest specialists from our farm sites highlights a potential limitation in the contribution of coffee agroforestry to *Eleutherodactylus* conservation. We detected *E. wightmanae* in two forest sites (ANGEF2, SAISF2) located within 100 m of corresponding farms sites (ANGE1, SAIS1), and suspect the low shade cover and scarcity of shade trees at these farms prevented colonization. *Eleutherodactylus wightmanae* is considered to be dependent on forests (Angulo, 2008) and in agricultural landscapes colonization and extinction rates are strongly influenced by forest cover (Monroe et al., 2017). During a period of widespread deforestation, densely shaded coffee farms likely formed the primary habitat for populations of forest-dwelling species of *Eleutherodactylus* and other forest taxa across the Central Mountains (Brash, 1987; Nir, 1988; Weaver & Birdsey, 1986) indicating extant species are not completely restricted

to undisturbed or mature forest habitats. Previous studies have demonstrated that within forested areas the degree of humidity and leaf litter, rather than stand diversity or composition, dictate the presence of amphibian species of the forest interior (Acevedo-Charry & Aide, 2019; Santos-Barrera & Urbina-Cardona, 2011). Forest-dependent *Eleutherodactylus* in Puerto Rico have colonized mid-successional secondary forests high in canopy cover, humidity and leaf litter (Acevedo-Charry & Aide, 2019). In our study, farm sites with dense shade and high leaf litter (e.g. CAAB1, TETU1) did not harbor forest specialists. However, the habitat potential of these farms could not be adequately evaluated because species such as *E. wightmanae* were also missing from recordings in surrounding secondary forest. Further studies targeting high-quality farms in areas where forest species are present in the landscape will be required to determine whether coffee farms under current management regimes have conservation value for Eleutherodactylids.

The prevalence in farms of non-forest *Eleutherodactylus* species abundant across Puerto Rico may be indicative of a larger pattern of biotic homogenization of amphibian communities, whereby narrowly distributed species are replaced by a small set of hardy species that perform well in simplified and fragmented habitats (Nowakowski et al., 2018; Pyron, 2018). This phenomenon has been observed among avian species in Puerto Rico, with omnivorous species and seed-eating species characteristic of open habitats expanding into the ranges of several endemic, forest-dependent species, and in a few cases contributing to population declines (Brash, 1987; Vázquez Plass & Wunderle Jr, 2013; Wiley, 1986). In Costa Rica, shifts toward disturbance-tolerant species communities following forest conversion to oil palm monocultures have been linked to reductions in structural complexity and microhabitat diversity (Gallmetzer & Schulze, 2015). Reductions in canopy and shrub cover as well as leaf litter and deadwood create hostile environments for many species, and the loss of oviposition sites in leaf litter accumulations, tree holes, and bromeliads may be driving the complete absence of common forest species from oil palm plantations. In the Central Mountains of Puerto Rico, the alteration of vegetation structure and reduction of shade cover caused by coffee farm intensification appears to be altering the suitability of agricultural landscapes for *Eleutherodactylus* species, promoting colonization by generalist and open-habitat species while reducing microhabitats with the potential to shelter forest-specialists. Ending the promotion of sun coffee and restoring structural complexity to simplified farms could help reverse the apparent homogenization of amphibian communities. Shade tree planting has been shown to increase the diversity of avian species on coffee farms in this region (Irizarry et al., 2018).

Greater canopy cover and leaf litter on farms may increase their attractiveness to forest-dwelling amphibians but can also promote the accumulation and persistence of pesticides in otherwise favorable microhabitats. Tropical agriculture contends with environmental conditions that favor rapid growth of weeds and the buildup of arthropod pests and plant pathogens as a trade-off for the benefit of year-round cultivation. The wide variety of herbicides, insecticides, and fungicides applied in response are economically and environmentally costly and can have negative effects on human health in

agricultural areas (Alavanja et al., 2004; Rosenstock et al., 1991; Wesseling et al., 1997). For instance Endosulfan, the primary pesticide applied to control coffee berry borer (*Hypothenemus hampei*) (Karp et al., 2013), can persist for several months in coffee plantations and runoff can contaminate soil, water and aquatic fauna. (D. E. Robinson & Mansingh, 1999). The negative impact of herbicide application on *Eleutherodactylus* richness and diversity in this study support the notion that reducing the effects of agricultural intensification on amphibians requires directly addressing chemical inputs to agroecosystems (Perfecto & Vandermeer, 2008). Studies have shown that major reductions in pesticide use can be achieved by providing proper training and detailed product information (D. E. Robinson & Mansingh, 1999). Weed growth and agricultural pests can be suppressed naturally by increasing shade levels and encouraging biological control through greater vegetative diversity. In coffee farms, enhancing conditions that promote predation of arthropods by birds (Greenberg et al., 2000; Perfecto et al., 2004), anoles (Monagan Jr. et al., 2017) or both (Borkhataria et al., 2006) can increase top-down pressure on agricultural pests. *Eleutherodactylus coqui* consume high numbers of prey items and are considered the most important consumer of nocturnal arthropods in Puerto Rico (Joglar, 1998), yet to date no studies have been conducted on the impacts of *Eleutherodactylus* species on coffee pests. Maintaining or increasing the structural complexity of coffee farms may simultaneously make them more permeable to forest amphibians and reduce the need for pesticide inputs.

Our study and that of Monroe et al. (2017) have established that coffee farms currently serve as habitat for several amphibian species in Puerto Rico. Yet the extent to which they can provide suitable habitat for local species of conservation concern, all forest specialists, remains uncertain. Directly examining species-specific habitat use within agricultural landscapes, with a focus on forest specialists, is a necessary next step in assessing the conservation value of agroecosystems for amphibians. A reduction of canopy cover accompanying management intensification is occurring in the context of a warming climate and increasing drought severity (Hayhoe, 2013). These conditions are exacerbating *Eleutherodactylus* susceptibility to chytridiomycosis infection (Burrowes, 2009; Burrowes et al., 2004) and may promote transmission among individuals by crowding them into fewer humid microhabitats (Longo, Burrowes & Joglar, 2006). In addition to curtailing the ability of farms to harbor forest species, the transition to sun coffee can diminish the habitat quality of adjacent forests for amphibians (Gallmetzer & Schulze, 2015; Santos-Barrera & Urbina-Cardona, 2011). Intensification and degradation of habitat in agricultural landscapes could be additional synergistic effects contributing to amphibian declines in Puerto Rico. Understanding the suitability of human-modified habitats for amphibian communities and enhancing habitat quality are urgent needs given rapid rates of amphibian extinctions in Puerto Rico and globally.

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6 | APPENDICES

APPENDIX A Landcover class areas by buffer size. Units are percent of total area. Secondary forest includes all forested areas; non-forest vegetation includes shrub and grass cover; agriculture includes shaded and unshaded crops where crops are visible from above; exposed soil includes bare ground and unpaved roads; structures include buildings and surrounding paved areas; impervious surfaces combines road and structure classes. Ring buffers are centred on audio recorders.

Buffer	Class	Minimum	Mean	Maximum
75 m	Secondary forest	0	16.1	94.3
	Non-forest vegetation	0	10	39.7
	Agriculture	0	58.3	94
	Exposed soil	0	10.8	28
	Water	0	0.1	0.8
	Road	0	3.2	12.2
	Structure	0	1.5	8.3
	Impervious	0	4.7	20.5
150 m	Secondary forest	3.6	40.2	89.5
	Non-forest vegetation	0	18.7	44.7
	Agriculture	0	27.3	83.3
	Exposed soil	0	8.6	18.3
	Water	0	1.3	23.6
	Road	0	2.6	12.4
	Structure	0	1.3	5.2
	Impervious	0	3.9	17.2
300 m	Secondary forest	14	58	87.8
	Non-forest vegetation	1.2	19.3	40.6
	Agriculture	0	12.9	48
	Exposed soil	0.6	5.1	12.5
	Water	0	1.6	21.3
	Road	0	2.1	5.8
	Structure	0	1	3.6
	Impervious	0	3.1	8.7
500 m	Secondary forest	24.6	69.4	90.1
	Non-forest vegetation	3.7	17.3	36.2
	Agriculture	0	7	32
	Exposed soil	0.3	3	7.5
	Water	0	0.8	10.1
	Road	0.2	1.8	6.3
	Structure	0	0.8	2.6
	Impervious	0.3	2.6	8.9

APPENDIX B Farm vegetation survey data for each of the 18 farm sites, including shade cover; the number of shade trees; average shade tree diameter at breast height (DBH); the total number of crop stems; the number of stems of: coffee, plantain, root crops, citrus; the percentage of plots at which dead plantain leaves had been removed from plantain stalks (Trimmed); average leaf litter depth; the average percentage of exposed soil in a plots; the percentage of plots at which herbicide had been applied; the farm management intensity index (FMI) score; and the average slope of farms.

Farm	Shade (%) †	Shade trees (no.) ‡	DBH (cm) †	Crop stems (no) ‡	Coffee (no.) ‡	Plantain (no.) ‡	Root crop (no.) ‡	Citrus (no.) ‡	Other crops (no.) ‡	Trimmed (%) †	Herbaceous height (cm) †	Litter depth (cm) †	Exposed soil (%) †	Herbicide (%) †	FMI (val.) ‡	Slope (deg.) †
ADJU2	38	4	48	468	317	53	46	52	0	0	16	4	15	85	4.92	13.9
ANGE1	33	7	31	408	279	90	16	20	3	91	11	4	29	35	6.03	20.3
ANGE3	26	11	28	503	391	91	1	18	2	62	17	5	14	60	5.57	4.28
CAAB1	89	42	27	503	469	5	25	4	0	0	34	8	14	0	1.61	13.3
CAGU1	59	20	30	481	365	26	38	52	0	80	19	3	18	25	4.92	5.42
CIAL1	25	1	30	891	439	339	106	7	0	65	5	5	50	5	6.53	13.9
CIAL2	30	9	32	416	206	56	145	8	1	70	17	4	27	5	5.25	18.8
CIAL3	49	28	31	608	231	204	160	13	0	21	16	3	47	0	4.73	13.2
JAYU1	54	16	44	469	343	115	0	8	3	79	5	4	32	75	5.80	14.8
JAYU4	43	7	46	1182	382	514	279	3	4	50	30	3	43	0	5.27	22.6
SAAR1	22	2	30	676	276	291	107	1	1	65	13	3	46	40	6.82	11.4
SAAR2	36	5	40	394	283	64	38	7	2	100	10	5	29	20	5.57	22.8
SAGA1	65	18	28	518	98	310	38	61	11	42	38	7	25	0	3.24	11.4
SAGA2	29	1	8	647	394	231	15	6	1	29	28	6	19	10	5.11	12
SAIS1	24	3	44	443	316	112	9	6	0	45	10	4	38	10	5.42	11
SAIS3	31	1	44	469	142	297	21	9	0	6	29	4	22	10	4.16	11.5
TETU1	70	22	14	696	181	400	110	4	1	55	42	9	16	0	3.08	15.3
TETU2	68	26	31	842	484	146	204	6	2	88	33	7	20	0	3.70	13.5

† Averaged single value from survey points at a site
‡ Site total from survey points

APPENDIX C Area of agriculture (AG), exposed soil (ES), non-forest vegetation (NF) including shrubs and grass, roads (RD), forest (SF), structures (ST) and water (WA) around farm sites at distances of 0-75 m, 75-150 m, 150-300 m, and 300-500 m from recorder locations. Total area of each ring is provided next to the buffer size.

	75 m (18 ha)							150 m (53 ha)						
Farm	AG	ES	NF	RD	SF	ST	WA	AG	ES	NF	RD	SF	ST	WA
ADJU2	10.9	1.74	0.86	0	4.21	0	0	16.1	2.37	9.02	0	25.5	0	0
ANGE1	16.6	0.96	0.03	0	0.08	0	0	19.9	3.84	5.56	0.15	23.5	0	0
ANGE3	4.52	1.32	7.01	0.27	4.37	0.18	0	2.26	1.3	9.87	0.89	37.4	1.33	0
CAAB1	0	0	0	0.76	16.7	0.14	0.1	0	0	0.42	1.61	37.8	0.74	12.5
CAGU1	8.8	0.66	4.82	0.73	1.59	1.04	0	9.84	1.75	22.6	6.55	9.74	2.56	0
CIAL1	11.9	2.36	0.24	0.51	2.23	0.47	0	15.1	4.25	9.6	1.59	21.5	1	0
CIAL2	11.1	4.48	1.21	0	0.87	0	0	14.6	8.87	12.9	1.13	15.4	0.17	0
CIAL3	8.01	3.2	3.62	1.34	1.1	0.39	0	3.21	3.76	23.7	1.52	20.5	0.34	0
JAYU1	11.7	4.94	0.93	0	0.12	0	0	19	8.46	7.65	0	17.7	0.17	0
JAYU4	15.6	2.07	0	0	0	0	0	44.2	5.74	0	0	1.91	1.22	0
SAAR1	7.7	0.7	5.05	2.16	0.57	1.46	0	13.1	2.52	17.5	4.21	12.9	2.78	0
SAAR2	9.9	1.2	3.38	1.1	1.72	0.37	0	10.8	4.01	15.9	1.62	20	0.64	0
SAGA1	12.3	0	0.01	0	5.23	0	0.14	7.79	0.1	11.1	1.1	32.4	0.46	0
SAGA2	12.5	4.44	0.65	0	0	0.08	0	24.0	9.7	8.14	0.58	9.89	0.66	0
SAIS1	13.5	3	0	0	1.15	0	0	27.6	9.56	8.07	0	7.83	0	0
SAIS3	13.8	2.71	0	1.03	0.12	0.05	0	19.1	8.12	7	0.54	18.1	0.16	0
TETU1	11.3	0.29	1.69	0.59	3.62	0.14	0	14.1	6.72	6.65	1.11	24.1	0.29	0
TETU2	5.24	0.27	2.33	1.57	7.67	0.59	0	0	0.61	2.53	2.23	47.5	0.17	0

	300 m (212 ha)							500 m (503 ha)						
	AG	ES	NF	RD	SF	ST	WA	AG	ES	NF	RD	SF	ST	WA
ADJU2	12.8	2.74	12.4	0.36	183	0.47	0	24.3	5.04	18.6	1.26	453	0.74	0
ANGE1	22.2	3.69	2.45	1.15	179	0	3.82	0	1.4	50.3	1.5	442	0.18	7.4
ANGE3	6.06	7.06	58.2	4.42	133	3.27	0	7.59	21.3	182	11.6	273	7.18	0
CAAB1	0	1.29	8.75	3.69	152	1.28	45.1	4.26	7.78	27.3	10.9	397	4.75	50.98
CAGU1	5.63	8.83	86.1	7.31	98.8	2.91	2.47	5.46	14.7	127	19.4	328	7.9	0
CIAL1	19.2	8.54	9.58	2.14	172	0.69	0	18.6	11.3	30.2	11.5	428	2.65	0
CIAL2	36.4	26.5	28.8	4.94	115	0.94	0	5.57	19.8	48.2	5.61	422	1.02	0
CIAL3	24.2	13.4	77.1	4.06	92	1.28	0	0.02	15.2	136	3.34	347	1.75	0
JAYU1	83.5	18.2	43	4.31	62.3	0.73	0	138	27.6	119	4.85	203	1.6	8.93
JAYU4	102	18.1	36.6	12.2	29.8	6.1	7.32	161	30.7	137	31.8	124	13	5.11
SAAR1	16.7	6.44	56.5	6.27	122	4.45	0	35.3	10	105	8.89	341	3.19	0
SAAR2	20.3	5.4	66.8	7.82	108	3.98	0	29.3	9.46	96.8	8.93	352	5.88	0
SAGA1	9.85	3.86	77.2	7.58	105	7.61	0.89	0	8.4	66.7	9.71	411	4.81	1.89
SAGA2	2.8	10.6	31.6	5.1	160	2.41	0	0	9.46	118	5.76	363	5.83	0.49
SAIS1	27	18.8	47.8	0	118	0.09	0	43.3	16.3	109	6.4	327	0.46	0
SAIS3	59.6	23.3	56.8	0.93	71.3	0.09	0	104	37.6	106	9.62	240	6.11	0