Acta Herpetologica 17(2): 177-186, 2022
DOI: 10.36253/a_h-13209

Occupancy and probability of detection of the introduced population of *Eleutherodactylus coqui* in Turrialba, Costa Rica

Jimmy Barrantes-Madrigal[1,*], Manuel Spínola Parallada[1], Gilbert Alvarado[2], Víctor J. Acosta-Chaves[3,4]

[1] *Instituto Internacional en Conservación y Manejo de Vida Silvestre, Universidad Nacional, Heredia, Costa Rica*
[2] *Laboratorio de Patología Experimental y Comparada (LAPECOM), Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica*
[3] *Sede del Atlántico, Universidad de Costa Rica Sede Atlántico, Cartago, Costa Rica*
[4] *School for Field Studies, Atenas, Costa Rica*
**Corresponding author*. Email: jimmybarrantesm@gmail.com

Submitted on: 2021, 13th September; revised on: 2022, 7th June; accepted on: 2022, 19th June
Editor: Andrea Costa

Abstract. The Puerto Rican Common coqui frog (*Eleutherodactylus coqui*) has a long history as an invasive species in places such as Hawaii. Since its introduction in Costa Rica, scarce information is available to understand why and how the habitat in the Turrialba town is suitable for the species. Our goal was to analyze the habitat selection of *E. coqui* to identify if there are key habitat features that explained its success there. We measured 9 site variables that may affect the habitat selection of *E. coqui* in 92 survey units of 10 m radius distributed over a 500 m radius from its introduction point. We registered the presence/pseudo-absence data of *E. coqui* and environmental variables in each survey unit during eight surveys. We ran occupancy models to determine the influence of the variables on the habitat selection and to estimate its detection probability. We found that sites near the introduction point, containing abundant vegetation, bromeliads, and palms have a higher probability to be occupied by *E. coqui*. The habitat selection in Costa Rica shares characteristics with the populations of Puerto Rico and Hawaii. But, unlike the case in Hawaii, in Costa Rica this species has maintained a limited dispersal because the potentially higher biotic resistance, as well a sedentary behavior. However, the microhabitat conditions used by *E. coqui* in the study site are common throughout the country. Therefore, active management in new populations and environmental education programs to avoid human transportation of the species is critical to reduce its dispersal.

Keywords. Amphibians, conservation, detection probability, invasive species, introduced species, occupancy models.

INTRODUCTION

The study of the factors that determine the establishment and dynamics of an exotic species in a new ecosystem is not only a vital component in the development of biological invasion management strategies, but it also provides important information for understanding the processes that take place in natural ecosystems (Jiménez-Valverde et al., 2011; Wan et al., 2019). In most scenarios the introduced species fail to establish or advance beyond the first stages of invasion (Zenni and Núñez, 2013). However, under the right conditions, these species can colonize and spread over large areas and ecosystems causing severe alterations (Mačić, 2018). Additionally, in some cases rapid evolutionary processes may occur that favor their adaptation to new conditions (Whitney and Gabler, 2008; Carneiro and Lyko, 2020), where characteristics such as behavior, morphological and reproductive traits, and genetic variability of populations of introduced species may differ considerably with respect to the populations in their native range (O'Neill et al., 2018).

ISSN 1827-9635 (print)
ISSN 1827-9643 (online)

The Common coqui frog (*Eleutherodactylus coqui*, Thomas 1966) is a species native from Puerto Rico with a long history as an invasive species (Lowe et al., 2004). In its native habitat *E. coqui* is one of the most abundant amphibians, and it can be found from the forest floor to the canopy, inhabiting almost all environments (Joglar, 1998). It breeds throughout the year (Townsend and Stewart, 1994). Neonates take 8 to 9 months to become sexually mature (Towsend and Steward, 1994) and lays on average 4-6 clutches of eggs per year, each containing 16-41 eggs per clutch (Towsend and Stewart, 1994). Eggs are generally deposited in covered sites that provide protection from rain and environmental conditions (Townsend, 1989; Beard and Pitt, 2012). Egg development is direct (Towsend and Steward, 1985) and hatch after 14-17 days (Towsend and Steward, 1994).

This anuran was introduced to the Hawaiian archipelago in the late 1980s, where in less than 10 years it had spread throughout an extensive area of the archipelago (Kraus and Campbell, 2002). As in Puerto Rico, *E. coqui* populations in Hawaii are abundant; it has been reported population densities of up to 91000 individuals per hectare at the archipelago, a number three times higher than the estimates reported in Puerto Rico (Beard et al., 2008). These extreme densities have caused not only ecosystem alterations such as changes in the invertebrate community (Choi and Beard, 2012), alteration in the nutrient cycle and herbivory regimes (Sin et al., 2008), but also social and economic effects due to noise pollution produced by their constant vocalizations and the measures required for its control (Beard et al., 2009).

In Costa Rica, the Common coqui frog was introduced around 1998 into the city of Turrialba (García-Rodríguez et al., 2010; Barrantes-Madrigal et al., 2019). Unlike its invasion process in Hawaii, in the Cartago Province it has been kept restricted to a few localities for almost two decades: Turrialba and Juan Viñas (Barrantes-Madrigal et al., 2019). Although Barrantes-Madrigal et al. (2019) provided an update of the invasion status of the species in Costa Rica, since then have been observed few individuals in San Antonio de Escazú (San José Province) (https://www.inaturalist.org/observations/48536340). To continue research on this topic is relevant to understand why this population survived in Turrialba, and what implications could it has with the years across the country.

Although there is much information in the literature about the ecology of *E. coqui*, this information comes mainly from islands (Puerto Rico and Hawaii) where the ecological conditions are different from the continental neotropical context found in Costa Rica. The objective of this work is to determine the habitat selection of the Common coqui frog (*Eleutherodactylus coqui*) population introduced in the town of Turrialba to identify habitat variables that favor its occupation. We predicted that the vegetation structure and the availability of breeding sites would play a relevant role in the selection of the microhabitat of this frog as it has been in its native (Townsend, 1989) and exotic range (Beard et al., 2003). This research is relevant to understand why this population survived in Turrialba, and what implications could it has with the years across the country.

MATERIALS AND METHODS

Study area

The study was carried out in the city of Turrialba, where the initial population of *E. coqui* was found in Costa Rica (9°53'42"-9º54'18"N and 83°40'48"-83°39'54"E; García-Rodríguez et al., 2010; Fig. 1). Turrialba is located on the Caribbean slope and belongs to the Canton of Turrialba, Province of Cartago. It has an elevation range between 600 and 650 m a.s.l, has a warm and humid climate with an average annual temperature of 22 °C, and, due to its location, it is exposed to humid northeast winds and in certain regions can receive up to 7000 mm of rain (Dufour, 1978).

The place where *E. coqui* was first detected is surrounded by an area of heterogeneous composition with residential and commercial areas, including the campus of the University of Costa Rica (Atlantic Branch), but also open areas, pastures, plantations, streams, and small patches of secondary forest such as the Botanical Garden of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE; Fig. 2).

Sampling design

We delimited a circular area of 500 m radius (78.5 ha) around the point where this species was first reported (García-Rodríguez et al., 2010) as the study site. The extension of the sampling area was defined according to a preliminary sampling where we did not find evidence of the presence of the Common coqui frog outside the 500 m radius area from the introduction site. We assumed that, since its introduction, the species has had the same probability of dispersal in any direction within the selected area. Within this area we delimited three strata: urban, forest and open areas, based on satellite images taken from Google Earth Pro (Google, 2016). In each stratum we randomly distributed 29 circular sampling units (SU) of 10 m radius (314.1 m^2), with a minimum separation of 30 m between each other to capture most of the micro-

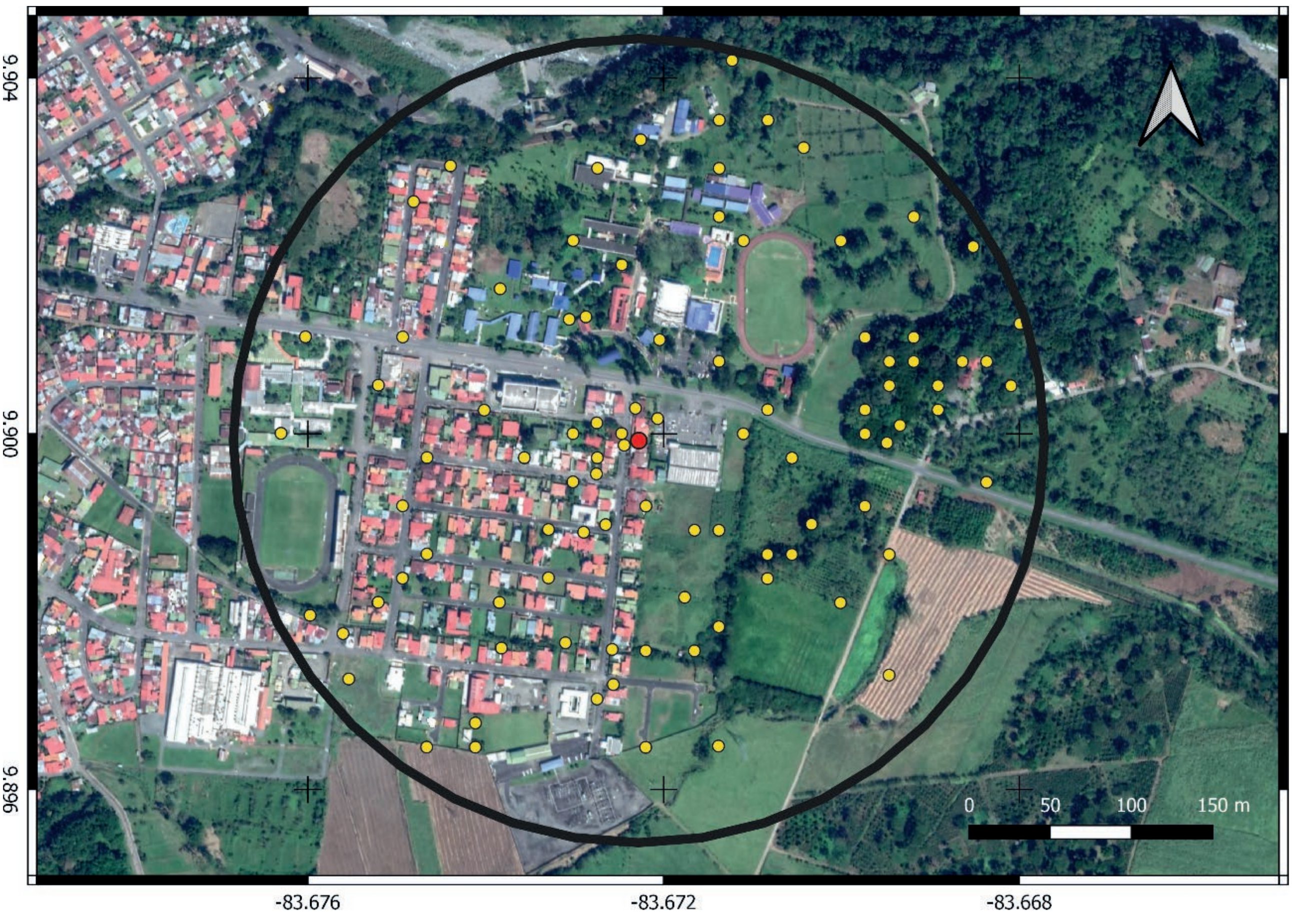

Fig. 1. Point of introduction of *Eleutherodactylus coqui* (red dot) and distribution of sampling units (yellow points) for the analysis of its habitat selection in Turrialba, Costa Rica.

habitat's variability in each stratum (Fig. 1). We considered 30 m as an adequate distance considering that *E. coqui* is a sedentary species, with movements of 3 4.5 m on average around its retreat sites (Woolbright, 1985).

Data collection

SUs were characterized based on nine site covariates distributed in four categories that we considered may influence the habitat selection of *E. coqui* (Table 1). The first category was vegetation, where we estimated volume of vegetation in three vertical strata and tree cover as habitat attributes that could be important in maintaining the environmental requirements of this species (e.g., temperature, humidity), as well as providing foraging sites or perches to vocalize. We registered bromeliads, palms, and leaf litter for their role as possible nesting or refuge sites (Stewart and Pough, 1983; Beard et al., 2003). Bromeliads were registered as presence or absence, where we considered less than five bromeliads as an absence. The percentage of palms and leaf litter in the SU, as well as the percentage of vegetation mentioned above, were calculated dividing the SU into four equal sections by drawing an imaginary line from the central point towards the four cardinal directions, in this way, we visually estimated the percentage of the covariate represented in each section and averaged the result for each SU.

On the category of water bodies, we quantified the distance to rivers as a measure to analyze the association with gallery forest environments. Additionally, to consider the dispersal capability of this species we measured the distance from the site where the first individuals were introduced. Both distance measures were calculated using the *distance* function of the *raster* package (Hijmans, 2016) in the statistical program R v3.3.2 (R Core Team, 2016).

We carried out a minimum of five and a maximum of eight nocturnal surveys (18:00 - 22:00 h) in each SU during October 2016 to February 2017. We implemented a five-minute survey in each SU using the visual and

Fig. 2. Representation of the types of environments contained in the study area for the habitat selection analysis of *Eleutherodactylus coqui* in Costa Rica. **A**. Forest, **B**. Gardens, **C**. Plantation, **D**. Open area-pasture, **E**. Green areas, **F**. Urban areas.

auditory encounter survey technique (Crump and Scott, 1994) to determine the presence of *E. coqui*. During each survey, we recorded if there was presence of the species in the sampling units (SU).

We registered three environmental variables at the beginning of each SU survey: relative humidity (hum), air temperature (temp) and the illuminated percentage of the moon (moon). These variables were chosen because there

Table 1. Detail of covariables used to analyze the habitat selection of the Common coqui frog (*Eleutherodactylus coqui*) in Costa Rica.

Covariable	ID code	Description
Vegetation		
Low height vegetation	veg_low	Percentage of the volume between 0 - 1 m in height within the SU occupied by vegetation
Medium height vegetation	veg_med	Percentage of the volume between 1 - 2 m in height within the SU occupied by vegetation
High height vegetation	veg_high	Percentage of the volume between 2 - 3 m in height within the SU occupied by vegetation
Canopy cover	can_cover	Percentage of canopy cover within the SU (measured with a densiometer)
Retreat sites		
Bromeliads	brom	Number of bromeliads within the SU at a height of less than 3 m.
Leaf litter	leaf_litter	Estimated percentage of leaf litter within the SU
Palms	palm	Percentage of the SU volume occupied by vegetation belonging to plants of the *Arecaceae* family
Water bodies		
Distance to rivers	dist_river	Distance in meters to the closest moving body of water
Dispersal		
Distance to origin	dist_origin	Distance in meters to the point of introduction of *Eleutherodactylus coqui* in Costa Rica.

is evidence in the literature that they influence the calling activity of *E. coqui* and other congeners (Joglar, 1998; Grant et al., 2012). Relative humidity and air temperature were quantified using a digital thermo-hygrometer (SE = ± 5% and ± 0.1 °C respectively). Additionally, the illuminated percentage of the moon was calculated as the percentage corresponding to the lunar phase, where 0% represents new moon and 100% full moon, using a lunar calendar.

Data analysis

We performed a habitat selection analysis using a single-season static occupancy model (Mackenzie et al., 2002). These models are especially useful when detection probability is less than 1, as it is expected for most amphibians. First, we standardized all variables (Mean = 0, SD = 1) due to their different value scales. We built a global model using the relative humidity, air temperature and the illuminated percentage of the moon as observation variables for the detection history, and vegetation, bromeliads, palms, leaf litter, canopy cover, distance to rivers and distance to origin as site covariates. Site and observation covariates were tested to evaluate their correlation, we built a global model with and without each of the correlated variables (Pearson $|r| < 0.6$) and kept those that resulted in the most parsimonious model evaluated by the Akaike Information Criterion (AIC; Burnham and Anderson, 2002). As result, we excluded leaf_litter, veg_low and veg_high from the global model. We assessed the goodness-of-fit and overdispersion of the global model with a parametric bootstrap approach based on the $\chi 2$ statistic with 1000 bootstrap samples (MacKenzie and Bailey, 2004).

We evaluated all possible combination of the global model and ranked the results by their AIC values using the *dredge* function of the MuMIn package (Barton, 2016). For occupancy and detection probability estimation we used a model averaging over the subset of models with a ΔAIC < 2.0 as all of them were considered robust (Weir et al., 2005). Finally, we calculated the relative importance of the estimated parameters for the habitat selection analysis using the importance function of the MuMln R package (Barton, 2016). This function ranks the variable according to the sum of the AIC weights in all models where the variable is included over all possible combinations of the global model. Models were built using the *unmarked* package (Fiske and Chandler, 2011) in the statistical program R v3.3.2 (R Core Team, 2016). All data and the R code used in the analysis is available as supplementary material.

RESULTS

We detected the presence of *E. coqui* in 30 of the 92 SUs on at least one occasion. The maximum distance from the point of introduction at which the species was recorded was 493 m, near the limit of the study area. A subset of 19 models with different combination of variables resulted with a ΔAIC < 2 (Table 2). The estimated c-hat value for site-occupancy model was close to 1 and did not indicate overdispersion or lack of fit (c-hat = 1.08; χ^2 = 781.74; P = 0.258). The AIC value was lower when we do not use any of the observation-level variables, however temperature and percentage illuminated of the moon were included in the subset of models with

Table 2. First 10 models of the set of models with the best fit (ΔAIC < 2) used in the habitat selection analysis of *Eleutherodactylus coqui*. p: detection probability; psi: selection probability; nPar: Number of parameters; AIC: Akaike's information criterion; ΔAIC: Difference with respect to the best model; wAIC: Akaike's weight.

Model formula	nPar	AIC	ΔAIC	wAIC
p(.) psi(brom + dist_origin + palm + veg_med)	5	313,04	0,00	0,106
p(.) psi(brom + dist_origin + veg_med)	6	313,29	0,25	0,094
p(.) psi(dist_origin + palm + veg_med)	5	313,47	0,43	0,085
p(.) psi(brom + can_cover + dist_origin + palm + veg_med)	4	313,58	0,54	0,081
p(.) psi(dist_origin + veg_med)	7	314,30	1,26	0,056
p(temp) psi(brom + dist_origin + palm + veg_med)	6	314,36	1,31	0,055
p(temp) psi(brom + dist_origin + veg_med)	6	314,52	1,48	0,051
p(.) psi(can_cover + dist_origin + palm + veg_med)	6	314,64	1,60	0,048
p(.) psi(brom + dist_origin + dist_river + palm + veg_med)	7	314,64	1,60	0,048
p(moon) psi(brom + dist_origin + palm + veg_med)	6	314,68	1,64	0,047

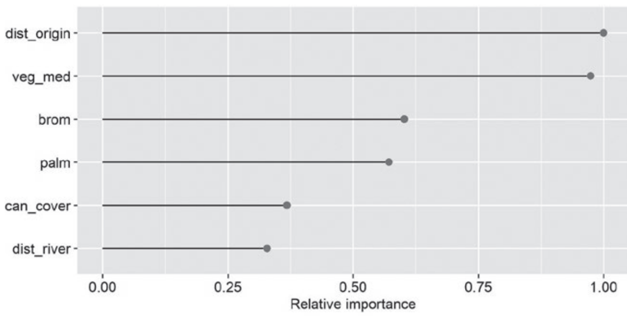

Fig. 3. Relative importance of variables in the habitat selection of *Eleutherodactylus coqui* in Turrialba, Costa Rica. dist_origin = distance to origin, veg_med = medium height vegetation, brom = bromeliads, palm = palms, can_cover = canopy cover, dist_river = distance to rivers.

ΔAIC < 2 (Table 2). The estimated detection probability using the averaged model was 0.666 (95% CI = 0.596 – 0.736). The variables mid vegetation (veg_med) and distance to origin (dist_origin) stand out as the most influential in the habitat selection of the species (Fig. 3). The presence of bromeliads (brom) also obtained a high value (0.60) as did the percentage of palms (palm) (0.57). The other site covariates presented relative importance values lower than 0.36.

DISCUSSION

The distribution of the Common coqui frog (*Eleutherodactylus coqui*) in the study area was explained by site features that favor its occupancy. We determined that the vegetation at a height of 1-2 meters, as well as the proximity to the site of introduction, are the site characteristics that best explain the occupation of the species on a microgeographic scale. In Puerto Rico, individuals of *E. coqui* have been observed from the ground to the top of the trees (Joglar, 1998), however, consistent with our observations, in our study area this species prefers perches with heights of approximately 1 m and has a negative association for higher places (Beard et al., 2003). The Common coqui uses plants to vocalize and forage, to select low vegetation for that purpose fit with previous habitat description and selection in Puerto Rico (Townsend, 1989). Dense and abundant low vegetation cover contributes to maintaining humidity conditions to avoid its desiccation (Beard et al., 2009; Klawinski et al., 2014).

The positive association with the abundance of bromeliads and palms could be explained by the reproductive biology of the frog, because previous research carried out in Puerto Rico and Hawaii highlights the importance of the availability and quality of nesting sites as a limiting factor for the Common coqui population, because the hatching success of the spawn is affected by the structure of the selected sites (Stewart and Pough, 1983; Townsend and Stewart, 1994; Beard et al., 2003). Plant species such as *Cecropia peltata*, epiphytic plants as bromeliads and palms (e.g., *Prestodea montana*) are important for the biology of species in Puerto Rico, especially due to leaf litter produced that could be shelter, nesting site or call perch (Townsend, 1989). In Turrialba this type of vegetation also occurs everywhere, especially in riparian and secondary forest, but not necessarily in gardens or sidewalks in our study site. However, also into gardens and sidewalks where ornamental introduced palms (e.g., *Areca* sp., *Wodyetia* sp.) or *Hybiscus* sp. bushes are common and frequently pruned to 1-2 m heigh. Structurally, our study site provides vegetation requirements that the Common coqui required for breeding and shelter, even

Fig. 4. Common coqui frog (*Eleutherodactylus coqui*) found in a bromeliad, Turrialba, Costa Rica. Photo by J. Barrantes.

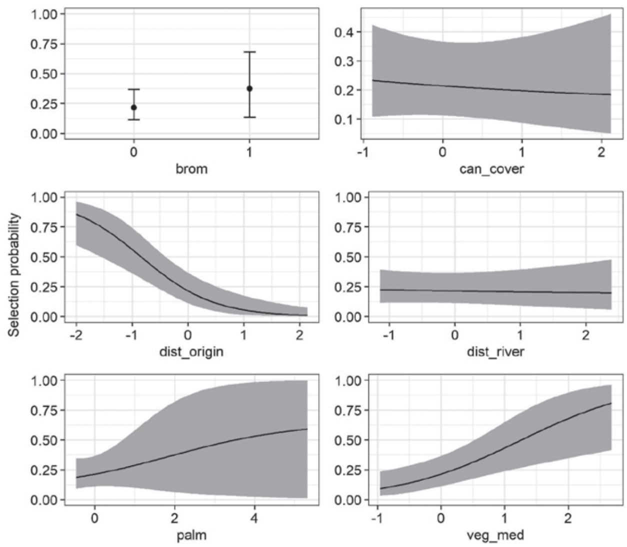

Fig. 5. Selection probability of the variables used to analyze the habitat selection of *Eleutherodactylus coqui* in Costa Rica.

when leaf litter was not abundant in our study site; the species could be using different types of substrates to lay eggs. We hypothesize that *E. coqui* uses bromeliads or other epiphytes (e.g., orchids, ferns) frequently found in trees and gardens for this purpose, because it was common to find individuals retreated inside bromeliads (Fig. 4) or perching in palm leaves. The use of bromeliads and epiphytic plants as shelters during the day is well known for the Common coqui biology (Ovaska, 1992; Fogarty and Vilella, 2003), as they provide a protected substrate where humidity conditions are maintained (Stewart and Pought, 1983), and the same conditions required to deposit their eggs (Townsend, 1989). Although it is common for *E. coqui* to lay its eggs on the ground or surroundings, this species prefers elevated substrates whenever they are available as it allows it to have greater hatching success and makes it easier for males to access high perches, close to the laying, where they can perform their vocalizations to attract females or defend territories (Townsend, 1989).

The detection probability (0.666, 95% CI = 0.596 – 0.736) is similar to values reported in a study from Hawaii (0.58 to 0.73; Olson et al., 2012). These results indicate that, despite being a relatively easy species to detect due to its constant vocalizations, at least three nocturnal surveys (2.73) to each site are required to avoid false negatives in detections of Common coqui individuals with a 95% of confidence. Even when none of the quantified environmental variables had a significant influence on the detection probability, previous studies indicate that the activity of this species is closely associated with humidity conditions (Pough et al., 1983). Humidity in Turrialba is relatively constant and high across the surveyed months (Dufour, 1978). This lack of variation could be the reason why we did not find a significant influence of these variables on the detection probability.

The observed distribution pattern suggests that there is a higher probability of finding Common coqui individuals near the introduction point (Fig. 5). This same pattern has been observed in Hawaii, where their populations are frequently found near points or routes of introduction such as roads or nurseries, and their dispersal throughout the archipelago is mainly due to transport facilitated by humans (Rauschert et al., 2017), with the natural dispersal movements being less important during the invasion process (Everman and Klawinski, 2013). This anuran is a very sedentary species, its movements at night are generally short and maintains an action range of just a few square meters (Woolbright, 1985), limiting its dispersal to more remote areas since its introduction in Costa Rica.

The limited dispersion documented can be related with the highly heterogeneous matrix with cover that contain potential barriers such as high-speed roads, neighborhoods, or even more complex rainforest fragments. Into the Jorge de Bravo neighborhood and surroundings, the Common coqui behaves like strong invader in disturbed areas near the introduction point, but it seems that would be a weak invader outside where natural ecosystems are more dominant because potentially there is more biotic resistance (Meyer et al., 2021). The biodiversity level in the Costa Rican Caribbean is much higher than in islands like Puerto Rico or Hawaii, especially vertebrate diversity such amphibian, reptiles (Savage, 2002), birds (Stiles and Skutch, 1989) or bats (LaVal and Rodríguez, 2002) that could be potential competitors or predators for a noisy species of *Eleutherodactylus*. For example, other native amphibians with a similar niche than the Common coqui such as Tink frog (*Diasporus diastema*), Pigmy rain frog (*Pristimantis ridens*), Fleischmann's glass frog (*Hyalinobatrachium fleischmanni*) or Green-boned tree frog (*Scinax elaeochrous*) also occur in the study area, including secondary growth, gardens, or perturbed lands (Savage, 2002). It is likely that competition, prey abundance, predation and other factors can influence the habitat selection and dispersal of this species. Previous work has highlighted that the way in which introduced species interact with native biota at different perturbation levels is an important determinant of their invasion success (Shea and Chesson, 2002; Meyer et al., 2021). Further studies are needed in this field to understand the influence of these interactions, both for the target species and for the native species with which it coexists.

Our study suggests that the habitat selection of the introduced population of *Eleutherodactylus coqui* in Costa Rica shares characteristics with the populations of Puerto Rico and Hawaii, where low vegetation and refuge sites during the day are decisive. However, unlike the case in Hawaii, in Costa Rica this species has maintained a limited dispersal because the biotic resistance and sedentary behavior discussed previously. Therefore, the scenario of a natural dispersion sounds like a less probable one based on what has been recorded in our study site into the Turrialba town thought the last 20 years (Barrantes-Madrigal et al. 2019). Moreover, all the populations in Turrialba, Juan Viñas, and potentially Escazú, where introduced on purpose or accidentally by humans (Barrantes-Madrigal et al., 2019). According with our results, the species could potentially colonize areas with open vegetation or crops with small bushes such as parks or sun coffee plantations from lowlands or middle elevations. Other species of *Eleutherodactylus* that also succeed in open vegetation are abundant in Puerto Rican sun coffee plantations (Monroe et al. 2017), for example. However, in the other hand, other similar species to the Common coqui such as *Eleutherodactylus planirostris* or *E. johnstonei* has been restricted to a single record or locality, without an important expansion or succeed to stablish new populations (e.g., *E. johnstonei*; Savage, 2002; Barquero and Araya, 2016). Thus, even when an extreme aggressive invasion scenario like the observed in Hawaii is unlikely to occur at country scale in Costa Rica at least soon, because the microhabitat conditions used by *E. coqui* in the study site are common in other neighboring towns in the lowlands from Caribbean or Pacific slopes, we consider that rural and peri urban areas with a mixed matrix of agropastoral-urban systems could be more likely to be invade by the Common coqui in further years only if transportation by humans continue.

Anecdotically, during surveys made by Barrantes-Madrigal et al. (2019), we identified that an important number of people from our study area sympathized with the sound produced by the Common coqui, even feeling proud of having the species living in their homes. This can increase the transportation risk of Common coqui frogs between people, both intentional and accidental, something that did not happened with other species like *E. johnstonei*. On the contrary, it was identified that other neighbors from our study area had noise problems due to the extreme local abundance of the frog in their gardens trying to manage the population with invasive and non-friendly environmental methods but with few succees. We encourage the environmental authorities from Minister of Environment (MINAE) to develop an early warning system and apply immediate management measures in new locations where this species is detected to prevent its establishment and spread. Additionally, we recommend increasing research and monitoring efforts on the possible negative effects on the ecosystem of the study area and to identify other pathways that could facilitate their dispersal to new regions, mainly those related to movement by humans. Our observations could serve as the basis for making microhabitat management decisions in parks or gardens in Turrialba where the species represents a nuisance to its inhabitants or a threat to other native species. It would be critical to develop an environmental education program to local people from Turrialba or Juan Viñas to avoid moving the species to new places where biotic resistance could be lesser or environmental conditions could be even more beneficial for the Common coqui establishment.

ACKNOWLEDGMENTS

We extend our thanks to the Rufford Foundation for funding this project, as well as Idea Wild for donating equipment to carry out this investigation. We also thank the Universidad de Costa Rica Sede Atlántico and the CATIE Botanical Garden for allowing us to enter the facilities, and the Central Conservation Area of the National System of Conservation Areas for the respective research permits. Finally, John Bohrman and two anonymous reviewers provided comments improving early version of this document.

SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found at < http://www.unipv.it/webshi/appendix> Manuscript number 13209.

REFERENCES

Barrantes-Madrigal, J., Parallada, M.S., Alvarado, G., Chaves, V.J.A. (2019): Distribution and invasion progress of *Eleutherodactylus coqui* (Anura: Eleutherodactylidae) introduced in Costa Rica. Phyllomedusa **18**: 101-107.

Barton, K. (2016): Package "MuMIn": Multi-Model Inference. R package, Version 1.15. 6. URL: https://cran. r-project. org/web/packages/MuMIn/index.

Barquero, M.D., Araya, M.F. (2016): First record of the Greenhouse frog, *Eleutherodactylus planirostris* (Anura: Eleutherodactylidae), in Costa Rica. Herpetol. Notes **9**: 145-147.

Beard, K.H., Al-Chokhachy, R., Tuttle, N.C., O'Neill, E.M. (2008): Population density estimates and growth rates of *Eleutherodactylus coqui* in Hawaii. J. Herpetol. **42**: 626-636.

Beard, K.H., McCullough, S., Eschtruth, A.K. (2003): Quantitative assessment of habitat preferences for the Puerto Rican terrestrial frog, *Eleutherodactylus coqui*. J. Herpetol. **37**: 10-17.

Beard, K.H., Pitt, W.C. (2012). *Eleutherodactylus coqui* Thomas (Caribbean tree frog). In: A handbook of global freshwater invasive species, pp. 317-325. Francis, R.A., Ed, Routledge, London.

Beard, K.H., Price, E.A., Pitt, W.C. (2009): Biology and Impacts of Pacific Island Invasive Species. *Eleutherodactylus coqui*, the Coqui Frog (Anura: Leptodactylidae). Pac. Sci. **63**: 297-316.

Carneiro, V.C., Lyko, F. (2020): Rapid epigenetic adaptation in animals and its role in invasiveness. Integr. Comp. Biol. **60**: 267-274.

Choi, R.T., Beard, K.H. (2012): Coqui frog invasions change invertebrate communities in Hawaii. Biol. Invasions **14**: 939-948

Crump, M.L., Scott, N.J. (1994): Visual encounter surveys. In: Measuring and monitoring biological diversity: standard methods for amphibians. Heyer, W.R., Donnelly, M.A., McDiarmid, R. W., Hayek, L., Foster, M. S., Eds, Smithsonian Institution Press, Washington.

Dufour, J. (1978): Desventajas del sitio de las ciudades en el medio volcánico e hiperhúmedo de Centroamérica. El caso de Turrailba, Costa Rica. Rev. Geogr. **86**: 207-225

Everman, E., Klawinski, P. (2013): Human-facilitated jump dispersal of a non-native frog species on Hawaii Island. J. Biogeogr. **40**: 1961-1970.

Fiske, I., Chandler, R. (2011): unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. J. Stat. Softw. **43**: 1-23.

Fogarty, J.H., Vilella, F.J. (2003): Use of native forest and eucalyptus plantations by Eleutherodactylus frogs. J. Wildl. Manag. **67**: 186-195.

García-Rodríguez, A., Chaves, G., Wainwright, M., Villegas, A. (2010): *Eleutherodactylus coqui* (Puerto Rican coquí). Herpetol. Rev. **41**: 320-321.

Grant, R., Halliday, T., Chadwick, E. (2012): Amphibians response to the lunar synodic cycle—a review of current knowledge, recommendations, and implications for conservation. Behav. Ecol. **24**: 53-62.

Hijmans, R. (2016): raster: Geographic Data Analysis and Modeling. R package versión 2.5-8. Available in: https://CRAN.R-project.org/package=raster

Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P., Lobo, J.M. (2011): Use of niche models in invasive species risk assessments. Biol. Invasions **13**: 2785-2797.

Joglar, R.L. (1998): Los coquíes de Puerto Rico: su historia natural y conservación. University of Puerto Rico, San Juan.

Klawinski, P.D., Dalton, B., Shiels, A.B. (2014): Coqui frog populations are negatively affected by canopy opening but not detritus deposition following an experimental hurricane in a tropical rainforest. For. Ecol. Manag. **332**: 118-123.

Kraus, F. Campbell, E.W. (2002): Human-mediated escalation of a formerly eradicable problem: the invasion of Caribbean frogs in the Hawai0ian Islands. Biol. Invasions **4**: 327-332.

LaVal, R.K., & Rodríguez, B. (2002): Costa Rica bats. Editorial INBio, Costa Rica.

Lowe, S., Browne, M., Boudjelas, S., De Poorter, M. (2004): 100 of the world's worst invasive alien species. A Selection From the Global Invasive Species Database. IUCN/SSC Invasive Species Specialist Group (ISSG), Auckland.

Mačić, V., Albano, P.G., Almpanidou, V., Claudet, J., Corrales, X., Essl, F., Marković, O. (2018): Biological invasions in conservation planning: a global systematic review. Front. Mar. Sci. **5**: 178.

MacKenzie, D.I., Bailey, L.L. (2004): Assessing the fit of site-occupancy models. J. Agric. Biol. Environ. Stat. **9**: 300-318.

MacKenzie, D.I., Nichols, J.D., Lachman, G. B., Droege, S., Royle, J., Langtimm, C.A. (2002): Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**: 2248-2255.

Meyer, S.E., Callaham, M.A., Stewart, J.E., & Warren, S.D. (2021): Invasive Species Response to Natural and Anthropogenic Disturbance. In: Invasive Species in Forests and Rangelands of the United States: A Comprehensive Science Synthesis for the United States Forest Sector. Heidelberg, pp. 85-110. Poland, T.M. Patel-Weynand, T., Finch, D.M., Ford, M.C., Hayes, D.C., Lopez, V.M., Eds, Springer International Publishing, Germany.

Monroe, K.D., Collazo, J.A., Pacifici, K., Reich, B.J., Puente-Rolón, A.R., & Terando, A.J. (2017): Occupancy and abundance of *Eleutherodactylus* frogs in coffee plantations in Puerto Rico. Herpetol. **73**: 297-306.

Olson, C.A., Beard, K.H., Koons, D.N., Pitt, W.C. (2012): Detection probabilities of two introduced frogs in Hawaii: implications for assessing non-native species distributions. Biol. Invasions **14**: 889-900.

O'Neill, E.M., Beard, K.H., Fox, C.W. (2018): Body size and life history traits in native and introduced populations of Coqui frogs. Copeia **106**: 161-170.

Ovaska, K. (1992): Short-and long-term movements of the frog Eleutherodactylus johnstonei in Barbados, West Indies. Copeia **1992**: 569-573.

Pough, F.H., Taigen, T.L., Stewart M.M., Brussard, P.F. (1983): Behavioral modification of evaporative water loss by a Puerto Rican frog. Ecology **64**: 244-252.

R Core Team. (2016): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Wien.

Rauschert, E.S., Mortensen, D.A., Bloser, S.M. (2017): Human-mediated dispersal via rural road maintenance can move invasive propagules. Biol. Invasions **19**: 2047-2058.

Savage, J.M. (2002): The amphibians and reptiles of Costa Rica: a herpetofauna between two continents, between two seas. University of Chicago press, Chicago.

Shea, K., Chesson, P. (2002): Community ecology theory as a framework for biological invasions. Trends. Ecol. Evol. **17**: 170-176.

Sin, H., Beard, K.H., Pitt, W.C. (2008): An invasive frog, *Eleutherodactylus coqui*, increases new leaf production and leaf litter decomposition rates through nutrient cycling in Hawaii. Biol. Invasions **10**: 335-345.

Stewart, M.M. Pought, F.H. (1983): Population Density of Tropical Forest Frogs: Relation to Retreat Sites. Science **221**: 570-572.

Stiles, F.G., Skutch, A.F. (1989): Guide to the birds of Costa Rica. Comstock, Ithaca.

Townsend, D.S. (1989): The consequences of microhabitat choice for male reproductive success in a tropical frog (*Eleutherodactylus coqui*). Herpetologica **45**: 451-458.

Townsend, D.S., Stewart, M.M. (1985): Direct development in *Eleutherodactylus coqui* (Anura: Leptodactylidae): a staging table. Copeia **1985**: 423-436.

Townsend, D.S. Stewart, M.M. (1994): Reproductive ecology of the Puerto Rican Frog *Eleutherodactylus coqui*. J. Herpetol. **28**: 34-40.

Wan, J.S., Rutherford, S., Bonser, S.P. (2019): The invasion triangle in the range dynamics of invasive species following successful establishment. Evol. Ecol. **33**: 299-312.

Weir, L.A., Royle, J.A., Nanjappa, P., Jung, R.E. (2005): Modeling anuran detection and site occupancy on North American Amphibian Monitoring Program (NAAMP) routes in Maryland. J. Herpetol. **39**: 627-639.

Whitney, K.D., Gabler, C.A. (2008): Rapid evolution in introduced species,'invasive traits' and recipient communities: challenges for predicting invasive potential. Divers. Distrib. **14**: 569-580.

Woolbright, L.L. (1985): Patterns of nocturnal movement and calling by the tropical frog Eleutherodactylus coqui. Herpetologica **41**: 1-9.

Zenni, R.D., Nuñez, M.A. (2013): The elephant in the room: the role of failed invasions in understanding invasion biology. Oikos **122**: 801-815.