Stochasticity determines the seasonality of an anuran assemblage in the Brazilian Cerrado

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ABSTRACT

Anurans are highly sensitive to environmental changes, particularly in Neotropical regions, such as the Cerrado. Therefore, we seek to understand how temperature, humidity, precipitation, photoperiod, and the evolutionary history of species, shape the patterns of anuran communities over time. We used Phylogenetic Generalized Linear Mixed Models to analyze the relationships between climatic variables and anuran abundance, incorporating species' evolutionary history as a covariate. Our results showed that precipitation has a positive influence on anuran abundance, while temperature alone had no significant effect. However, we observed that the interaction between precipitation and temperature was not statistically significant and negative. These results suggest that only precipitation favors abundance, while temperature appears to act by reducing abundance. Additionally, species phylogeny and variability in sampling campaigns also contributed to explaining variations in abundance, as closely related species tend to exhibit similar ecological responses to environmental changes. We emphasize that precipitation is essential for anuran survival and reproductive behavior, especially in seasonally dry environments like the Cerrado. As, an important predictor of species distribution, climate also shows that evolutionary proximity among species reflects niche conservatism. These findings reinforce the importance of furthern research on climatic and evolutionary impacts to guide conservation strategies in biodiversity-rich Neotropical ecosystems.

Key-words: Neotropical Anurans; Cerrado; Evolutionary Ecology; Anuran Community

1. INTRODUCTION

Ectothermic animals have an intrinsic relationship with the thermal conditions of their environment, making them highly sensitive to climatic variations (Reider et al. 2020; Rosa et al. 2022; Petrović et al. 2023; Roberto & Cascon, 2023). In some tropical ecoregions, there is significant seasonal fluctuation in temperature and humidity, which can determine the presence and abundance of animals throughout the year (Stephenson et al. 2022). Among the many ecoregions in the Neotropics, the Cerrado is one of the most seasonal, varying from dry (April to September) to wet seasons (October to March) (Vital et al. 2022). In the Cerrado, the anurofauna stands out for its diversity of species, characterized by its richness and endemicity (Valdujo et al. 2012).

Climatic factors such as temperature, humidity, and precipitation directly influence the ecology of anurans, affecting community composition, species richness, abundance, growth, reproductive phenology, and daily activity patterns (Roberto & Cascon 2023). For example, higher temperatures can increase anuran survival and accelerate their development (Niehaus et al. 2006; Bernal-Bautista et al. 2016). This pattern varies according to the thermal background of each population (Ruthsatz et al. 2018). Meanwhile, more humid environments tend to support a greater diversity of anurans due to the increased availability of microhabitats and suitable breeding sites (Vasconcelos et al. 2009). The interaction between species composition and climatic variables can vary seasonally (Ceron et al. 2020), and the combination of humidity, temperature, and precipitation is crucial for modeling the temporal dynamics of anuran communities, regulating their ecological patterns over time (Fontana et al. 2023; Roberto & Cascon 2023).

In addition, photoperiod (i.e. day length) acts as a biological clock that synchronizes various physiological and behavioral processes in many animals (Zinn et al. 1986; Kukita et al. 2015; Pall et al. 2022). During the summer, longer days contrast with shorter days in winter, while spring and autumn bring more balance between day and night (Moreira 2019). This variation in daily light significantly impacts processes such as growth, reproduction, and behavior in anurans, shaping the seasonal rhythms of many species (Paniagua et al. 1990; Borah et al. 2022; Neptune et al. 2023). Studies show that photoperiod drives the phenological calling patterns of anurans, allowing them to synchronize their physiology and behavior throughout the year (Sluys et al. 2011; Rosa et al. 2021).

Furthermore, phylogenetically related amphibian species often share similar ecological traits, such as activity patterns and niche occupation (Campos et al. 2019). However, in highly diverse communities, competition for resources can lead to niche differentiation, promoting the coexistence of closely related species (Peng et al. 2022). Phylogenetic diversity, reflecting evolutionary history, provides valuable insights into the processes that shape community assembly, including the evolution of environmental sensitivities (Montero-Mendieta et al. 2021). By considering phylogenetic relationships, we can infer the adaptive traits that have emerged over time in response to various selective pressures (Losos 1996; Hof et al. 2010).

Given the importance of climatic and environmental factors in evolutionary processes that regulate biodiversity across spatial and temporal scales, this study aims to evaluate the specific influence and synergism of these variables on the seasonality of an anuran Cerrado assemblage, seeking to understand the dynamics of this assemblage throughout the year. We expect species to distribute across different periods in response to climatic variation according to their evolutionary history.

2. METHODS

1. Study area

Fieldwork took place at the Private Natural Heritage Reserve (PNHR) Fazenda Santa Fé, situated in the municipality of Campo Grande, Mato Grosso do Sul, Brazil (-20°51'31" S; -54°72'77" W), at elevations between 300 and 600 a.s.l. The studied lagoon spans 3,358 m^2 and has a depth of 2.5 meters. The region experiences an average temperature of 22.8 °C and an annual precipitation of 1,533 mm. The tropical climate features two distinct seasons: a dry winter (April to August) and a wet summer (September to March) (Moroti et al., 2021). The reserve covers 38 hectares surrounded by soybean and corn monocultures. Its Cerrado vegetation is in various stages of conservation and restoration, with springs that shape and influence the Brejo Bonito wetland, a habitat for a wide variety of species.

2. Sampling design

We conducted data collection at 14-day intervals from August 2023 to March 2024 and monthly from April to July 2024, considering the dry and wet seasonality of the Cerrado, covering a full year. During each campaign, we observed community composition for two hours, starting 15 minutes after sunset, using the acoustic survey method described by Zimmerman (1994). A total of 19 campaigns were conducted, accumulating 38 hours of sampling. To estimate seasonal vocal activity, we counted the number of calling males, following the methodology of Gottsberger and Gruber (2004).

3. Climatic variables

Climatic data, including air temperature and relative humidity, were measured with a digital thermo-hygrometer at the start and end of each sampling session to capture thermal variation. Precipitation data, sourced from a meteorological station 15 km from the study area, were provided by the National Institute of Meteorology (NIM). Daily photoperiods (measured in sunlight minutes) were obtained from the National Observatory of Brazil (Ceron et al., 2020). To ensure the independence of climatic variables, researchers assessed their correlation using the Variance Inflation Factor (VIF) in R software v. 4.4.1 (R Core Team, 2024). Since factors like temperature, humidity, precipitation, photoperiod, and seasonality affect anuran assemblages and are shaped by the species' evolutionary history, these factors were categorized based on predefined causal assumptions (Table 1).

4. Bayesian phylogenetic analysis

The community phylogenetic tree was built using 15 sequences from individuals previously sequenced by Moroti et al. (2021) at the study site and deposited in GenBank, along with additional COI sequences retrieved from the database (Table S1). Researchers edited and aligned the sequences using MEGA 11 (Molecular Evolutionary Genetics Analysis version 11) (Tamura, Stecher, & Kumar, 2021) with the MUSCLE algorithm under standard parameters (Edgar, 2004). The TIM2+G model, identified as the best fit for nucleotide substitution using the Bayesian Information Criterion in jModelTest 2 (Darriba, Taboada, Doallo, & Posada, 2012), was applied. Bayesian phylogenetic analysis was performed with BEAST v2 (Suchard et al., 2019) for 50 million generations, sampling every 5,000 steps with the Yule tree model. The analysis's stability was verified through trace plot inspections, ensuring that effective sample size (ESS) values exceeded 200, as assessed in Tracer v1.7 (Rambaut et al., 2018). The first 10% of genealogies were discarded as burn-in, and the maximum clade credibility tree was generated using TreeAnnotator v1.8 (Figure 1) (Drummond & Rambaut, 2007).

5. Data analysis

A Pearson correlation matrix identified potential collinearities among predictor variables (Santos, 2021). After detecting correlations, researchers constructed Phylogenetic Generalized Linear Mixed Models (PGLMMs) for each predictor variable, with species abundance as the response variable and phylogeny as a covariate. Sampling campaigns were included as random factor. The models were built using the *pglmm* function, and their quality was evaluated using Akaike Information Criterion (AIC) and Pseudo-R^2 values derived from AICc and community PGLMM functions (Brewer et al., 2019). Eleven mixed-effects models were developed to explore the relationships between environmental variables and species abundance, considering species phylogeny (Figure 1) and variations across sampling campaigns.

3. RESULTS

We recorded a total of 1001 individuals belonging to 30 species, distributed in four families: Bufonidae (n=1), Hylidae (n=14), Leptodactylidae (n=14), and Microhylidae (n=1) (Table S2). Model 3, which included the interaction between daily precipitation and average air temperature, had the lowest AIC value (800; Table 2), indicating it was the best-fitting model for the data. Model 3 revealed several important relationships between environmental variables and species abundance (Table 3). The main effects of average air temperature were not statistically significant on their own (p = 0.12), nor in interaction with daily precipitation (p = 0.69). However, the interaction between daily precipitation and average air temperature was negative and not significant (β = -0.06; p = 0.69), indicating that the combined effect of these variables reduces species abundance. On the other hand, daily precipitation alone was positive and significant (β = 0.22; p = 0.04; Figure 2), suggesting that higher precipitation levels increase abundance. Model 3 also included random effects to capture variation between species and sampling campaigns. The variance associated with the random effect of sampling campaigns (0.14) was greater than that associated with species (0.13), suggesting that variation between sampling campaigns is more relevant for explaining abundance than variation between species.

The residual variance was 0.39, indicating that the variation in abundance is well-explained by the predictors included in the model. To assess model fit, we calculated Pseudo-R^2 for both the fixed effects component and the full model (fixed + random effects). The Pseudo-R^2 for the fixed effects was 0.62, indicating that approximately 62% of the total variance in abundance is explained by the fixed effects (daily precipitation and average air temperature). When considering random effects, the Pseudo-R^2 increased to 12.02, suggesting the total variance in abundance is explained by the full model, highlighting the importance of accounting for phylogeny and sampling campaigns in abundance modeling.

4. DISCUSSION

Our analyses revealed that anuran abundance in the study area is influenced by environmental and evolutionary factors. Although our initial predictions pointed to other variables, the most suitable model highlighted the interaction between precipitation and temperature, suggesting that species abundance results from an interaction between these two factors. However, the anuran community proved to be more sensitive to precipitation variations, with higher rainfall volumes being associated with increased populations of various species. This phenomenon can be explained by the greater availability of resources and the creation of microhabitats favorable for reproduction (Roberto & Cascon 2023). On the other hand, mean air temperature did not have a direct and significant effect on anuran abundance. Nevertheless, we observed that the interaction between temperature and precipitation was negative, indicating that the impact of temperature is conditioned by precipitation levels. During periods of high precipitation, elevated temperatures do not seem to limit anuran activity. In contrast, during dry seasons, high temperatures can increase dehydration and mortality (Roberto & Cascon 2023).

In the Neotropical region, anurans rely heavily on rainfall and mild temperatures for their reproductive and calling activities (Vieira et al. 2008). This dependence on water is even more pronounced in savanna environments, such as the Caatinga (Vieira et al. 2008), the Cerrado (Maffei et al. 2011), and the Chaco (Schalk & Sáenz 2016), where extreme climatic conditions, with prolonged droughts and high temperatures, pose significant challenges for the survival of these amphibians. To overcome these adversities, anuran species have developed various adaptive strategies, such as explosive breeding in response to rainfall events (Fouquet et al. 2020), burrowing in underground shelters during droughts, and selecting microhabitats with higher humidity (Nomura et al. 2009).

Additionally, the phylogeny of species and the variability between sampling campaigns played a crucial role in explaining the variation in abundance. Our results do not rule out the niche conservatism hypothesis, as the studied species share a close phylogenetic relationship and, consequently, similar ecological niches (Saban et al. 2023). This evolutionary proximity influences how species respond to environmental variables, such as precipitation and temperature. The high variance associated with the random effect of sampling campaigns suggests that uncontrolled temporal factors, such as short-term climate fluctuations or stochastic events, may significantly impact species abundance at different times. Thus, our findings emphasize the importance of environmental variables in predicting species abundance and highlight the role of phylogeny and sample variability in improving the model.

TABLES

Table 1. Overview of components that may influence anuran abundance in the Neotropical region.

Variable	Justification	Reference
Anuran abundance	The diversity of anuran species in the Neotropical region is influenced by various environmental factors, with hydroperiod being one of the most influential. Thus, species with different adaptations to the hydrological regime coexist by exploiting specific ecological niches and minimizing competition. Additionally, temperature and relative humidity directly affect community assembly.	Valério et al. 2016; Villa et al. 2019; Roberto & Cascon 2023.
Precipitation	The calling activity of tropical anurans is concentrated in the rainy season due to their physiology. Species found in the Cerrado, for example, show higher water absorption rates and sensitivity to dehydration. In this context, the rainy season	Villa et al. 2019; Ceron et al. 2020; Roberto & Cascon, 2023

	provides more favorable environmental conditions for reproduction.	
Temperature	In the Neotropical region, temperature significantly affects anuran abundance. Higher and more constant temperatures accelerate the physiological processes of these amphibians. In more favorable temperatures, the larval development time is reduced, decreasing the exposure of tadpoles to predators, thereby increasing their chances of survival until metamorphosis.	Bernal-Bautista 2016; Villa et al. 2019; Ceron et al. 2020; Santos, 2021; Roberto & Cascon 2023
Humidity	The spatial distribution and composition of anuran communities are directly influenced by humidity. In drier regions, the occurrence of anurans is more limited compared to more humid areas, as humidity is essential to prevent skin desiccation in these animals.	Villa et al. 2019; Pereira-Ribeiro et al. 2019; Ceron et al. 2020; Roberto & Cascon 2023

Photoperiod	The photoperiod drives the calling patterns of anurans in tropical forests, as it allows them to synchronize their physiology and behavior with more favorable environmental conditions for reproduction.	Rosa et al. 2021; Roberto & Cascon 2023
Phylogenetics	Phylogenetic composition plays a fundamental role in understanding the abundance and distribution of anuran species in the Neotropical region. By analyzing the evolutionary relationships between species within a community, we can infer the historical and ecological processes that have shaped its assembly.	Montero-Mendieta 2021; Fontana et al. 2023

Table 2. Comparison of models with different combinations of environmental variables and their respective Akaike Information Criterion (AIC) values.

Model	**Interactions**	**AIC**
1	Daily Precipitation * Mean Air Temperature * Humidity x Photoperiod	1008
2	Daily Precipitation * Mean Air Temperature * Humidity	900
3	Daily Precipitation * Mean Air Temperature	800
4	Mean Air Temperature * Humidity * Photoperiod	1007
5	Humidity * Photoperiod	988
7	Daily Precipitation * Humidity * Photoperiod	990
8	Daily Precipitation * Mean Air Temperature * Photoperiod	963
10	Daily Precipitation * Humidity	850
11	Mean Air Temperature * Photoperiod	971

Table 3. Results of the fixed effects and interactions of model 3 (Daily Precipitation x Mean Air Temperature) based on a phylogenetic generalized linear mixed model (PGLMM).

Effect	**Estimate**	**Standard Error**	**Z-score**	**p-value**
Intercept	1.042	0.130	7.962	<0.001
Daily Precipitation	0.220	0.111	1.981	0.047
Mean Air Temperature	0.167	0107	1.550	0.120
Daily Precipitation * Mean Air Temperature	-0.060	0.156	-0.389	0.696

FIGURE CAPTIONS

Figure 1. Phylogenetic relationship of species recorded in the study area. Deli: *Dendropsophus elianeae*; Djim: *D. jimi*; Dnan: *D. nanus*; Dmin: *D. minutus*; Balb: *Boana albopunctata*; Bran: *B. raniceps*; Bpun: *B. punctata*; Sfusov: *Scinax fuscovarius*; Snas: *S. nasicus*; Sfuscom: *S. fuscomarginatus*; Sacu: *S. acuminatus*; Ppla: *Pseudis platensis*; Ttyp: *Trachycephalus typhonius*; Pazu: *Pithecopus azureus*; Ebic: *Elachistocleis bicolor*; Rdip: *Rhinella diptycha*; Lele: *Leptodactylus elenae*; Lmys: *L. mystacinus*; Lfur: *L. furnarius*; Lfus: *L. fuscus*; Llab: *L. labyrinthicus*; Lmac: *L. macrosternum*; Lpod: *L. podicipinus*; Adip: *Adenomera diptyx*; Pmot: *Pseudopaludicola motorzinho*; Palb: *Physalaemus albonotatus*; Pcen: *P. centralis*; Pbil: *P. biligonigerus*; Pcuv: *P. cuvieri*; Pnat: *P. nattereri*.

Figure 2. Relationship between Daily Precipitation and Abundance.

FIGURES

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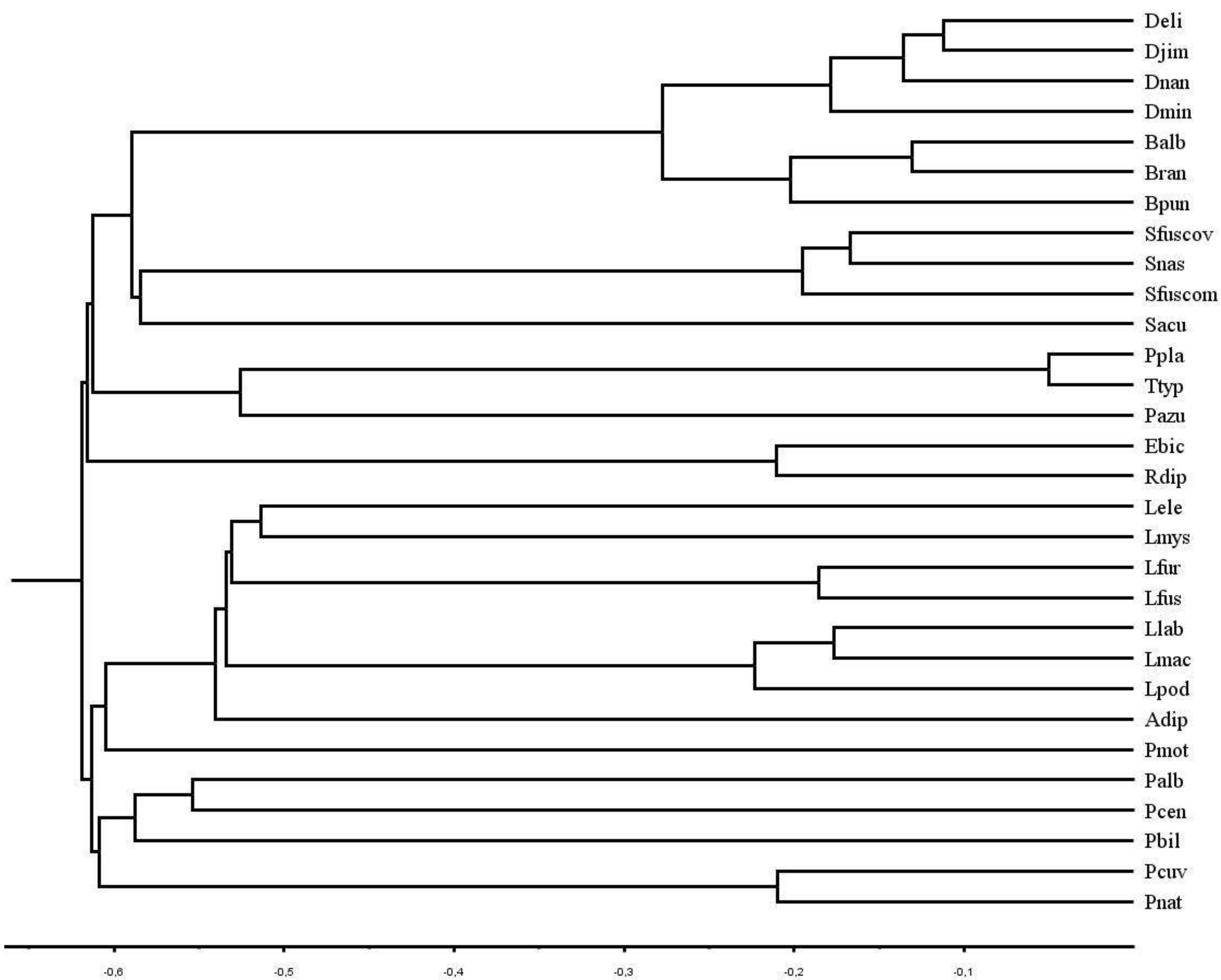

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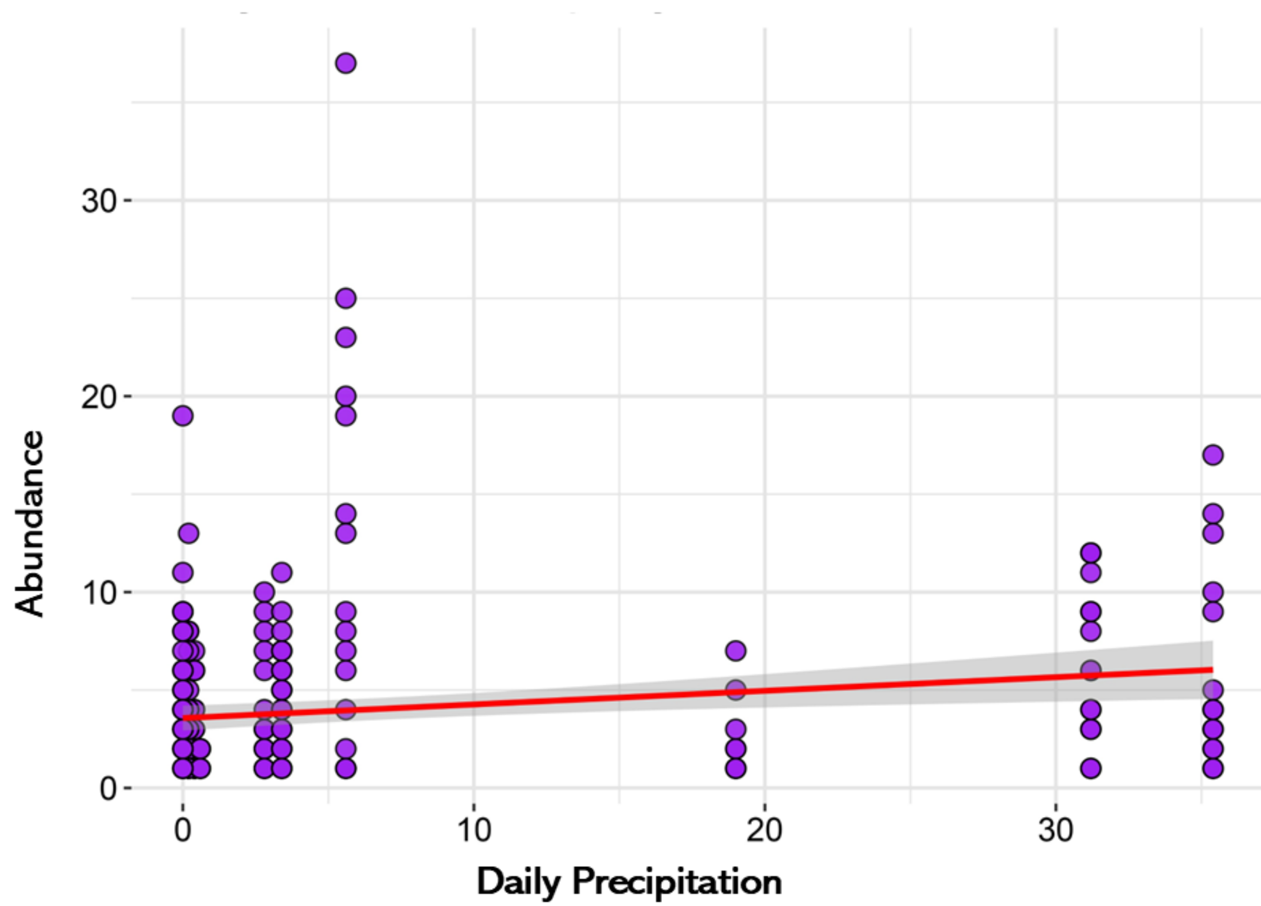

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DISCLOSURE STATEMENTS

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

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SUPPLEMENTARY INFORMATION

Supplementary Material 1. GenBank details: species and accession number.

GendBank/BOLD number	Genus	Species
OR248765.1	*Adenomera*	*diptyx*
MT583106.1	*Boana*	*raniceps*
MT583096.1	*Boana*	*albopunctata*
MT583102.1	*Boana*	*punctata*
MT583121.1	*Dendropsophus*	*nanus*
MT583119.1	*Dendropsophus*	*minutus*
MT583115.1	*Dendropsophus*	*jimi*
MN420388.1	*Dendropsophus*	*elianeae*
ON873601.2	*Elachistocleis*	*bicolor*
MT583151.1	*Leptodactylus*	*podicipinus*
MN153848.1	*Leptodactylus*	*mystacinus*
KU494532.1	*Leptodactylus*	*labyrinthicus*
MT583142.1	*Leptodactylus*	*fuscus*

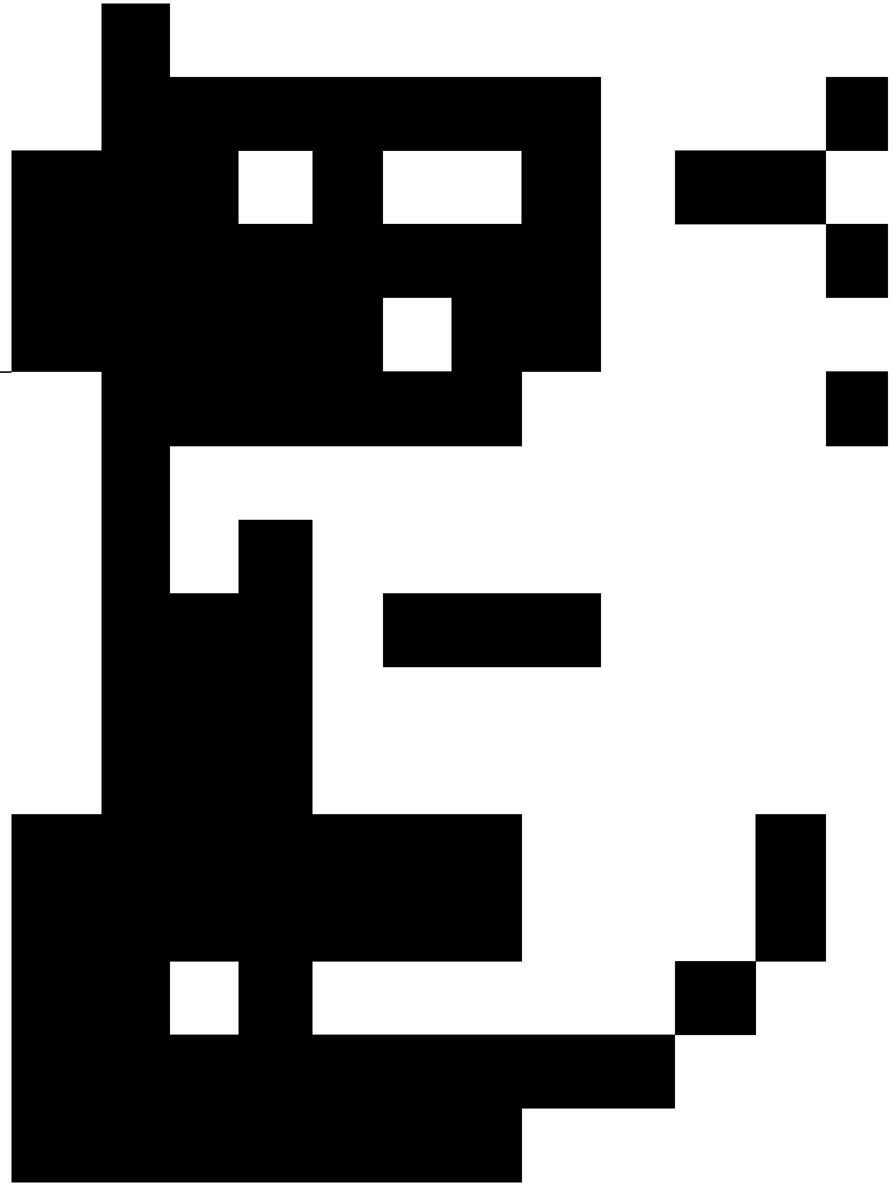
MT583141.1	*Leptodactylus*	*furnarius*
MW316308.1	*Leptodactylus*	*elenae*
MT496546.1	*Leptodactylus*	*macrosternum*
MT583171.1	*Physalaemus*	*nattereri*
MT583169.1	*Physalaemus*	*cuvieri*
MW201204.1	*Physalaemus*	*centralis*
KP145988.1	*Physalaemus*	*biligonigerus*
OR458898.1	*Physalaemus*	*albonotatus*
MF926328.1	*Pithecopus*	*azureus*
MT996155.1	*Pseudis*	*platensis*
KJ147040.1	*Pseudopaludicola*	*motorzinho*
MT583183.1	*Rhinella*	*diptycha*
MT583193.1	*Scinax*	*nasicus*
KU494759.1	*Scinax*	*fuscovarius*
MT583187.1	*Scinax*	*fuscomarginatus*
OQ934392.1	*Scinax*	*acuminatus*

MT996188.1	*Trachycephalus typhonius*

Supplementary Material 2. Species recorded each month from August 2023 to July 2024. Aug – August, Sep – September, Oct – October, Nov – November, Dec – December, Jan – January, Feb – February, Mar – March, Apr – April, May – May, Jun – June, Jul – July.

Family	Species	Months sampled											
		Aug	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**
Bufonidae	*Rhinella dyptcha*	■	■	■	■				■				
Hylidae	*Boana albopunctata*	■	■	■	■								
	Boana punctata							■					
	Boana raniceps	■	■	■	■	■	■	■	■	■		■	
	Dendropsophus elianeae		■										
	Dendropsophus jimii		■	■	■	■		■					
	Dendropsophus minutus	■	■	■	■	■	■	■	■	■		■	
	Dendropsophus nanus	■	■	■	■	■	■	■					
	Pithecopus azureus	■	■	■	■			■	■				
	Pseudis platensis	■	■	■	■		■	■					

	Scinax acuminatus
	Scinax fuscomarginatus
	Scinax fuscovarius
	Scinax nasicus
	Trachycephalus typhonius
Leptodactylidae	*Adenomera diptyx*
	Leptodactylus elenae
	Leptodactylus furnarius
	Leptodactylus fuscus
	Leptodactylus
	labyrinthicus
	Leptodactylus
	macrosternum
	Leptodactylus mystacinus
	Leptodactylus podicipinus
	Physalaemus albonotatus



	Physalaemus biligonigerus	■										
	Physalaemus centralis	■	■	■	■		■					
	Physalaemus cuvieri	■	■	■	■		■					
	Physalaemus nattereri		■									
	Pseudopaludicola motorzinho	■	■	■	■	■	■	■	■	■	■	■
Microhylidae	*Elachistocleis bicolor*			■	■		■				■	