

COMPOSITION, PHENOLOGY, AND HABITAT USE OF ANURANS IN A CERRADO REMNANT IN NORTHEASTERN BRAZIL

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Abstract.—Breeding anurans are commonly used for assessing biodiversity and identifying priority areas for conservation. Here we describe the diversity, composition, calling phenology, and habitat use of anuran species in a poorly known area of the Cerrado biome in the south-central portion of the state of Maranhão in northeastern Brazil, and examine the influence of environmental and climatic factors on activity patterns of the species observed. Between December 2013 and February 2015, we surveyed seven sites every two months using active visual search and auditory census. We recorded 31 anuran species from five families and 11 genera: Leptodactylidae (14 species), Hylidae (12), Bufonidae (three), Microhylidae (one), and Phyllomedusidae (one). In general, environments with greater heterogeneity had greater species diversity. We found high replacement of species (β diversity) among the different water bodies sampled. Similarity analysis revealed that species differed in use of calling sites and identified six groups of species with various degrees of overlap. Abundance was correlated with minimum temperature in the week prior to data collection, whereas species richness was not correlated with any climatic variable analyzed. We observed a marked decrease in species richness, abundance, and vocalization, however, during the dry season (June and August). Our study provides important data on the occurrence and activity patterns of anurans in the northern portion of the Cerrado, especially in the state of Maranhão. This region has high biodiversity and is currently threatened by the advance of agriculture. Thus, our data will be useful in formulating management plans and supporting future conservation strategies in the region.

Key Words.—anuran fauna; β diversity; climatic factors; environmental heterogeneity; Mirador; species composition

INTRODUCTION

Amphibians are one of the most diverse and conspicuous groups of vertebrates in the world, occurring in tropical, subtropical, and temperate regions, and having diverse life histories, ranging from oviparity to viviparity with aquatic, semi-aquatic, or terrestrial habitats (Wells 2007; Duellman and Trueb 1994). Amphibians are exposed to a multitude of complex natural and anthropogenic ecological pressures, which generate distinct spatiotemporal occurrence patterns of species because of their different requirements and levels of tolerance to environmental variation (Duellman and Trueb 1994). Factors related to physiological and reproductive needs and biotic interactions with other species are major determinants of composition and structure of amphibian communities (Blaustein and Bancroft 2007). For anuran amphibians, reproductive characteristics are a primary determinant of community structure because differences in breeding site location,

timing of vocalization, and acoustic parameters allow for spatial and temporal division of habitats and the coexistence of different species (Duellman and Trueb 1994; Vasconcelos et al. 2010). Small temperature variations affect the assimilation and energy utilization rates of individuals (Vitt and Caldwell 2014), directly influencing the immunological, physiological, ecological, and behavioral characteristics of individuals, including those related to reproduction, development rate, and demand for food (Maciel and Juncá 2009; Blaustein et al. 2010; López-Alcaide and Macip-Ríos 2011). Precipitation is important for initiating and sustaining reproductive behavior in many species and also affects hydroperiod of aquatic breeding sites as well as soil moisture (Vonesh 2001; Toledo et al. 2003; Beja and Alcazar 2003; Bastazini et al. 2007).

In South America, the Cerrado biome is a biogeographic region of great interest for studies on patterns of diversity and distribution of amphibians. The varied degrees of vegetation structural complexity,

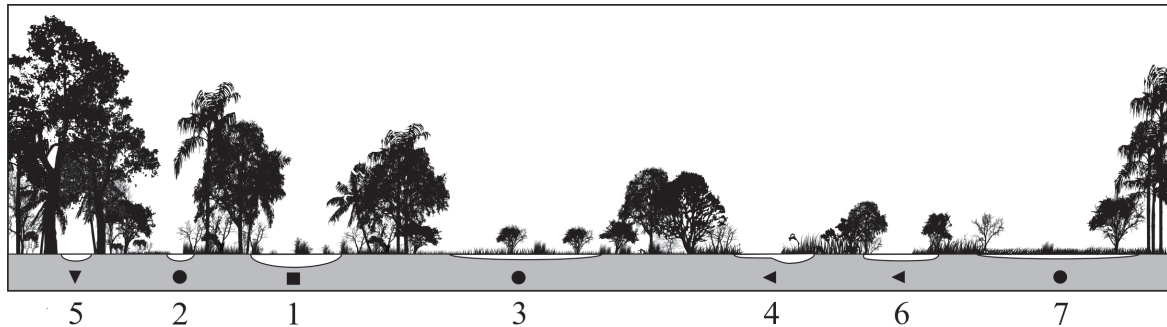


FIGURE 1. Schematic profile (no scale) of the vegetation around the water bodies surveyed in the Parque Estadual do Mirador, Maranhão, Brazil. Sampling sites (P1 to P7) are represented by numbers 1–7. The order of the sites in scheme does not correspond to the sampling order. Triangles represents the direction of the water flow: (▼) from top to bottom and (◄) from right to left. Circle (●) represents standing water, and the square (■) represents water with little movement.

with open and forested areas, create a matrix of environmental conditions that support a large number of species (Oliveira-Filho and Ratter 2002; Ribeiro and Walter 2008). Despite its ecological importance, the Cerrado has been heavily impacted by human activities, mainly due to major agricultural expansion and intense local exploitation of native resources (Klink and Machado 2005). Therefore, it is urgent to increase efforts to understand the composition and distribution of species in this biodiversity hotspot (Myers et al. 2000; Barreto Rocha et al. 2004).

Despite the growing number of studies and species lists published in recent years (Maffei et al. 2011; Valdujo et al. 2011, 2012; Santoro and Brandão 2014; Santos et al. 2014; Andrade et al. 2017), the composition and distribution of amphibians in the Cerrado is still poorly known, especially in its northern portion (Diniz-Filho et al. 2005; Valdujo et al. 2011; Vasconcelos and Nascimento 2014; Andrade et al. 2017). The state of Maranhão contains a large part of the northern Brazilian Cerrado, about 216,000 km² distributed in almost 60% of the state (Instituto Brasileiro de Geografia e Estatística. 2011. Mapas de vegetação, geologia e solos do Maranhão. Available at <http://cod.ibge.gov.br/1XUKN> [Accessed 15 April 2016]). Despite the great expanse of Cerrado in Maranhão, data on the composition and distribution of anurans are scarce (Barreto 2007; Brasileiro et al. 2008; Andrade et al. 2017).

Breeding anurans are commonly used as biological models for assessing different biodiversity metrics, such as species richness, species compositional variation among habitats (i.e., beta diversity), and phylogenetic diversity, among others (Santoro and Brandão 2014; Miranda et al. 2015; Andrade et al. 2016, 2017; Lourenço-de-Moraes et al. 2019). These metrics are useful for identifying areas with high biological diversity and importance for conservation. The goal of the present study is: (1) to determine the diversity and composition of anuran species in a Cerrado remnant in the south-central portion of the state of Maranhão;

(2) to describe the calling phenology, and habitat and microhabitat use by the anurans; (3) to determine which component of beta diversity best explains patterns of species occurrence across sites; and (4) to evaluate the influence of environmental and climatic factors on species richness and abundance.

MATERIALS AND METHODS

Study area.—We conducted this study in the Parque Estadual do Mirador (PEM; 06°10'–06°42'S; 44°43'–45°54'W), located in the south-central region of the state of Maranhão in northeastern Brazil. The Park is situated between the Itapecuru and Alpercatas rivers and encompasses the municipalities of Mirador, Formosa da Serra Negra, and Fernando Falcão. The PEM, the largest Conservation Unit in the state of Maranhão with approximately 767,000 ha (Estado do Maranhão 2009), is located in a Cerrado area (Conceição and Castro 2009), on litholic, stony, and rocky soils (Alcântara 2004). It has a dry and sub-humid climate (Aw¹), with annual rainfall of 1,200 to 1,400 mm and average annual temperatures ranging from 19.5° to 33° C (Alcântara 2004).

We selected seven sampling sites through diurnal and nocturnal expeditions in October and November 2013 to establish the presence of water bodies (temporary or permanent) used as breeding sites by anurans (Fig. 1):

P1 (6°37'49.60"S; 45°52'44.00"W). Permanent pond with a maximum depth of 1.5 m formed from the springs of the Alpercatas River, in which there were some floating aquatic macrophytes and a small cluster of plants inside the pond formed by emergent vegetation (*Juncus* sp.). The surrounding vegetation consisted of medium (5–10 m) to large (> 10 m) trees, including some palm. It had a soaked margin and a large amount of litter under the trees.

P2 (6°36'10.6"S; 45°50'32.0"W). Small temporary pond, with a maximum depth of 0.6 m. It had a large amount of emergent aquatic macrophytes, including

large Buriti palms (*Mauritia flexuosa*). On the periphery, the vegetation included a few spaced trees and abundant herbaceous plants. It had wet margins partially sloping with little or no litter.

P3 (6°36'27.65"S; 45°50'29.58"W). Extensive flooded field with a maximum depth of 0.5 m in the rainy season. Located among spaced trees, it contained little vegetation other than a few clumps of shrubs. It had flat and dry margins, and no litter deposition around it.

P4 (6°36'13.30"S; 45°49'1.50"W). Permanent stream located in an area with campo sujo physiognomy (Moraes 2014). Much of the stream extent was covered by shrubby vegetation, except for a small area interrupted by an unpaved road. It had partially sloping dry margins. Upstream, the stream was narrow (width < 2 m) and deep (depth about 1.5 m) with a strong current. The stream then widened (width about 5 m) when crossing the unpaved road forming a shallow area (depth about 0.3 m), after which it continued flowing downstream through vegetation.

P5 (6°36'37.30"S; 45°47'59.20"W). Permanent stream inside a gallery forest with large palms. It had a flat and soaked margin for much of its length and accumulation of palm leaves on the ground. There was no vegetation within the stream. In the lower portion, there was a small pool with an average depth of 0.5 m, which was used as a water source by local inhabitants of the park.

P6 (6°36'34.20"S; 45°46'43.90"W). Permanent stream in a field area with some scattered palm trees. The marginal vegetation was open for a great part of its extent; however, a small bush forest in which the water penetrates was present after crossing an unpaved road. It had a maximum depth of 0.8 m and the vegetation within was composed mainly of grasses and reeds. The margins were flat and dry.

P7 (6°47'28.20"S; 45°28'25.10"W). Flooded field formed in the rainy season from the waters of the Itapecuru River. The flooded field had a large area and is covered by emergent vegetation with average height of 0.8 m. It had a few, widely spaced trees and some palm trees. The soil was sandy and remained flooded throughout the rainy season.

Data collection.—We sampled for anurans every two months, from December 2013 to February 2015, during both rainy (December-May) and dry (June-November) seasons. We used active visual search and auditory census (Heyer et al. 1994) in different microhabitats used by frogs (on vegetation, under marginal vegetation, under litter leaves, under fallen logs, and in rock crevices, among others). These methods are considered the most efficient in terms of documenting the largest number of species in the shortest time (Valdujo et al. 2009). We recorded all individuals seen and estimated

the total abundance of vocalizing males (Vasconcelos and Rossa-Feres 2005; Santos et al. 2007).

During each sampling period, three researchers carried out field activities during three consecutive days, starting around 1800 and ending at 2400. Only one researcher was present for all eight periods whereas other researchers were substituted throughout the study. Sampling effort was proportional to the size and structural complexity of the water bodies (Scott and Woodward 1994), with a minimum duration of 40 min and maximum of 160 min. We sampled each site once per period and alternated the starting time of the sampling at each site in order to sample different periods of the night and increase the chance of detecting species (Valdujo et al. 2011).

We obtained climate data (accumulated rainfall, mean maximum temperature, mean minimum temperature, and mean relative humidity of the 7 d prior to the sampling period) from Banco de Dados Meteorológicos para Ensino e Pesquisa-BDMEP (Meteorological Database for Teaching and Research) of the Instituto Nacional de Meteorologia-INMET (National Institute of Meteorology), Substation of Balsas - Maranhão (about 90 km from PEM). We collected and deposited two individuals of each species at the Delta do Parnaíba Zoological Collection (CZDP 11) of the Universidade Federal Delta do Parnaíba-UFDPar, Parnaíba, Piauí, Brazil.

Data analysis.—We used the Shannon-Wiener (H') and Pielou equitability (J') indices to determine the species diversity at each sampling site (Krebs 2000). To obtain a reference value, we consider the logarithm of the number of species used in the analysis as the total diversity (H' total) and the maximum theoretical diversity (H' max) as the logarithm of the number of species at each collection site. Thus, we consider high diversity when $H' \geq 60\%$ of the total log of species (H' total) and $H' \geq 60\%$ of the total log of species in each site (H' max; adapted from Conte and Rossa-Feres 2006). We estimated species abundances using the sum of the calling males and visualized individuals (males and females) in each sampling site. To avoid overestimation resulting from recounting individuals across multiple sampling periods, we adopted the number of individuals recorded in the period of greatest occurrence as total abundance (Conte and Rossa-Feres 2006; Santos et al. 2008).

To assess β diversity among the different sampling sites (i.e., the variation in species composition among sites), we computed the LCBP indices (i.e., Local Contributions to Beta Diversity; sensu Legendre and De Cáceres 2013) using the Sorensen dissimilarity index of the Baselga family for species abundance data (Legendre 2014). The LCBP indices represent how much each

sampling site contributes to beta diversity (BD_{total}) and can be decomposed into species replacement (turnover) and nestedness components (Legendre and De Cáceres 2013; Legendre 2014). In addition, we used the Mantel test (Manly 2000) with 1,000 permutations to assess the influence of geographical distance on the species composition among sampling sites, using the Bray-Curtis similarity index.

We visually estimated the vertical occupation of species using height classes of calling perch for those species whose males vocalized in the vegetation (0–1 m; > 1–3 m; > 3–5 m; > 5 m), and horizontal occupation using the distance classes of the calling male to the nearest water body (0–0.5 m; > 0.5–1 m; > 1–2 m; > 2 m). We used the non-parametric Kruskal-Wallis (*H*) test to test for differences in vertical and horizontal space use in calling males of species ($\alpha = 0.05$). Microhabitat use was determined from substrates used by males as call sites (herbaceous vegetation, shrub, tree, reed, dry soil, soaked soil, litter, partially submerged, or floating). We quantified overlap in microhabitat use with the Morisita-Horn similarity index (CH) using species abundance in each microhabitat, followed by unweighted mean clustering (UPGMA; Krebs 2000). Clusters with similarity values higher than 60% (CH > 0.60) were considered to have high overlap (adapted from Melo et al. 2007). We used the cophenetic correlation coefficient (Pearson's *r*) to evaluate the representativity of the similarity matrix, obtained from the dendrogram, in relation to the original similarity matrix, with low values considered $r < 0.8$ (Rohlf 2000).

Finally, we evaluated the correlation of climatic factors (accumulated rainfall, mean maximum temperature, mean minimum temperature, and mean relative humidity for the 7 d prior to sampling period) with abundance and species richness using the Spearman rank-order correlation test (*rs*; Zar 1999). Reproductive modes are according to Haddad and Prado (2005). We calculated diversity metrics and performed correlation tests and similarity analysis using the software PAST 1.4 (Hammer et al. 2001) and R 3.5.1 (R Core Team 2018).

RESULTS

We recorded 31 anurans species in the PEM representing five families and 11 genera (species number in parenthesis): Leptodactylidae (14 species), Hylidae (12), Bufonidae (three), Microhylidae (one) and Phyllomedusidae (one; Table 1). We recorded *Adenomera* sp., *Leptodactylus mystaceus* (Basin White-lipped Frog) and *Rhinella ocellata* (Ocellated Toad) near but not in the sampling sites and we found only one individual of *Leptodactylus petersii* (Peters' Thin-Toed Frog), therefore we excluded these four species from analyses. Individuals of *Adenomera* sp. vocalized

hidden under litter in forest regions near sites P1 and P7. We found the only individual of *L. mystaceus* on the margins of a small stream near site P1 and some males of *R. ocellata* vocalized in a terrestrial environment among tufts of grass near site P2.

Based on our criteria, species diversity was high in four sampling sites (P1, P2, P3, and P5; Table 1). Sites P4, P6, and P7 exhibited low diversity, although P7 was close to the cutoff value. Site P4 had the lowest species richness (five species) and species diversity, whereas site P5 had the greatest species richness (17 species) and the highest *H'* diversity (Table 1). Although site P1 had fewer species than P5, species abundances were more equitable, giving it the highest *J'* diversity (Table 1).

Seven species called for most of sampling period (*Dendropsophus branneri* [no common name], *Dendropsophus minutus* [Guianan Dwarf Treefrog], *Boana multifasciata* [Many-banded Treefrog], *Pithecopus azureus* [no common name], *Scinax fuscomarginatus* [Brown-bordered Snouted Treefrog], *Scinax nebulosus* [Spix's Snouted Treefrog], and *Scinax* aff. *ruber* [Common Snouted Treefrog]), whereas two species called in only one period (*Boana boans* [Giant Gladiator Treefrog] and *Adenomera hylaedactyla* [Dark-spotted Thin-toed Frog]; see Fig. 2). Three species were widely distributed in PEM (11.11% of species): *Boana punctata* (Dotted Treefrog) and *B. multifasciata* occurred in six sampling sites and *S. nebulosus* occurred in five sites. On the other hand, four species (14.81%) occurred only in one site (*Adenomera saci* [no common name], *Leptodactylus sertanejo* [no common name], *Leptodactylus troglodytes* [Pernambuco White-lipped Frog], and *Pseudopaludicola jaredi* [no common name]).

There was low similarity in species composition among sites (BD_{total} = 0.383), with species replacement best explaining beta diversity patterns (70% of BD_{total}; Fig. 3). The turnover in species composition was highest for P7 as this site contained the largest number of exclusive species. Difference in composition was caused mainly by site P3, which had the largest species abundance (LCBD = 0.194; $P = 0.001$). In addition, there was no correlation between the geographic distance between sites and similarity in their species compositions ($r = 0.141$; $P = 0.312$). Sites P1 and P2, and P2 and P5, had the greatest similarity in species composition (Table 2). By contrast, sites P3 and P7 exhibited the lowest similarity, sharing only one species (Table 2).

There was a significant difference in vertical ($H = 13.48$; $df = 3$ $P < 0.001$) and horizontal ($H = 30.77$; $df = 3$, $P < 0.001$) space use among species. Of the 31 species recorded, 18 (58.1%) were classified as ground-dwelling and 13 (41.9%) as arboreal. The cluster analysis of microhabitat use clearly showed segregation between

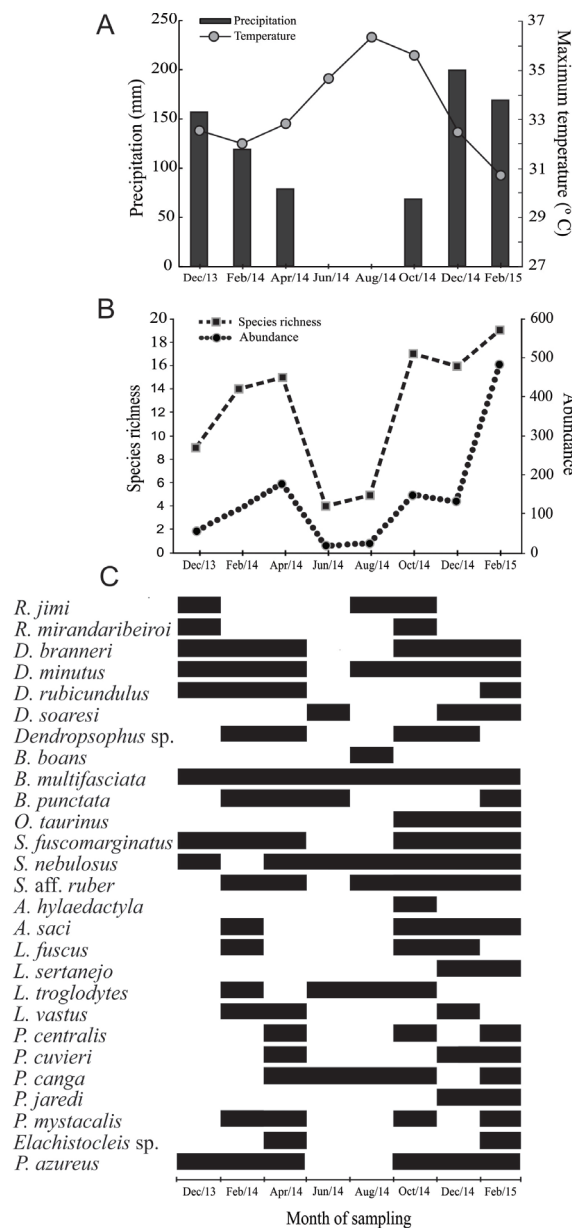


FIGURE 2. Environmental data and species richness (number of species), abundance (number of individuals), and vocalization periods for anuran species recorded in the Parque Estadual do Mirador (PEM), Maranhão, Brazil, between December 2013 and February 2015. (A) Monthly precipitation and the mean monthly maximum temperature recorded in the sampling periods. (B) Species richness and abundance of anurans recorded in the PEM during the sampling periods. (C) Temporal distribution of the anuran species recorded in the PEM; the horizontal bars represent the occurrence of male calling during the sampling period. The complete names of the species and common names are listed in Table 1. Four species are not included (see Results and Table 1 for more information).

hylids and non-hylids, with the formation of six groups (Fig. 4). Groups 1 and 4 were formed by unique species that used microhabitats differently from other species:

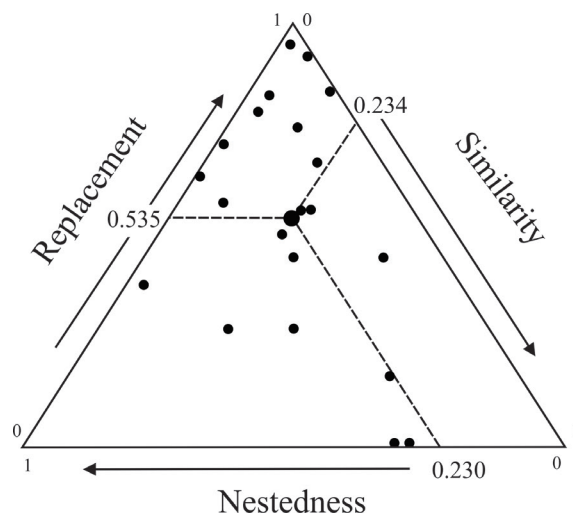


FIGURE 3. Triangular plot of the relationships among pairs of sampling sites studied in the Estadal do Mirador Maranhão, Brazil, showing the values of similarity, replacement, and nestedness. The dotted lines represent the links between the mean values, which are listed on the three axes.

L. troglodytes vocalized only under the litter whereas *Rhinella jimi* (no common name) always vocalized in areas of dry soil. Group 2 contains ground-dwelling species that vocalize on the ground, which includes: (1) species that vocalize predominantly on swampy, or eventually dry soil (*Leptodactylus fuscus* [Fuscous Foam Frog], *Leptodactylus vastus* [Northeastern Pepper Frog] and *Rhinella mirandaribeiroi* [no common name]); (2) species that vocalize on swampy soil in clear field areas with a predominance of herbaceous vegetation (*A. saci*, *L. sertanejo*, *Pseudopaludicola canga* [no common name], *P. jaredi* and *Pseudopaludicola mystacalis* [Cope's Swamp Frog]); and (3) a single species that predominantly vocalizes on swampy soils, but which can also be found under litter near water bodies in gallery forests (*A. hylaedactyla*).

Group 3 contains species that vocalize within the water while floating with the body partially submerged in temporary ponds and in flooded areas (*Physalaemus centralis* [Central Dwarf Frog], *Physalaemus cuvieri* [Cuvier's Foam Froglet] and *Elachistocleis* sp.). Group 5 comprises species with similar vocalization sites, perching on small to medium vegetation (0.4 to 2.5 m high), which includes: (1) species that had high abundance in shrub vegetation and reeds within the pond (*D. branneri*, *Dendropsophus* sp. and *S. fuscomarginatus*); (2) species that were more abundant in the marginal vegetation (*B. multifasciata*, *D. minutus*, *Dendropsophus rubicundulus* [Lagoa Santa Treefrog], *Dendropsophus soaresi* [Picos Treefrog], *P. azureus*, *S. nebulosus* and *S. aff. ruber*); and (3) a single species that despite being found vocalizing on shrubby vegetation, had its highest abundance in herbaceous vegetation,

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TABLE 1. Number of anurans recorded at seven sampling sites (P1-P7; see description in Materials and Methods) in the Parque Estadual do Mirador, south-central region of the state of Maranhão, Brazil, between December 2013 and February 2015. Reprod. mode: number indicates reproductive mode of the species (see Results for details). An asterisk (*) indicates species not considered in statistical analyses and that have not had their reproductive modes determined; the question mark (?) indicates unidentified species.

Taxon	P1	P2	P3	P4	P5	P6	P7	Reprod. mode
BUFONIDAE (three species)								
<i>Rhinella jimi</i> (no common name)	1	1	0	0	2	3	0	1
<i>Rhinella mirandaribeiroi</i> (no common name)	4	0	0	0	0	9	0	1
<i>Rhinella ocellata</i> (Ocellated Toad)*	0	6	0	0	0	0	0	*
HYLIDAE (12 species)								
<i>Dendropsophus branneri</i> (no common name)	20	26	2	0	0	0	0	1
<i>Dendropsophus minutus</i> (Guianan Dwarf Treefrog)	5	5	46	0	0	0	0	1
<i>Dendropsophus rubicundulus</i> (Lagoa Santa Treefrog)	0	9	58	0	1	0	0	1
<i>Dendropsophus soaresi</i> (Picos Treefrog)	0	0	45	0	11	0	0	1
<i>Dendropsophus</i> sp.	0	0	0	0	7	0	5	?
<i>Boana boana</i> (Giant Gladiator Treefrog)	0	1	0	0	0	0	3	4
<i>Boana multifasciata</i> (Many-banded Treefrog)	11	8	0	6	22	8	21	1
<i>Boana punctata</i> (Dotted Treefrog)	17	5	0	5	8	11	4	1
<i>Osteocephalus taurinus</i> (Manaus Slender-legged Treefrog)	7	0	0	0	7	0	0	1
<i>Scinax fuscomarginatus</i> (Brown-bordered Snouted Treefrog)	16	13	54	0	0	0	0	1
<i>Scinax nebulosus</i> (Spix's Snouted Treefrog)	15	4	0	4	5	2	0	1
<i>Scinax</i> aff. <i>ruber</i> (Common Snouted Treefrog)	0	0	30	0	16	0	9	1
LEPTODACTYLIDAE (14 species)								
<i>Adenomera hylaedactyla</i> (Dark-spotted Thin-toed Frog)	0	6	2	0	0	2	0	32
<i>Adenomera saci</i> (no common name)	0	0	0	0	0	0	41	32
<i>Adenomera</i> sp.*	0	0	0	0	0	5	14	?
<i>Leptodactylus fuscus</i> (Fuscous Foam Frog)	0	2	23	2	7	0	0	30
<i>Leptodactylus mystaceus</i> (Basin White-lipped Frog)*	1	0	0	0	0	0	0	*
<i>Leptodactylus petersii</i> (Peters' Thin-toed Frog)*	0	0	0	0	1	0	0	*
<i>Leptodactylus sertanejo</i> (no common name)	0	0	0	0	0	0	31	30
<i>Leptodactylus troglodytes</i> (Pernambuco White-lipped Frog)	0	0	2	0	0	0	0	30
<i>Leptodactylus vastus</i> (Northeastern Pepper Frog)	0	0	1	0	2	0	0	13
<i>Physalaemus centralis</i> (Central Dwarf Frog)	0	0	28	0	0	1	0	11
<i>Physalaemus cuvieri</i> (Cuvier's Foam Froglet)	0	1	23	0	7	0	0	11
<i>Pseudopaludicola canga</i> (no common name)	8	4	0	0	4	0	35	1
<i>Pseudopaludicola jaredi</i> (no common name).	0	0	0	0	0	0	8	1
<i>Pseudopaludicola mystacalis</i> (Cope's Swamp Frog)	4	0	30	0	3	0	0	1
MICROHYLIDAE (one species)								
<i>Elachistocleis</i> sp.	0	0	0	0	4	0	3	?
PHYLLOMEDUSIDAE (one species)								
<i>Pithecopus azureus</i> (no common name)	0	12	9	1	2	0	0	24
Species richness (S)	11	14	14	5	17	7	10	
Shannon-Wiener diversity (H')	2.193	2.269	2.286	1.461	2.493	1.671	1.927	
Pielou equitability (J')	0.914	0.860	0.866	0.908	0.899	0.858	0.837	
H'/H' max (%)	91.45	86.00	86.62	90.80	89.91	85.87	83.00	

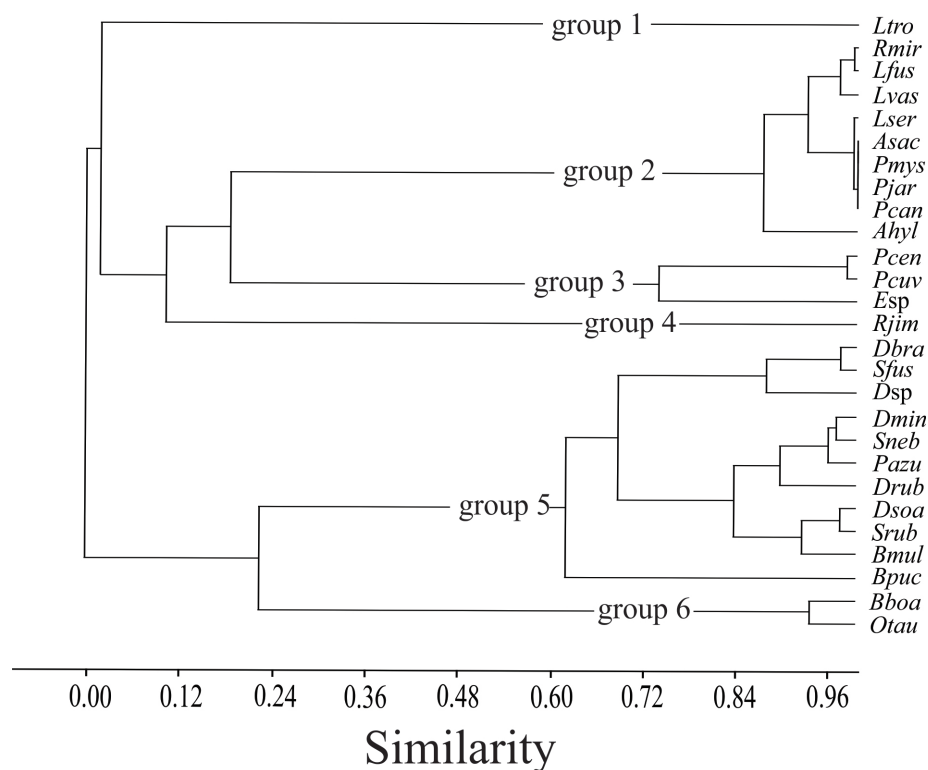


FIGURE 4. Overlap in the use of calling sites using the Morisita-Horn similarity index among 27 of the 31 species recorded in the seven studied water bodies in the Parque Estadual do Mirador, Maranhão, Brazil, showing formation of six groups. Species: *Ltro* = *Leptodactylus troglodites*; *Rmir* = *Rhinella mirandaribeiroi*; *Lvas* = *Leptodactylus vastus*; *Lfus* = *Leptodactylus fuscus*; *Asac* = *Adenomera saci*; *Lser* = *Leptodactylus sertanejo*; *Pmys* = *Pseudopaludicola mystacalis*; *Pjar* = *Pseudopaludicola jaredi*; *Pcan* = *Pseudopaludicola canga*; *Ahyl* = *Adenomera hylaedactyla*; *Pcen* = *Physalaemus centralis*; *Pcu* = *Physalaemus cuvieri*; *Esp* = *Elachistocleis* sp.; *Rjim* = *Rhinella jimi*; *Dbra* = *Dendropsophus branneri*; *Sfus* = *Scinax fuscomarginatus*; *Dsp* = *Dendropsophus* sp.; *Dmin* = *Dendropsophus minutus*; *Sneb* = *Scinax nebulosus*; *Pazu* = *Pithecopus azureus*; *Drub* = *Dendropsophus rubicundulus*; *Dsoa* = *Dendropsophus soaresi*; *Srub* = *Scinax* aff. *ruber*; *Bmul* = *Boana multifasciata*; *Bpun* = *Boana punctata*; *Bboa* = *Boana boans*; *Otau* = *Osteocephalus taurinus*. Common names are provided in Table 1. Cophenetic correlation coefficient (r) = 0.961.

vocalizing near the soil (*B. punctata*). Group 6 was formed only of *B. boans* and *Osteocephalus taurinus* (Manaus Slender-legged Treefrog), large hylids that vocalize perched on tree branches.

There was a positive correlation between minimum temperature and abundance ($r_s = 0.829$, $P = 0.016$), but there was no correlation between species richness and any of the climatic parameters (all $P > 0.05$). The highest rainfall values in the region occurred between

December 2014 and February 2015, which was also the period with greatest observed abundance and species richness in PEM (Fig. 2). The months with the least amount of rainfall were June and August 2014, when there was a marked reduction in the number of calling male anurans (Fig. 2).

Among the 27 analyzed species that exhibited calling activity, seven reproductive modes are represented (Table 1). Most species (15 species, 55.55% of the

TABLE 2. Similarity in composition of anuran species among the seven sampling sites (P1 to P7) studied in the Parque Estadual do Mirador, Maranhão, Brazil. Similarity between the paired combinations was calculated from Sorensen index of the Baselga family (non-italicized numbers) and geographic distance (m) among the water bodies sampled (italicized numbers).

	P1	P2	P3	P4	P5	P6	P7
P1		5,068	4,828	7,447	9,024	11,303	48,210
P2	58.54		529	2,779	4,765	7,043	45,771
P3	11.71	19.11		2,738	4,627	6,933	45,468
P4	23.81	31.30	1.62		2,045	4,268	2,310
P5	36.11	27.32	20.83	28.57		43,265	41,239
P6	36.11	27.07	1.56	48.15	22.78		39,277
P7	17.17	13.23	3.51	11.24	34.33	12.25	

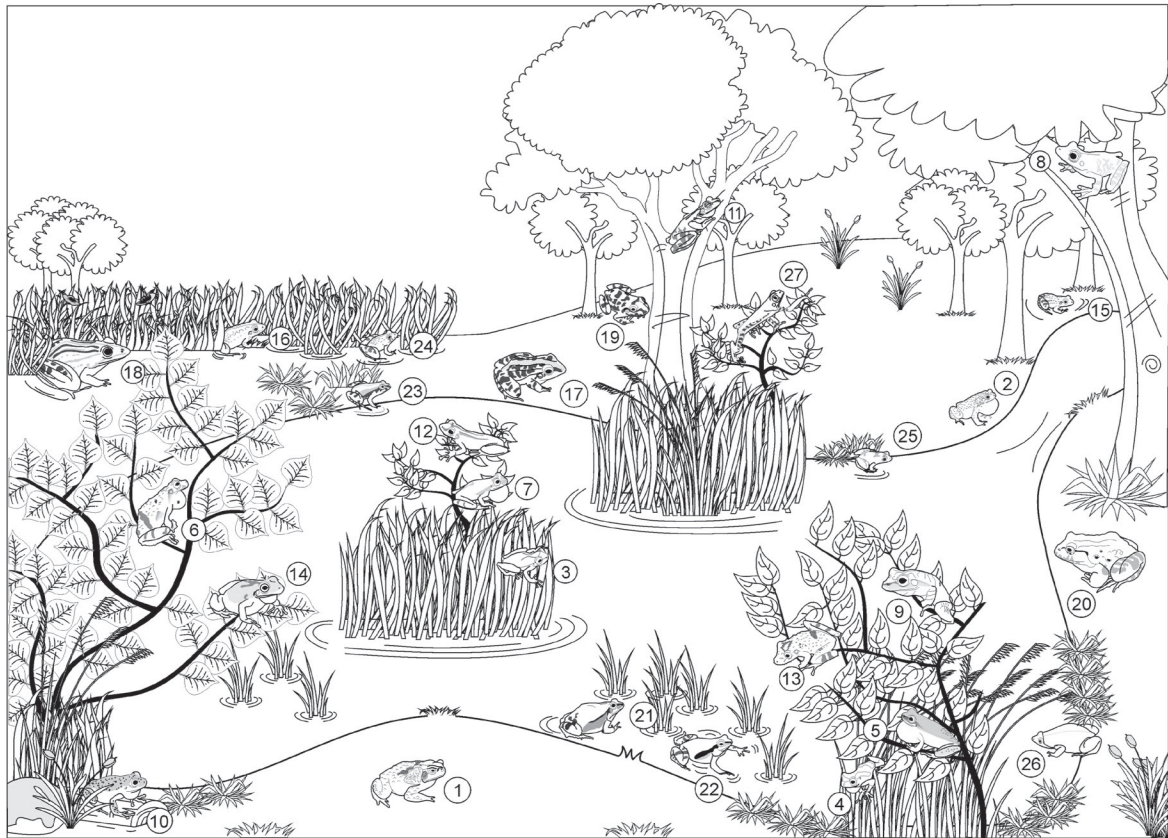


Figure 5. Diagrammatic representation of male calling site and habitat use of the 27 species of anurans analyzed (see results and Table 1 for more information) that were vocalizing in the Parque Estadual do Mirador, Maranhão, Brazil. Species: (1) *Rhinella jimi*; (2) *Rhinella mirandaribeiroi*; (3) *Dendropsophus branneri*; (4) *Dendropsophus minutus*; (5) *Dendropsophus rubicundulus*; (6) *Dendropsophus soaresi*; (7) *Dendropsophus* sp.; (8) *Boana boans*; (9) *Boana multifasciata*; (10) *Boana punctata*; (11) *Osteocephalus taurinus*; (12) *Scinax fuscomarginatus*; (13) *Scinax nebulosus*; (14) *Scinax* aff. *ruber*; (15) *Adenomera hylaedactyla*; (16) *Adenomera saci*; (17) *Leptodactylus fuscus*; (18) *Leptodactylus sertanejo*; (19) *Leptodactylus troglodytes*; (20) *Leptodactylus vastus*; (21) *Physalaemus centralis*; (22) *Physalaemus cuvieri*; (23) *Pseudopaludicola canga*; (24) *Pseudopaludicola Jaredi*; (25) *Pseudopaludicola mystacalis*; (26) *Elachistocleis* sp.; (27) *Pithecopus azureus*. Common names are provided in Table 1.

total) have reproductive mode 1, in which both egg deposition and tadpole development occurs in lentic environments. Eight species deposit their eggs in foam nests, of which: three (11.11%) laid the eggs in foam nests in underground chambers and the tadpoles are exotrophic (mode 30), two (7.40%) lay the eggs in holes in the soil and the tadpoles are endotrophic (mode 32), two (7.40%) lay the eggs in a floating foam nest on the water surface and the tadpoles are exotrophic (mode 11), and one species (3.70%) lays the eggs in floating foam nests on water accumulated in basins constructed in the soil and the tadpoles are exotrophic (mode 13). Only *B. boans* (3.70%) lays the eggs in natural or artificial basins on soil (mode 4). *Pithecopus azureus* (3.70%) lays the eggs on the vegetation with exotrophic tadpoles falling into the water after hatching (mode 24). *Dendropsophus* sp. and *Elachistocleis* sp. (7.40%) did not have their reproductive modes classified because we could not identify them at specific levels.

DISCUSSION

With 31 species, the PEM has the second highest anuran species richness in the state of Maranhão. This number is higher than that recorded by Barreto et al. (2007) in the Balsas River Basin (23 species) and by Andrade et al. (2012) in the region of the Parnaíba River Delta (nine species). Species richness reported here is similar to that recorded in the Reserva Biológica do Gurupi (Freitas et al. 2017) and in the Tocantins River Basin (Brasileiro et al. 2008), with 31 and 33 amphibian species, respectively. In addition, species richness in the PEM was greater than several other studies in different Cerrado regions (Silva-Leite et al. 2008; Oda et al. 2009; Kopp et al. 2010; Dal Vechio et al. 2013). With high richness and 19.35% of species considered endemic to the Brazilian Cerrado (Valdujo et al. 2012; Andrade et al. 2017), the PEM is of great importance in terms of anuran diversity not only for the state of Maranhão but for the northern region of the Cerrado.

Diversity indices, which take into account abundance and species richness, are widely used to assess and compare the structure of biological communities (Krebs 2000; Magurran and McGill 2011). Diversity values are strongly dependent on sample size, however, which makes comparisons between different communities difficult, and they are sometimes indicative of environmental heterogeneity (Silva et al. 2011). The PEM has high availability of diverse microhabitats, which strongly influences the occurrence of different species groups (arboreal and terrestrial; Santoro and Brandão 2014; Andrade et al. 2016). Increases in environmental heterogeneity are directly linked to increases in anuran species richness (Vasconcelos and Rossa-Feres 2008; Melo et al. 2013), especially in the Cerrado (Maffei et al. 2011; Vasconcelos et al. 2011; Santos et al. 2014). The influence of structural complexity on diversity can be observed at site P5, where there is a small permanent stream in the middle of gallery forest. The overflowing of the stream forms small flooded areas, both in open and enclosed areas, increasing the availability of sites for reproduction (Afonso and Eterovick 2007; Andrade et al. 2016). Similarly, the low diversity and species richness at site P7, our most homogeneous site, may be due to low diversity of microhabitats, which consisted only of vegetation typical of flooded environments. The dominant species, *A. saci*, *L. sertanejo*, and *P. canga*, are commonly observed vocalizing under clumps of herbaceous plants in flooded fields (Carvalho and Giaretta 2013; Araújo et al. 2015; Lima et al. 2015; Andrade et al. 2016, 2017).

Species richness is often directly related to the extent of overlap in resource use by species (Piatti and Souza 2011). In the PEM, the overlap in calling sites was higher among terrestrial species, especially those that vocalize in and around the margins of ponds, as is commonly observed among species of the Bufonidae, Leptodactylidae, and Microhylidae (Vasconcelos and Rossa-Feres 2008). This high overlap reflects the low availability of specific microhabitats for each species and may promote segregation in other dimensions of their ecological niches (Santos and Rossa-Feres 2007; Vasconcelos and Rossa-Feres 2008). For anurans, this segregation may occur through the use of different vocalization periods, differences in structural parameters of the advertisement call (Rossa-Feres and Jim 1996, 2001; Vasconcelos and Rossa-Feres 2008) or use of different environments as breeding sites (call sites and oviposition sites; Santos et al. 2007; Miranda et al. 2015; this study). In the PEM, although most species exhibit reproductive mode 1, we observed a difference in occupancy of call sites.

Use of distinct environments for reproduction is a striking feature of anurans (Gascon 1991) and occurs among different vegetative strata (Pires and Prance 1985) of forested areas (vertical heterogeneity) or among

different phytophysiognomies of open areas (horizontal heterogeneity) (Colli et al. 2002). In open areas, higher horizontal habitat diversity increases the availability of ecological niches (Garda et al. 2013) and supports a greater number of reproductive modes (Andrade et al. 2016), mainly in ground-dwelling species (Cardoso et al. 1989). In the PEM, we observed a high replacement of species between sites. In this case, beta diversity reflects a fundamental component of the spatial pattern of regional biodiversity (Gaston and Williams 1996). This is particularly interesting in the Cerrado because the biome has high phytophysiological diversity (Colli et al. 2002), ranging from completely open fields to forested areas (Ribeiro and Walter 2008).

Although abundance of anurans in the PEM was influenced by temperature, species richness was not related to any climatic parameters analyzed; however, 66.67% of species (18 species) vocalized exclusively in the rainy season, while other species showed variable vocalization periods in the rainy or dry seasons. Only *B. boans* vocalized exclusively in a period with low rainfall, confirming previous observations of reproductive activity of this species during the dry season (Bernarde 2007; Matavelli et al. 2013). In tropical regions where temperature and humidity are high, precipitation is the determining factor initiating and maintaining reproductive activity of most amphibians (Duellman and Trueb 1994; Bertoluci and Rodrigues 2002; Vasconcelos et al. 2010). Studies carried out in several regions in Brazil support the influence of precipitation and temperature on reproduction of anuran amphibians (Conte and Machado 2005; Bernarde 2007; São Pedro and Feio 2010; Kopp et al. 2010). Monthly and annual climate fluctuations commonly occur in some regions influencing rainfall regularity and pond hydroperiod, however, generating changes in reproductive patterns of anuran species (Vasconcelos and Rossa-Feres 2005; Abruñhosa et al. 2006; Vieira et al. 2007; this study).

Phenological differences in anuran reproduction are linked mainly to the reproductive modes of species (Gottsberger and Gruber 2004; Abruñhosa et al. 2006). In general, anurans with derived reproductive modes involving eggs deposited in foams nests or in underground holes (Leptodactylidae; Haddad and Prado 2005) occupy the ponds at the beginning of the rainy season (Abruñhosa et al. 2006; Santos et al. 2007). These species have adaptations against desiccation, allowing them to minimize the effects of seasonal variation in areas with low water availability (Duellman and Trueb 1994; Ávila and Ferreira 2004; Vieira et al. 2007). On the other hand, species with ancestral reproductive modes (mode 1), in which the eggs are deposited directly into the water (Haddad and Prado 2005), occupy ponds later and have a longer reproductive period because successful reproduction depends on availability and stability of water levels at breeding sites (Arzabe 1999;

Abrunhosa et al. 2006; Santos et al. 2007). This also explains the observation that permanent ponds support more hylids than do temporary ponds (Arzabe 1999).

Our study provides important data on the occurrence and activity patterns of anuran species in the northern portion of the Cerrado, especially in the state of Maranhão. Parque Estadual do Mirador is located in a typical Cerrado area with a great diversity of phytophysognomies (e.g., *cerradão*, *cerrado sensu stricto*, *campo cerrado*, *campo sujo*, and *campo limpo*; Moraes 2014), which supports a wide variety of anuran species, including species typical of other environments (Andrade et al. 2017). The PEM is currently threatened by the advance of agriculture in the region, which may alter the natural environments and consequently change the composition of anuran species. Greater monitoring of PEM is essential, especially in areas of conflict near park boundaries. Our data on the phenology, distributions, and breeding habitats of anuran amphibians will be useful in formulating management plans for species in PEM and the south-central region of Maranhão as well as in the development of biodiversity conservation strategies for the northern portion of the Brazilian Cerrado.

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