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Predictors of Abundance of a Rare Bromeliad-Dwelling Frog (*Crossodactylodes itambe*) in the Espinhaço Mountain Range of Brazil

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ABSTRACT.—**Although tank bromeliads are used by many anuran species, bromeligenous frogs (species strictly dependent on bromeliads for reproduction) occur less frequently and are poorly understood. *Crossodactylodes* are small frogs confined to bromeliads where they lay their eggs and complete their life cycle without leaving the plant. The genus comprises five species and little information exists on their natural history. We focused on *Crossodactylodes itambe*—a species confined to a single summit of $<$0.5 km^2 at 1,700 m above sea level in the Espinhaço Mountain Range of Brazil. We surveyed frogs in 75 individual bromeliads during two consecutive years, and we used a Generalized Linear Model to investigate the drivers of species abundance related to habitat structure and local climate. We recorded 446 adults, 267 tadpoles, and 40 juveniles over the two years. Most bromeliads contained one adult frog with a mean number of 2–3 tadpoles. The structure of bromeliads influenced species abundance more than local climate. We found that bromeliad size, volume of central tank, and presence/absence of invertebrates and of water influenced frog abundance. Abundance increased in larger bromeliads at higher elevation. Changes in the structure and size of bromeliads might, therefore, affect abundance. We provide the first species assessment and evaluation of threat categories for this poorly known species.**

Bromeliads are arboreal or terrestrial plants that collect water, leaf litter, and detritus in a central tank (also known as a phytotelm; Lehtinen 2004). Because of their complex structure, bromeliads provide a wide range of microhabitats and contain a diverse associated fauna (Rocha et al., 2000; Armbruster et al., 2002; Teixeira et al., 2002; Jabiol et al., 2009; Silva et al., 2011; Brouard et al., 2012; Dézerald et al., 2014). Anuran amphibians represent the highest animal biomass and the richest vertebrate group associated with bromeliads (Oliveira et al., 1997; Silva et al., 2011). These plants are used by many anuran species (Teixeira et al., 2002; Lacerda et al., 2009; Pertel et al., 2010; Silva et al., 2011), but most of them are nonresident and only occasionally are observed. For example, species such as *Elachistocleis ovalis* (Andrade et al., 2009), *Aparasphenodon brunoi* (Teixeira et al., 2002), and *Scinax cuspidatus* (Domingos et al., 2015) use bromeliads during periods of inactivity or as shelter. In contrast, and less frequently, some anurans complete their entire life cycle within bromeliads and are defined as bromeligenous (sensu Peixoto, 1995).

In Brazil, there are at least 50 bromeligenous anurans (Sabagh et al., 2017), and the best documented examples are *Phyllodytes* species (Giaretta, 1996; Teixeira et al., 1997; Eterovick, 1999; Ferreira et al., 2012; Cunha and Napoli, 2016; Mageski et al., 2016; Motta-Tavares et al., 2016; Ruano-Fajardo et al., 2016) and the *Scinax perpusillus* group (Peixoto, 1995; Oliveira and Navas, 2004; Alves-Silva and Silva, 2009; Lacerda et al., 2009; Sabagh et al., 2012). Less well-documented, the genus *Crossodactylodes* comprises five species endemic to the Atlantic rain forest in Brazil: *Crossodactylodes pintoi* (Cochran, 1938), *Crossodactylodes bokermanni* and *Crossodactylodes izecksohni* (Peixoto, 1983), *Crossodactylodes septentrionalis* (Teixeira et al., 2013), and *Crossodactylodes itambe* (Barata et al., 2013). *Crossodactylodes* species have highly restricted distributions, and most of them are only recorded from type localities (Bokermann, 1966; Peixoto, 1981, 1983; Barata et al., 2013; Teixeira et al., 2013). These small frogs are strictly dependent on bromeliads where they lay their eggs (Peixoto, 1981; Santos et al., 2017) and spend the entire life cycle within the plant (Peixoto, 1981; Barata et al., 2013; Teixeira et al., 2013).

Although the genus was described in 1938 (Cochran, 1938), little is known about the biology of *Crossodactylodes* species, but some aspects of natural history have been revealed in recently described species (Barata et al., 2013; Teixeira et al., 2013; Santos et al., 2017). Overall, almost half of the bromeligenous frogs occurring in Brazil are considered as threatened, and for 35%, the conservation status is still unknown (Sabagh et al., 2017). Until now, only three *Crossodactylodes* species have been evaluated by the IUCN Red List: two Near Threatened species (*C. bokermanni* and *C. izecksohni*) are close to qualifying for Vulnerable, with declining populations living in restricted areas (Silvano and Peixoto, 2004a,b); and one Data Deficient species (*C. pintoi*) was last recorded in 1909 (Peixoto and Carvalho-e-Silva, 2004). We focused this study on *C. itambe*, a bromeligenous species known from only the type locality in an area of $<$0.5 km^2 at 1,700 m above sea level (a.s.l.) (Barata et al., 2013). Adults and tadpoles of *C. itambe* are reported to exclusively use a single species of bromeliad, *Vriesea medusa* (Barata et al., 2013; Santos et al., 2017), a night-blooming tank bromeliad also with a small distributional range (Versieux, 2008).

The bromeliad characteristics that determine abundance or presence of anurans are poorly understood and vary between and among species groups. Bromeligenous frogs show a strong indication of habitat selection (Mageski et al., 2016; Sabagh et al., 2017), and different species show different habitat preferences and use (Eterovick, 1999; Schineider and Teixeira, 2001; Oliveira and Navas, 2004; Cunha and Napoli, 2016; Motta-Tavares et al., 2016). Nonetheless, these aspects have never been investigated for *Crossodactylodes* species. Given the highly restricted distribution of both *C. itambe* and its host bromeliad *V. medusa*, we ask the question: what are specific habitat characteristics that influence species abundance at the study site? Here, we describe the effects of habitat structure and local climate on abundance within the only known population of *C. itambe*. We also provide the first species assessment and recommend the threat category to which this rare bromeliad-dwelling species should be allocated according to the IUCN

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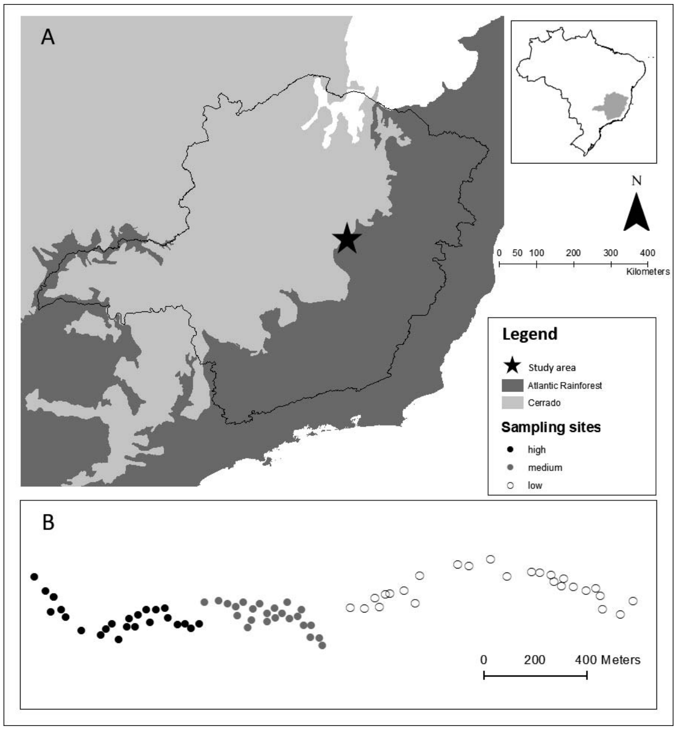

FIG. 1. Location of study area in Minas Gerais state in southeastern Brazil (Pico do Itambé State Park) showing (A) the limits of the Cerrado and the Atlantic rain forest. Sampling sites (B) are also shown grouped in three elevation categories: low (1,704–1,815 m a.s.l.), medium (1,838–1,925 m a.s.l.) and high (1,998–2,060 m a.s.l.).

guidelines (IUCN Standards And Petitions Subcommittee, 2017).

MATERIALS AND METHODS

Study Area and Data Sampling.—Pico do Itambé State Park (equivalent to IUCN categories I and II; Dudley, 2008) is located in the state of Minas Gerais, southeastern Brazil (18°23′S, 43°20′W; datum WGS84; Fig. 1A), encompassing 4,700 ha and including the Itambé summit. The area is a quartzite massif characterized by open field habitats with vegetation growing on rocky outcrops above 800 m (defined as campos rupestres; Eiten, 1978). The Itambé summit is the highest point of the Espinhaço Range, a mountain chain that geographically divides two hotspot biomes: the Cerrado (to the west) and the Atlantic rain forest (to the east). The Itambé summit receives the Atlantic moist wind that increases rainfall and mist, but the area is also influenced by the Cerrado that provides open grassland habitats with herbs and shrubs covering an extensive outcrop. This ecotone area hosts 14% of Brazilian vascular plants in <1% of the country's surface (Silveira et al., 2016) and is severely threatened by human activity (Alves et al., 2014; Monteiro et al., 2017), including climate change (Bitencourt et al., 2016). To the best of our knowledge, *C. itambe* is restricted to campos rupestres at the Espinhaço Range, living in a single species of tank bromeliad *V. medusa* in high elevation areas. *Vriesea medusa* grows on rocky outcrops, is 1.6–2.2 m tall with a funnel-like central tank comprising a rosette of 55–80 cm diameter (approximately 70 cm high) (Versieux, 2008).

Considering the restricted distribution of *C. itambe* on the Itambé summit (Barata et al., 2013), we used individual bromeliads occurring between 1,700 m and 2,062 m a.s.l. as sampling sites. We randomly selected 75 bromeliads, which we tagged with individual numbered labels, allowing repeated visits over different years. Sampling sites were at least 25 m apart from each other and were grouped according to three elevation categories (Fig. 1B) delimited by topography: low (1,704–1,815 m a.s.l.); medium (1,838–1,925 m a.s.l.); and high (1,998–2,062 m a.s.l.). The 75 sampling sites comprised 25 sites at each elevation category. To investigate frog abundance in relation to habitat structure, we characterized each sampling site according to elevation (m a.s.l.), size (bromeliad height × width in cm), volume of the central tank (hereafter rosette, height × width in cm), and number of neighboring bromeliads touching the edge of the labelled bromeliad.

We searched for *C. itambe* using visual encounter surveys (Crump and Scott, 1994) in two consecutive years (February to May 2015; February to June 2016), encompassing both wet (February to March) and dry (April to June) seasons. Each monthly survey consisted of 4–6 consecutive night visits made by one team of two investigators, starting after dusk. During our study period, we surveyed only those sites that were individually tagged. Because some experience is required to detect frogs in bromeliads (Barata et al., 2017), only one trained observer searched for the species. By standardizing our survey to a single observer (detectability of $P = 0.6$, see Barata et al., 2017), we are confident we eliminated the effect of observer bias in detection. For each bromeliad studied and on each sampling occasion, we recorded total number of individuals and stage of development (adults, juveniles, and tadpoles). Because of reduced size and coloration of *C. itambe*, we did not mark individuals, and males were not distinguished from females, because sex cannot be determined without capture and close examination of sexually dimorphic characteristics. To investigate changes in abundance in relation to sampling occasion, we recorded time of survey, presence and absence of water in the rosette, and presence and absence of invertebrates (potential predators of tadpoles and/or competitors for resources). We also installed data loggers at the three different elevation ranges to record daily climatic variables: maximum (max) and minimum (min) temperature, mean temperature, and relative humidity (RH). Monthly rainfall and UV radiation was recorded by a weather station located in the study area (at the top of Itambé summit).

Data Analyses.—Although we registered adults, tadpoles, and juveniles (hereafter, total counts) during our study period, our data analysis included records from only adults. Therefore, the total number of adults occupying a bromeliad in a given sampling occasion (i.e., abundance) was considered as our response variable, and we investigated predictors of abundance according to sampling occasion and habitat characteristics. Although our sampling sites are considered independent, for the purpose of our analysis, we did not assume the population was closed. Additionally, as variables that are survey-specific (i.e., vary by both site and sampling occasion, such as presence/absence of invertebrates) cannot be fitted as predictors of abundance in models that account for detectability (Royle, 2004), we used a generalized linear model (GLM) to identify predictors of species abundance in the study area. Our models included explanatory variables relating to sampling occasion (presence/absence of water and invertebrates at the time observation was made, year and season); local climate (max–min temperature, rainfall, UV radiation, and RH); and habitat structure (size, volume, elevation as a continuous variable, and number of neighbors). Exploratory analyses showed that

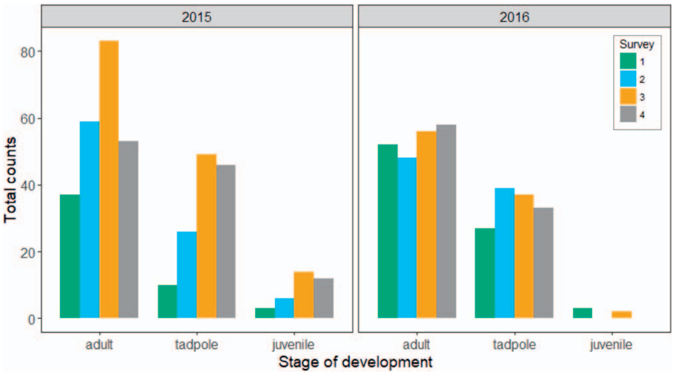

FIG. 2 Total counts of individuals of *Crossodactylodes itambe* during two consecutive years, according to stage of development (adult, tadpole, or juvenile) in four surveys (February to May 2015; February to June 2016).

variables were not correlated (Pearson *r*-values for all variable pairs were <0.5); thus, they were treated as independent predictors in the models.

We fitted models using a Poisson distribution (in abundance data the mean was equal to the variance, = 0.2), and model selection was performed using the Akaike Information Criteria (AIC; Akaike, 1973). Models with ΔAIC < 2 were interpreted as having strong support, whereas those with a ΔAIC of >2 were considered to have less support (Burnham and Anderson, 2002). We tested the goodness of fit of the models using a chi-square test (model was considered good when $P > 0.05$). We reported the results of GLM after model averaging using the parameter estimates (β), unconditional standard errors (SE), and upper and lower confidence intervals (CI). Statistical analyses were performed using R (R Core team 2015) with the “MuMIn” package (Barton, 2016). We report summary statistics as means ± SD.

RESULTS

We counted a total number of 446 adults, 267 tadpoles, and 40 juveniles over 2 yr of sampling in the 75 bromeliads we surveyed (Fig. 2). Considering all sampling sites, the total counts of adults, tadpoles, and juveniles were similar for both years ($N = 398$ in 2015, $N = 355$ in 2016; Fig. 2), as were the total counts between seasons ($N = 310$ wet season; $N = 443$ dry season, for 2 yr). In almost 80% of occupied bromeliads ($N = 273$ of 349 occasions), we recorded only one adult (mean = 1.3 ± 0.6), and the maximum number of adults recorded in a single bromeliad was four. Nevertheless, this distribution was random rather than overdispersed (mean and variance = 0.2; Poisson test $P = 0.94$). The mean number of tadpoles in occupied bromeliads for each year was 2–3, with a maximum of eight individuals (mean = 2.4 ± 1.7). We had more counts of adults, tadpoles, and juveniles at high elevations, between 1,998 and 2,062 m a.s.l. ($N = 486$; 65% of total counts). Only 4% of our counts were made at low altitude, below 1,815 m a.s.l., and were exclusively adults ($N = 33$) with no tadpoles or juveniles occurring at low elevation.

Only two models were considered to have a good fit (i.e., ΔAIC < 2), and both included habitat and climatic variables, as well as presence/absence of invertebrates and water (Table 1). The third model had ΔAIC > 2 and little explanatory power, but variables describing abundance were similar to those included in the selected models, showing consistency in model selection (Table 1). Our best model included a wide set of explanatory variables and explained 48% of adult abundance, whereas the second model explained 34% (Table 1). We observed a positive and significant relationship between abundance and the presence of water inside the rosette, and there was a negative relationship with the presence of invertebrates in the bromeliad

TABLE 1. Summary of top three Generalized Linear Models showing estimates for predicted variables with estimated parameter (β) and standard error (SE); and parameters of model selection showing number of parameters within each model (N Pars), Akaike Information Criteria (AIC), ΔAIC, and AIC weights (AIC *w*). Models are ranked according to AIC values and significant variables are highlighted in **bold**. Total number of adults occupying a bromeliad in a given sampling occasion was considered as our response variable and fitted models included explanatory variables.

	Model rank					
	1		2		3	
Variable	β	±SE	β	±SE	β	±SE
Estimates for predicted variables						
Intercept	−2.48	0.21	−2.48	0.24	−2.48	0.24
Invertebrates	**−0.35**	**0.1**	**−0.35**	**0.1**	**−0.35**	**0.1**
Water	**0.55**	**0.2**	**0.56**	**0.2**	**0.58**	**0.2**
Elevation	**0.51**	**0.06**	**0.49**	**0.07**	**0.48**	**0.07**
Size	0.11	0.06	0.11	0.06	0.11	0.06
Neighbors	−0.1	0.05	−0.1	0.05	−0.1	0.05
Volume	**0.24**	**0.07**	**0.24**	**0.07**	**0.24**	**0.07**
Year	**0.33**	**0.14**	**0.38**	**0.15**	0.31	0.18
RH	−0.1	0.06	**−0.14**	**0.07**	**−0.15**	**0.07**
T max	0.11	0.06	0.09	0.06	0.1	0.06
T min	−0.12	0.06	**−0.18**	**0.08**	**−0.18**	**0.08**
Elevation: size	**0.28**	**0.06**	**0.28**	**0.06**	**0.28**	**0.06**
Season	–		0.16	0.14	0.21	0.16
Pluviosity	–		–		−0.05	0.08
Parameters of model selection						
N Pars	12		13		14	
AIC	2313.4		2314.1		2315.7	
ΔAIC	0		0.71		2.27	
AIC *w*	0.48		0.34		0.15	

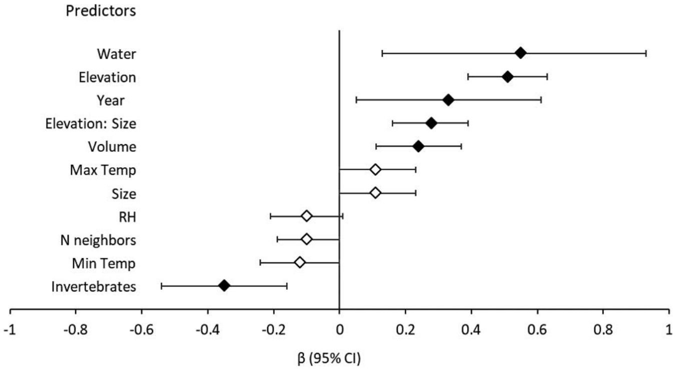

FIG. 3. Variation in parameter estimate (β) with 95% confidence interval for variables included in the best fitting model, after model averaging and selection. Significance of predictors of frog abundance (black diamonds = significant effect) is given when confidence intervals do not cross zero. (Legend: Water = presence of water; Elevation: Size = interaction of elevation and size of bromeliad; Volume = volume of central tank; Max Temp = maximum temperature; Size = size of bromeliad; RH = relative humidity; N neighbor = number of neighbors; Min Temp = minimum temperature; invertebrates = presence of invertebrates).

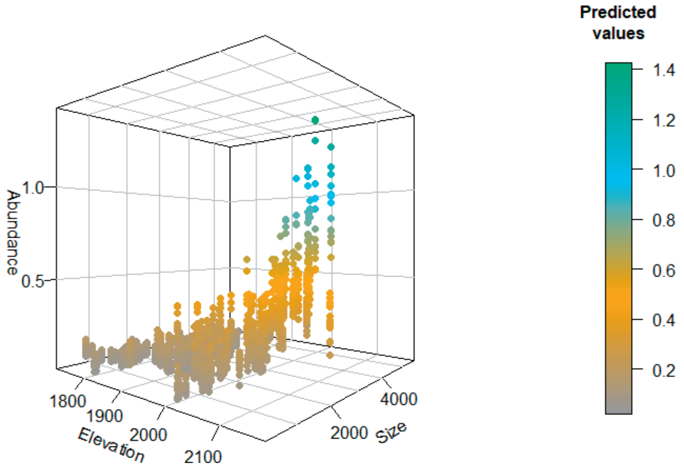

FIG. 4. Relationship between predicted values of abundance (total counts of adults per bromeliad) and the interaction of elevation (in meters above sea level) and bromeliad size (given by bromeliad height × width in centimeters).

(Fig. 3), both variables changing with survey occasion. Elevation and size of the bromeliad are considered habitat variables and the interaction between those two had a positive effect on frog abundance at sampled sites (Fig. 4). Although bromeliad size had high relative importance in our models, the effect of this variable alone was not considered significant (Fig. 3). Volume of rosette had a positive effect on adult abundance. Although included in the best model, climatic variables did not significantly explain abundance of adults inside the bromeliad (Fig. 3; Table 1).

DISCUSSION

Although a quarter of bromeligenous frogs are reported to use a single species of bromeliad, further investigations of habitat selection are still needed (Sabagh et al., 2017). We recorded only *C. itambe* using *V. medusa*, confirming previous suggestions that this frog species is restricted to a single bromeliad (Barata et al., 2013; Santos et al., 2017). Although *C. bokermanni* was also reported to occupy a single species of *Vriesea*, *C. izecksohni* was recorded using different *Vriesea* species (Sabagh et al., 2017). Different species of bromeliads are used by bromeligenous frogs (Alves-Silva and Silva, 2009; Lacerda et al., 2009; Mageski et al., 2016; Motta-Tavares et al., 2016; Sabagh et al., 2017); however, *Vriesea* sp. is one of the most common bromeliads used (often preferred) by *Phyllodytes luteolus* and *S. perpusillus* (Eterovick, 1999; Schineider and Teixeira, 2001; Oliveira and Navas, 2004; Ferreira et al., 2012). *Vriesea* sp. are preferred for a variety of reasons, such as the large number of leaf axils (Schineider and Teixeira, 2001; Mageski et al., 2016), complexity of their structure (Eterovick, 1999; Ferreira et al., 2012), or position close to the ground (Oliveira and Navas, 2004).

For *C. itambe*, elevation may influence the distribution of adults (Barata et al., 2013) and tadpoles (Santos et al., 2017), which also affects species occupancy (Barata et al., 2017). Indeed, we found elevation to be an important determinant of species abundance. All other four *Crossodactylodes* species are restricted to high elevations, from 650–1,200 m a.s.l. (Peixoto and Carvalho-e-Silva, 2004; Silvano and Peixoto, 2004a,b; Teixeira et al., 2013); however, habitat use has never been investigated for other *Crossodactylodes* species. Santos et al. (2017) suggested that preferential breeding sites for *C. itambe* occurred above 1,977 m a.s.l. We found the interaction of elevation and bromeliad size was positive and significant, showing an increase in the number of individuals occurring in larger bromeliads at higher elevations.

Bromeliad selection by *S. perpusillus* males was mostly influenced by plant size (Oliveira and Navas, 2004), but for *C. itambe* size alone was not a significant predictor. Larger bromeliads usually contain a larger number of leaves, which can be correlated with water storage capacity (Cogliatti-Carvalho et al., 2010; Freschi et al., 2010) and may offer some advantage to reduce predation (Ferreira et al., 2012) and avoid competition (Schineider and Teixeira, 2001; Cogliatti-Carvalho et al., 2010). We found that the volume of the rosette positively influenced abundance. Larger tanks can hold more nutrients for tadpole development and are less susceptible to unpredictable droughts that can cause mortality of the offspring (Lehtinen, 2004). *Vriesea* is the most diverse genus within Bromeliaceae in the state of Minas Gerais (Versieux and Wendt, 2007) and varies widely in water storage capacity (Alves et al., 1996; Schineider and Teixeira, 2001; Cogliatti-Carvalho et al., 2010). Because it holds a large rosette, *V. medusa* can retain large volumes of water from mist and rain, making it available throughout the year and reducing chances of bromeliad tank desiccation.

Tank bromeliads are capable of holding water even in dry environments (Cogliatti-Carvalho et al., 2010). We observed that most bromeliads retained water during periods of reduced rainfall (from April to June). Holding water in the dry season may favor tadpole development and survival throughout the year and may also reduce the influence of seasonality in species abundance. Although year was an important predictor of abundance, number of individuals did not seem to vary with season, because we had similar numbers in both dry and wet seasons. In fact, season and rainfall were not important variables in our model, and other climatic variables were also unrelated to abundance. Similar patterns occur in bromeligenous species *P. luteolus* (Schineider and Teixeira, 2001; Ferreira et al., 2012), for which reproduction was not influenced by thermal fluctuations throughout the seasons (Oliveira and Navas, 2004).

The presence of water is vital for bromeligenous frogs, and we argue that simple presence of water inside the bromeliad is as important as water volume (we observed an increasing number of frogs in bromeliads where water was available). Indeed, only on rare occasions did we record individuals in bromeliads with no water (8% of total counts). Although preferences for bromeliads with large water reservoirs were recorded for two other bromeligenous species (Oliveira and Navas, 2004; Mageski et al., 2016), water depth and volume stored in the rosette were not important for *Phyllodytes melanomystax* (Cunha and Napoli, 2016) and *P. luteolus* (Eterovick, 1999; Schineider and Teixeira, 2001). Therefore, we argue that the simple presence of water (not the volume stored by the tank itself) might be considered as the main factor influencing the abundance of *C. itambe*.

We found that presence of invertebrates can have a negative effect on the abundance of *C. itambe* in the bromeliad. Microhabitats with water bugs are avoided by tadpoles in streams (Eterovick and Barata, 2006), but this was not investigated for bromeligenous tadpoles. In spite of being an unpredictable environment (e.g., food availability or desiccation risks), a phytotelm has fewer predators than ponds and streams (Schiesari et al., 2003; Lehtinen, 2004). Although invertebrates were not identified to genus level, we observed bromeliads being frequently used by spiders, known to prey upon small frogs and tadpoles (Menin et al., 2005). Our data suggest that bromeliads with presence of invertebrates might be avoided by breeding adults and, therefore, preferred for tadpole development.

For bromeligenous species, clusters of bromeliads increase the number of available tanks and provide access to several oviposition sites (Oliveira and Navas, 2004; Cunha and Napoli, 2016), which are also preferentially used by males of *S. perpusillus* (Oliveira and Navas, 2004) and calling males of *P. melanomystax* (Cunha and Napoli, 2016). Surprisingly, we found that abundance of frogs was not influenced by the number of neighboring bromeliads. We recorded up to four adults and eight tadpoles inside a bromeliad, which is similar to *P. luteolus* (Schineider and Teixeira, 2001) and *P. melanomystax* (Cunha and Napoli, 2016). For *C. itambe*, clusters of adults with varying number of tadpoles and/or eggs using the same bromeliad were previously reported (Santos et al., 2017). Nonetheless, we usually observed one individual in each bromeliad (80% of our records), which was also recorded for other bromeligenous frogs (Schineider and Teixeira, 2001; Ferreira et al., 2012; Motta-Tavares et al., 2016).

Over 60% of bromeliads occurring at the Espinhaço Range are endemic, including *V. medusa* (Versieux and Wendt, 2007). Over the past centuries, fire was used by dairy farmers to manage natural pasture in our study site (Versieux, 2008). Although burning has not been commonly practiced since the Itambé summit became a protected area, occasional fires have recently occurred. Bromeligenous frogs are more likely to be threatened by the loss of their breeding sites (Sabagh et al., 2017), and we found that, for *C. itambe*, the structure of bromeliads had a greater influence determining adult abundance than local climate. Therefore, fire may change the structure of bromeliad and have a negative effect on population abundance, which can potentially cause extinction of local populations. Although we found the species to be locally abundant in the study area, extent of occurrence is limited to 0.5 km^2 (Barata et al., 2013) and no other population is known thus far. Based on IUCN criteria of geographic range, population number and decline in habitat quality, *C. itambe* could be classified as Critically Endangered (CR) under criteria B1ab(iii) and B2ab(iii), or Vulnerable (VU) under criteria A1c and D2, both considered high levels of threat categories.

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