

Contribution of environmental variables to anuran community structure in the Caatinga Domain of Brazil

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Abstract

Contribution of environmental variables to anuran community structure in the Caatinga Domain of Brazil. To ascertain the influence of environmental variables on the structure of anuran communities, we conducted tests to determine which variables best explain the spatial distribution patterns of different communities of anurans in a rocky, montane environment characterized mainly by open habitats and gallery forests. The study area is the Sete Passagens State Park in the State of Bahia, Brazil, an area included in the Chapada Diamantina Region and in the Caatinga Morphoclimatic Domain. We sampled 20 plots (60 × 25 m) during two rainy seasons, and measured 13 environmental variables. The environmental matrix was reduced to four synthetic axes through the principal component analysis, and the anuran community matrix was reduced to a synthetic axis through the non-metric multidimensional scaling method. We tested the association between environmental axes (independent variables) and community composition (dependent variable) using a multiple regression analysis. The single axis significantly associated with the species of anurans found in any given plot is Principal Component 1, in which the major contributors to variation are factors involving vegetation structure, listed in descending order, as follow: percentage of leaf litter, density of trees, canopy height, soil moisture, and percentage of understory, shrub, and herb layers. The ordination of the anuran community showed an environmental gradient from the Campo Rupestre to Semi-deciduous Forest patches, characterized mainly by the gradual increase of layering in the vegetation.

Keywords: Altitude, Brazilian Semi-arid, Campo Rupestre, Chapada Diamantina, environmental gradient, Semi-deciduous Forest.

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Resumo

Contribuição de variáveis ambientais à estrutura de comunidade de anuros no Domínio da Caatinga of Brazil. O objetivo do presente estudo foi verificar a influência de variáveis ambientais na estrutura de comunidade de anuros, testando quais variáveis ambientais melhor explicam os padrões de distribuição espacial das comunidades dos anuros em ambiente montanhoso caracterizado essencialmente por ambientes abertos e florestas de galeria. A área de estudo é o Parque Estadual das Sete Passagens, no Estado da Bahia, Brasil, uma área incluída na região da Chapada Diamantina e no Domínio Morfoclimático da Caatinga. Amostramos 20 réplicas (60 × 25 m) durante duas estações chuvosas e mensuramos 13 variáveis ambientais. A matriz ambiental foi reduzida a quatro eixos sintéticos através da análise dos componentes principais e a matriz da comunidade de anuros foi reduzida a um eixo sintético por meio do método de escalonamento multidimensional não-métrico. Testamos a hipótese nula de ausência de associação entre os eixos ambientais (variáveis independentes) e a composição da comunidade (variável dependente) por meio da análise de regressão múltipla. O Componente Principal 1 foi o único eixo significativamente associado à composição de anuros, com variáveis de maior contribuição diretamente relacionadas à estrutura da vegetação (ordem decrescente): porcentagem de serapilheira, densidade de lenhosas, altura do dossel, umidade do solo e porcentagem de subbosque, arbustos e herbáceas. A ordenação da comunidade de anuros evidenciou um gradiente ambiental do Campo Rupestre para manchas de Floresta Semi-decidual, principalmente caracterizado pelo aumento gradual da estratificação da vegetação.

Palavras-chave: Altitude, Campo Rupestre, Chapada Diamantina, Floresta Semidecidual, gradiente ambiental, Semiárido brasileiro.

Introduction

The identification of factors that regulate spatial distribution patterns and species abundance is an important step in understanding which processes determine the biological diversity of communities (Magurran 1988, Underwood *et al.* 2000). Such patterns arise from different processes, reflecting specific habitat requirements (Pianka 1973, Sredl and Collins 1992), resource distributions (Duellman 1990, Mesquita *et al.* 2006), and extensions of the social interactions (Connell 1980, Eterovick 2003).

Research on anuran community ecology is still largely dominated by descriptive approaches (e.g., Duellman 1978, Feio and Ferreira 2005, Santos *et al.* 2007, Uetanabaro *et al.* 2007); few studies have attempted to discern the effects of environmental variables on patterns of species distributions. The relationship between community structure and environmental variables usually is evaluated in studies of phenological variation (e.g., Donnelly and Guyer 1994, Canavero *et al.* 2008), in which temperature

(Bertoluci 1998), rainfall (e.g., Aichinger 1987, Rossa-Feres *et al.* 1999, Bernarde 2007), or both factors (e.g., Jørgensen 1992, Conte and Machado 2005, Zina *et al.* 2007) repeatedly have been identified as the main determinants of seasonal variation in anuran community activity. Methodological studies based on experimental designs that avoid the effects of temporal variation on organisms remain scarce (e.g., Vallan 2002, Krishnamurthy 2003, Bastazini *et al.* 2007).

Environmental heterogeneity is an environmental variable that might affect patterns of species distribution; it is known to be associated with species richness and composition of distinct taxonomic groups (MacArthur and MacArthur 1961, Parris 2004). However, the effect of environmental heterogeneity may vary substantially, depending on the type of habitat utilized by the taxon in question (Tews *et al.* 2004). Therefore, the structure of anuran communities can be determined by different groupings of environmental variables, depending on the habitat in which the community occurs. Thus, the question of which variables best explain the

structure of an anuran community may differ with each distinct type of environment. In Brazil, studies addressing this issue were conducted mainly in the Atlantic Forest Domain (e.g., Giaretta *et al.* 1999, Afonso and Eterovick 2007, Bastazini *et al.* 2007); there are no such studies focusing on anuran communities in the Caatinga Morphoclimatic Domain (defined by Ab'Sáber 1977).

Remarkably little is known about the species composition of the Caatinga Domain of the Brazilian Semi-arid Region; hence, there is an urgent need for studies to maximize conservation efforts of these anuran populations, especially in regions for which detailed data on diversity, abundance, and spatial distributions of taxa are lacking. At elevations exceeding 700 m above sea level, some environments are characterized by temperature and moisture conditions that accommodate unique ecosystems, such as the Campo Rupestre, and Deciduous and Semi-deciduous Forests; the latter usually are termed dry forests. (The Campo Rupestre was characterized by Rizzini 1979.) Zones of forested vegetation punctuate the xeric environments of the Caatinga Domain and are termed "exception zones" (defined by Ab'Sáber 2003). Sete Passagens State Park is one such exception zone in the Caatinga Domain; this park is located in the Serra de Jacobina Mountains, a regional name applied to the northern sector of the Serra do Espinhaço Mountain Range in the State of Bahia, Brazil. Studies of the structure of the anuran community of Sete Passagens State Park would inform the conservation efforts for the Caatinga Domain (MMA 2007), because such research would elucidate ecological requirements for species survival, and help guide management actions and conservation strategies in a region for which there are few data on ecology and species composition (Rodrigues 2003, Leal *et al.* 2005).

The goal of the present study is to determine which environmental variables best explain the spatial distribution patterns of an anuran community distributed along two main phyto-

siogonies in a montane environment of the Caatinga Domain—the Campo Rupestre and the Semi-deciduous Forest.

Materials and Methods

The study was carried out at the Sete Passagens State Park (Parque Estadual das Sete Passagens [PESP]; 11°26' S, 40°33' W) in the Municipality of Miguel Calmon, State of Bahia, Brazil (Figure 1). The park is located in the northern part of the Serra do Espinhaço Mountain Range (Davis *et al.* 1997), which is included in the Chapada Diamantina Ecoregion (Velloso *et al.* 2002). The Chapada Diamantina is part of the Caatinga Morphoclimatic Domain, which is characterized by vegetation morphologically and physiologically adapted to semiarid conditions (Ab'Sáber 1977). At the PESP, elevations range from approximately 800–1300 m, with an area of 2821 ha. The topography is mountainous with deep valleys and steep cliffs, and is classified as extremely unstable with moderate slopes ranging from 30–45°. The headwaters of nearly all the rivers in the vicinity of the park are located inside its boundaries. According to the Köppen classification, the climate is of the semi-arid BShw type—i.e., rainy in the summer and dry during winter. The rainy period is from October–April, and the wettest months are from November–January. At the high elevations, minimum winter temperatures are less than 14°C, whereas in the surrounding areas, the temperature is as high as 20°C. The vegetation cover at these higher elevations consists of seasonal Semi-deciduous Forests and the environments of Campo Rupestre, and differs from that of the lowland areas surrounding the park (up to ca. 500 m a.s.l.), in which shallow soils support typical Caatinga vegetation (Ab'Sáber 2003).

The sampling design followed that of Bastazini *et al.* (2007). We used 20 sample units (SUs) (plots: P1–P20) in the PESP; each plot was 60 × 25 m, and plots were located in both the Campo Rupestre and patches of seasonal Semi-deciduous Forests (Figure 1). The sample

units were located along existing trails to facilitate access to plots in the extremely hilly region by day and at night. This restriction prevented similar sampling effort in forest patches and areas of Campo Rupestre. The plots were separated by a minimum distance of 300 m. We identified six main types of environments in the PESP, based primarily on a combination of the following parameters: type of plant cover, including presence/absence of bromeliads; presence/absence and type of body of water; and

extension and conservation degree of forest patches. These physiognomic environmental types were not used as categorical variables in statistical analyses; they were used only as an aid to understanding the spatial distribution pattern of the anuran community along the environmental gradient.

We sampled SUs in two periods of consecutive rainy seasons, each sampling period lasting 5 days: 10 SUs from 18–22 November 2006 (P1–P10); and 10 SUs from 16–20 January 2007

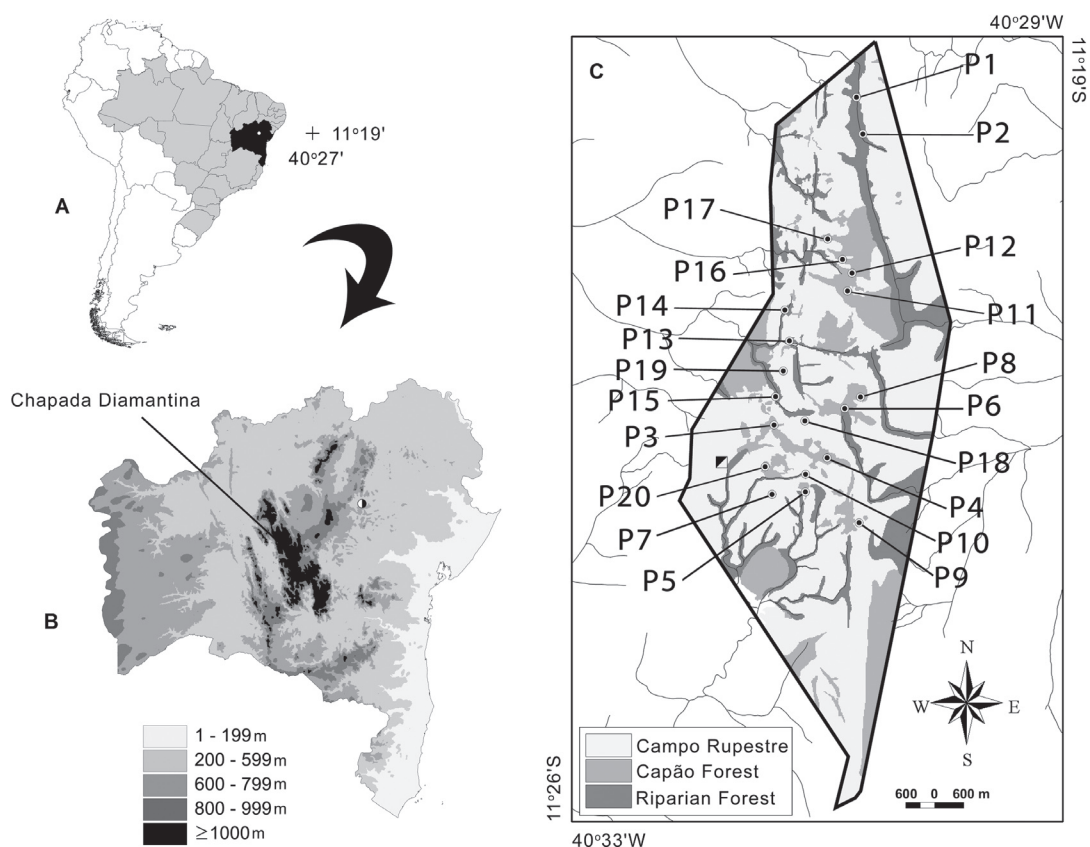


Figure 1. Distribution map of the 20 sample units within the limits of the Sete Passagens State Park (PESP), Municipality of Miguel Calmon, State of Bahia, Brazil. (A) South America; in gray, Brazil; in black, Bahia State; white circle, geographical position of the PESP headquarters. (B) Topographic map of the State of Bahia, highlighting PESP's position in the Ecoregion of the Chapada Diamantina Complex. (C) PESP's polygon, highlighting its vegetation, hydrography, sample units (circles), and State Park headquarters (square). The Capão Forest is a forest patch inside an open area owing to natural causes or to human activities this name commonly is used for this type of physiognomy by native inhabitants of the area studied.

(P11–P20). We distributed 50% of the SUs in the forested areas and the other 50% in open habitats of Campo Rupestre in each field season to control for temporal biases in the characterization of the SUs. Therefore, environmental temporal variation will have an equal affect on the sampling of each of these physiognomic environmental types, and reduce confusion of habitat or microhabitat effects with temporal effects.

We looked for anurans in each SU for 40 min/day, after 1800 h; thus, the total time devoted to active searching was 6 h and 40 min per day or 66 h and 40 min for the total of 10 sampling days. The same team of four researchers assayed the SUs throughout the study. Each pair of observers surveyed five SUs per night; the pairs of observers and the sampling sequence of SUs were changed randomly during the sampling period. Voucher specimens are deposited in the Amphibian Collection of the Zoological Museum of the Universidade Federal da Bahia (UFBA). Names of the taxa follow Frost (2011).

We measured 13 environmental variables in each SU: (1) relative humidity and (2) air temperature were measured with a thermo-hygrometer Minipa MT 242 every night in each SU before the searching began. (3) We calculated the percent water cover of the SU by dividing the SU into four quadrants and then estimating the percentage of water cover in each. (4) We calculated the average velocity of water flow by measuring the rate of movement of a matchstick (0.082 g and 3.5 cm long) across 1 m of water for three consecutive trials. (5) We measured the maximum depth and (6) maximum width of the body of water, and counted the numbers of (7) terrestrial and (8) epiphytic bromeliads. (9) We measured soil moisture by collecting one soil sample from each of 10 points in each SU. Samples were mixed and sealed in a plastic bag and moisture was measured by the "Moisture at 65°C" analysis (Embrapa 1997). (10) We estimated percentages of (11) leaf litter and understory, shrub, and herb layers (covering of forest layers between canopy and litter layers) as ordinal variables ranging from 0–4 (0 [0%], 1

[1–25%], 2 [25–50%], 3 [50–75%], and 4 [75–100%]). (12) Canopy height was treated as an ordinal variable, ranging from 0–4 (1 [0–5 m], 2 [6–10 m], 3 [10–15 m], and 4 [>15 m]) and (13) density of trees was estimated by the point-quarter method of Krebs (1999). Environmental variables 8–13 were assessed at 10 points chosen at random in the SU, following a point map defined in Bastazini *et al.* (2007); points were not changed during the study. A circle with a diameter of 3 m was drawn and centered at each point to limit the area of measurement.

Only SUs with anurans were included in the analyses; no anurans were observed in plots P7–P9 and P19. The assumptions of linearity, normality and homoscedasticity were examined and treated. We produced four data matrices: (A) a matrix of 16 SUs (objects) versus abundances of 15 anuran species (attributes), representing the dependent variable of the study, termed community composition; (B) a matrix with relative abundances, calculated from the Matrix A by dividing each cell by the line sum to reduce differences in the weight of sample units in analysis; (C) a second matrix of relative abundances, calculated from the Matrix A by dividing each cell by the column sum, to reduce differences in weight of species in the analysis; (D) a matrix with 16 SUs versus 13 environmental variables, representing the independent variables in the analysis.

We used the Nonmetric Multidimensional Scaling method (NMS), an ordination technique, to find and display the most robust anuran community structure based only the anuran species data set (Matrix B; McCune and Grace 2002). We selected only one dimension (ordination axis) for the NMS solution and used the Bray-Curtis distance measure. To avoid the local minimal problem, we made 50 starting configurations, using as stability criteria the instability value of 0.0005, with 20 iterations to evaluate the stability of the solution, and 500 as the maximum number of iterations. The Monte Carlo randomization test was used to evaluate whether the NMS extracted a stronger axis than expected

by chance (500 iterations for the randomized results). The proportion of variance represented by the NMS axis was obtained by a standardized Mantel test (r) based on the correlation between distance in the ordination space (NMS scores; Euclidian distance) and dissimilarity in the original space (Matrix B, Bray-Curtis distance).

The use of the NMS to search for strong organization patterns within our data (Matrix B, species composition) implies that we are performing an indirect gradient analysis. We chose this method because environmental gradients were not previously known in the PESP, especially gradients that might be related to anuran community composition. Therefore, the resulting NMS axis represents an indirect ordination of sample units (SUs)—that is, the plots were ordered using only the relative abundances of species; thus, the ordination is not a direct result of the environmental variables measured (direct ordination). To check whether the indirect ordination resulting from the analysis could efficiently represent a clear pattern of gradual species substitution along the NMS axis (x -axis), we generated a composite graph. Each individual graph represents the relative abundance of a given species (Matrix C) (y -axis) per sample units (x -axis), where sample units were ordered following NMS scores. The graphs then were sorted following the weighted averaging.

Stress is an important measure to be considered in the NMS analysis. It represents a distance measure of the departure from the monotonicity in a relation between distance in ordination space (scores of the NMS axis) and dissimilarity in original space (real data, Matrix B; McCune and Grace 2002). In other words, as the stress increases, the quality of the ordination represented in the synthetic axis decreases. The presence of very abundant species regularly distributed in nearly all plots in the data matrix might influence the quality of ordination, and produce high stress values. In the PESP, the brachycephalid *Ischnocnema paulodutra* was represented in all 16 SUs considered for analysis, showing high abundances in forested areas, as

well as in the Campo Rupestre. Consequently, we removed this taxon from the analysis, because the removal of species occurring in more than half SUs leads to a lower final stress (McCune and Grace 2002).

The association between the community composition (ordination of sample units along the NMS axis, dependent variable) and the spatial distribution of SUs (geographic distances between sample units, independent variable) was tested with the spatial autocorrelation analysis (Sokal and Oden 1978). A spatial correlogram was constructed using Moran's I-coefficients in four distance classes, for which the maximal limits (in km) were: 1.3, 2.1, 3.1, and 6.4. Each distance class contained approximately the same number of distance pairs of SUs. For each distance class, we computed a correlation coefficient; the statistical significance of the overall correlogram was tested by the Bonferroni criterion, in which a correlogram is considered significant if at least one Moran's I value is significant at $p \leq 0.05/k$, where "k" is the number of distance classes. Significant and positive Moran's I-coefficients indicate that plots a given distance apart are similar for the variable under analysis (NMS axis: community composition), whereas significant and negative Moran's I-values indicate dissimilar plots for that variable at this distance (Diniz-Filho *et al.* 2000).

We used the principal component analysis (PCA) to reduce the environmental data set (Matrix D) to a smaller number of orthogonal, synthetic variables that represent most of the original information. Eigenvectors and associated eigenvalues were obtained from a correlation matrix. Principal components with eigenvalues greater than 1.0 were rotated to a new varimax solution (McCune and Grace 2002). The degree of contribution of each environmental variable was determined by correlation between the original variables and the scores (loadings).

The association between the environmental data set (principal components, independent variables) and the anuran community composition (NMS axis, dependent variable) was tested by

the multiple regression analysis. The α -level ($p \leq 0.05$) was Bonferroni corrected (Bland 2004) for partial regression analyses developed with the same set of subjects.

Results

Composition and Structure of the Anuran Community

We registered 567 anurans belonging to five families, nine genera, and 15 species (Table 1). The family with the highest number of individuals was Hylidae, followed by Brachycephalidae. The five most abundant species were *Ischnocnema paulodutraii* (44.8%), *Ischnocnema* sp. nov. (16.6%), *Bokermannohyla oxente* (14.5%), *Scinax* sp. 1 (*S. ruber* Group) (6.3%), and *Proceratophrys* sp. nov. (allied to *P. schirchi*) (4.4%). These five species accounted for 86.6% of the total sampled individuals. Anurans occurred in all forested sample units (SUs). *Scinax pachycrus* was the single species found exclusively in the Campo Rupestre. *Bokermannohyla circumdata*, *Proceratophrys* sp. nov., *Rhinella crucifer*, *Scinax eurydice*, *Scinax* sp. 2 (*S. catharinae* Group), and *Trachycephalus mesophaeus* were restricted to forested areas. *Bokermannohyla oxente*, *Scinax* sp. 1 (*S. ruber* Group), and *Ischnocnema* sp. nov. were the most widespread species in PESP; the first two occurred mainly in forested environments, whereas *Ischnocnema* sp. nov. occurred mainly in the Campo Rupestre. Species common to forested environments and the Campo Rupestre were *S. pachycrus*, *Hypsiboas crepitans*, *H. faber*, and *Phyllomedusa bahiana*, all of which often were found at the edges of the forest and/or open habitats with lentic bodies of water.

The NMS axis was able to express community structure, as can be seen in Figure 2 and Table I by explaining 68% of the original variance (Mantel test: $r = 0.81$, $p \leq 0.001$). The Monte Carlo test resulted in a probability of 0.02, indicating that the NMS extracted a stronger axis than expected by chance. Although stress associated with NMS axis is high (24.5), this

does not mean that the interpretative value is low, because stress tends to increase when the number of objects is similar to number of variables (McCune and Grace 2002), as is the case for our data (16 objects [SUs] vs. 15 variables [species]).

The NMS axis ordered the anuran community through an environmental gradient that reflects the six main environments (physiognomies) that we identified when we gathered data (Figure 2, Table 1). Environment 1 (P20) is mostly an open area (80%) covered by Campo Rupestre, marked by sparse treelets and shallow soil. The area has a narrow, deep body of water and a patch of semi-deciduous forest (20%). Environment 2 (P10, P16, P17, P18) resembles Environment 1, but lacks water. *Scinax pachycrus* was exclusive to P16 and *Ischnocnema* sp. nov. reached its highest abundance values in P18. Environment 3 (P6, P13) comprises heterogeneous areas, characterized by mixed features of open areas (herbaceous vegetation and bare rocks) and riparian forests. Vegetation is not dense; there is an understory layer and bodies of water. *Hypsiboas crepitans*, *H. faber*, *Scinax* sp. 1, *Phyllomedusa bahiana*, and *Proceratophrys* sp. nov. were associated with this environment; the anurans often were captured in forested areas, but also at forest edges and in open areas. Environment 4 (P3, P4) consists of forest areas lacking bodies of water, and having many epiphytic bromeliads, herbaceous vegetation, and bryophytes. The forest cover of Environments 3 and 4 suffered different degrees of deforestation by human activities during the last 20 years, and is at present in an initial stage of natural forest recovery. *Strabomantis aramunha* was restricted to plots of this physiognomy, but also was captured from open areas external to the sampled plots in cavities under rocks beside a stream. Environments 5 (P1, P5, P11, P14, P15) and 6 (P2, P12) include the largest forest patches in the PESP, and are covered by dense vegetation. These areas are somewhat inaccessible because of the rugged relief. Environments 5 and 6 differ by the presence of bodies of water in the former.

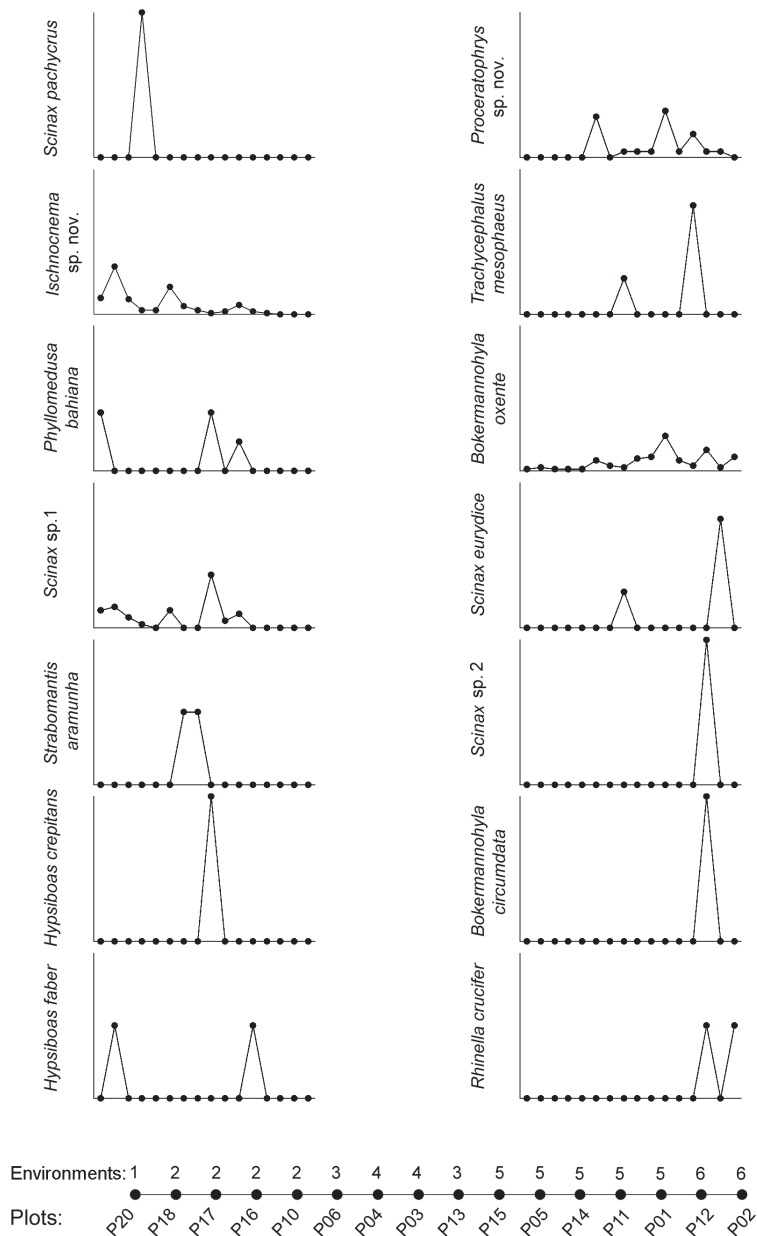


Figure 2. Composite graph of the anuran community structure from the Sete Passagens State Park based on weighted averaging from the NMS ordination. X-axis, sample units; Y-axis, relative abundances (in percentage) of an anuran species per sample unit (Matrix C). Arabic numerals represent six main types of environment identified during the data taking phase: 1, Campo Rupestre with bodies of water; 2, Campo Rupestre without bodies of water; 3, heterogeneous areas (mix of forest patch with streams and open areas of Campo Rupestre); 4, forest patches without bodies of water, but with elevated air moisture and high density of epiphytes and herbaceous vegetation; 5, dense forests with bodies of water; 6, dense forests without bodies of water. See text for more detailed descriptions of environments.

Table 1. Abundances of anuran species in the Sete Passagens State Park (PESP), and surrounding lowland area (xeric or Caatinga plant cover). Prevailing physiognomies of the PESP are ordered following PCT ordination scores of 16 sample units used in the account, and species based on weighted averaging from NMS ordination except for *Ischnochnema paulodutrai*, which was not included in the analysis (Material and Methods). Abundances from areas outside the PESP are not given owing to different sampling strategies. Species unique to this area are alphabetically ordered. A hybrid habitat is a mix of forest patch with streams and open areas of Campo Rupestre. CAA = Caatinga plant cover; DAM = human-made water reservoir constructed as a barrier in a stream, characterized by slow backwaters; LEN = lentic environment; LFP = lowland forest patches outside the PESP limits; LOT = lotic environment, characterized by springs and streams of noticeably flowing waters; WWA = areas without water bodies. Acronyms in parentheses indicate anuran families: BR = Brachycephalidae; BU = Bufonidae; CY = Cycloramphidae; HY = Hylidae; LE = Leptodactylidae; LP = Leiuperidae; ST = Strabomantidae. E1–E6, main types of environment identified in the PESP, characterized in text.

Species (Family)	Surrounding area						Sete Passagens State Park					
	Campo Rupestre			Hybrid habitat			Semi-deciduous Forest					
	CAA	LFP	E1	E2	E3	E4	E5	E6				
			LEN	WWA	LOT	DAM	WWA	LOT	WWA			
Sample units:	—	—	P20	P10, P16–18	P6	P13	P3–4	P1, P5, P11, P14–15	P2, P12			
<i>Ischnochnema paulodutrai</i> (BR)	—	—	33	69	6	8	65	87	19			
<i>Corythomantis greeningi</i> (HY)	—	•	—	—	—	—	—	—	—			
<i>Dendropsophus branneri</i> (HY)	•	—	—	—	—	—	—	—	—			
<i>Dendropsophus minutus</i> (HY)	•	—	—	—	—	—	—	—	—			
<i>Dendropsophus oliveirai</i> (HY)	•	—	—	—	—	—	—	—	—			
<i>Leptodactylus fuscus</i> (LE)	•	—	—	—	—	—	—	—	—			
<i>Leptodactylus macrosternum</i> (LE)	•	—	—	—	—	—	—	—	—			
<i>Leptodactylus vastus</i> (LE)	•	—	—	—	—	—	—	—	—			
<i>Odontophrynus carvalhoi</i> (CY)	•	—	—	—	—	—	—	—	—			
<i>Phyllomedusa nordestina</i> (HY)	•	—	—	—	—	—	—	—	—			
<i>Physalaemus cf. kroyeri</i> (LP)	•	—	—	—	—	—	—	—	—			
<i>Proceratophrys</i> sp. nov. (CY)	•	—	—	—	—	—	—	—	—			

Table 1. Continued.

Species (Family)	Sete Passagens State Park											
	Surrounding area			Campo Rupestre			Hybrid habitat			Semi-deciduous Forest		
	CAA	LFP	LEN	E1	E2	WWA	LOT	DAM	WWA	E4	E5	E6
	—	—	P20	P10, P16–18	P6	P13	P3–4	P1, P5, P11, P14–15	P2, P12			
Sample units:												
<i>Pseudopaludicola</i> sp. (LP)	•	—	—	—	—	—	—	—	—	—	—	—
<i>Rhinella granulosa</i> (BU)	•	—	—	—	—	—	—	—	—	—	—	—
<i>Rhinella jimi</i> (BU)	•	—	—	—	—	—	—	—	—	—	—	—
<i>Scinax pachyctrus</i> (HY)	•	—	—	2	—	—	—	—	—	—	—	—
<i>Ischnocnema</i> sp. nov. (BR)	—	—	12	52	20	1	9	12	—	—	—	—
<i>Phyllomedusa bahiana</i> (HY)	•	—	2	—	—	2	—	1	—	—	—	—
<i>Scinax</i> sp. 1 (<i>S. ruber</i> Group) (HY)	—	—	5	10	5	15	—	6	—	—	—	—
<i>Strabomantis aramunha</i> (ST)	—	—	—	—	—	—	2	—	—	—	—	—
<i>Hypsiboas crepitans</i> (HY)	•	—	—	—	—	1	—	—	—	—	—	—
<i>Hypsiboas faber</i> (HY)	•	—	1	1	—	—	—	1	—	—	—	—
<i>Proceratophrys</i> sp. nov. (CY)	—	—	—	—	7	1	1	15	1	—	—	—
<i>Trachycephalus mesophaeus</i> (HY)	—	—	—	—	—	—	1	3	—	—	—	—
<i>Bokermannohyla oxente</i> (HY)	—	•	1	5	6	7	5	49	10	—	—	—
<i>Scinax eurydice</i> (HY)	—	—	—	—	—	—	1	3	—	—	—	—
<i>Scinax</i> sp. 2 (<i>S. catharinae</i> Group) (HY)	—	—	—	—	—	—	—	2	—	—	—	—
<i>Bokermannohyla circumdata</i> (HY)	—	—	—	—	—	—	—	1	—	—	—	—
<i>Rhinella crucifer</i> (BU)	—	—	—	—	—	—	—	1	—	—	—	—
Total number of species:	17	2	6	6	5	7	7	11	5	11	7	5

Bokermannohyla circumdata, *Rhinella crucifer*, and *Scinax* sp. 2 (*S. catharinae* Group) were restricted to these latter two environments.

Environmental Variables

Principal Components Analysis applied to 13 environmental variables generated four principal components with eigenvalues greater than 1.0 (Table 2), which represented 84.1% of the total variance after the varimax solution. The first principal component accounts for 40.0% of the total variance and has high loadings (≥ 0.7) on variables related to the vegetation structure. In

decreasing order, these are: (1) percentage of leaf litter, (2) density of trees, (3) canopy height; (4) soil moisture, and (5) percentage of understory, shrub, and herb layers. On the second axis (19.5%), the variables that contributed to most of the variance are associated to characteristics of bodies of water; in decreasing order, these are: (1) maximum width of the water body, (2) maximum depth of the water body, (3) percentage of water cover in the SU, and (4) flow of water body. On the third axis (14.9%), two of the three most important variables are related to atmospheric features—(1) air temperature, (2) air moisture, and (3) number of

Table 2. Loadings from Principal Components Analysis (after varimax rotation) for 13 environmental variables of 16 combined sample units from the Sete Passagens State Park, Municipality of Miguel Calmon, State of Bahia, Brazil. The projection of component scores is in Figure 3. Loadings ≥ 0.7 are in bold.

Environmental variables	PC1	PC2	PC3	PC4
Percentage of leaf litter	0.9	0.1	0.1	0.1
Density of trees	0.8	0.1	-0.3	0.0
Canopy height	0.8	0.2	0.1	-0.1
Soil moisture	0.7	0.6	0.4	0.0
Percentage of understory, shrub, and herb layers	0.7	0.2	0.0	0.7
Number of epiphytic bromeliads	0.3	0.4	0.2	-0.9
Maximum width of body of water	0.2	0.9	0.0	-0.1
Maximum depth of body of water	-0.1	0.9	-0.3	0.1
Percentage of water cover in the SU	0.3	0.8	-0.1	-0.0
Flow of water body	0.3	0.8	0.3	-0.3
Air temperature	0.3	0.2	-0.8	-0.1
Air moisture	0.3	-0.1	0.8	0.3
Number of terrestrial bromeliads	-0.1	-0.1	0.7	-0.2
Eigenvalues:	5.2	2.5	1.9	1.2
% Total variance:	40.1	19.5	14.9	9.6

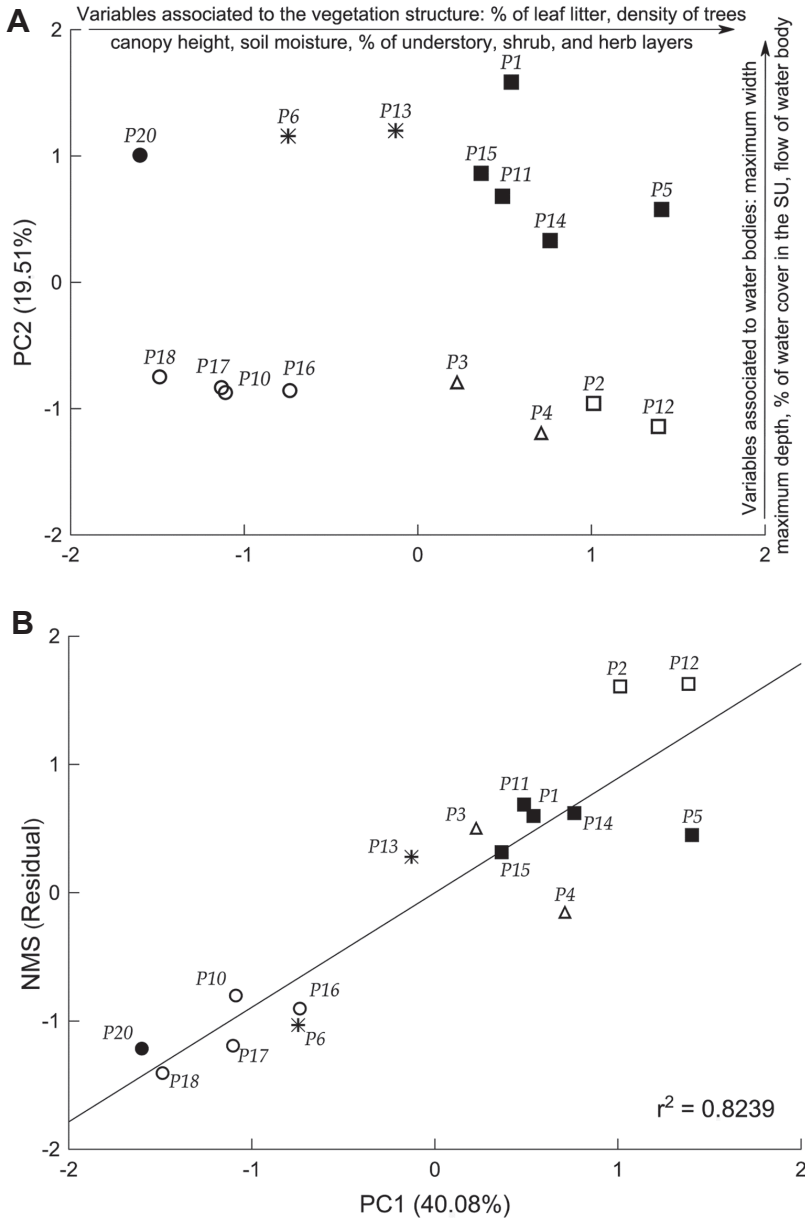


Figure 3 - (A) Projection of individual scores resulting from the principal component analysis for 13 environmental variables of the combined 16 sample units (SUs) used in the account in the space of the first (PC1) with the second (PC2) axis. (B) Partial regression plot of PC1 (environmental variables) on the nonmetric multi-dimensional scaling axis (NMS; anuran species composition). Regression was significant ($p < 0.0004$, Bonferroni corrected). Symbols represent types of environment: open and closed symbols, SUs without and with water bodies, respectively; asterisk, heterogeneous areas (caption of Figure 2); circle, Campo Rupestre; square, dense forest; triangle, forest patch with many epiphytic bromeliads, herbaceous vegetation, and bryophytes.

terrestrial bromeliads. On the fourth axis (9.6%) the variables that contributed to most of the variance also are related to the vegetation structure—(1) number of epiphytic bromeliads and (2) percentage of understory, shrub, and herb layers.

In the projection of the first (PC1) with the second (PC2) principal component, three groups of sample units (SUs) are discriminated (Figure 3A): (1) SUs with water bodies (P1, P5, P6, P11, P13–P15, P20); (2) SUs without water bodies in open areas (P10, P16–P18); and (3) SUs without water bodies in forested or transitional areas (P2–P4, P12). In areas lacking water, the ordination of SUs follows a plant-cover gradient throughout PC1, with moderately forested SUs (P3, P4) lying between non-forested (P10, P16–P18) and forested plots (P2, P12) in the ordination plan. A similar plant-cover gradient is observed for SUs with bodies of water: (1) open areas with 80% of the SU covered by a matrix of Campo Rupestre (P20); (2) transitional areas with riparian forest (55% of the SU) along with a matrix of Campo Rupestre (45% of the SU), the latter covered by herbaceous vegetation (P13) or by rocks and bromeliads (P6) with P13 having more forest than P6; (3) forested areas (P1, P5, P11, P14–A15) characterized by the greatest density of trees, with diameters at breast height up to 40 cm and canopy heights up to 15 m.

Anuran Community vs. Environmental Variables

We tested the association between the environmental data set (independent variables: principal components with eigenvalues ≥ 1.0) and anuran community composition (dependent variable: NMS axis) using a multiple regression analysis, which was strongly significant ($p < 0.0001$). However, of four possible partial regressions, only PC1 vs. NMS axis is significant ($p < 0.0004$, Bonferroni corrected). The partial regression plot of PC1 vs. NMS axis (Figure 3B) accounts for 82% of the original variation and reflects an environmental gradient that transitions

from open areas of Campo Rupestre to forest environments. This gradient is characterized by a gradual increase of leaf litter, tree density, canopy height, and understory, shrub, and herb layers.

The absence of spatial autocorrelation among the SUs is not rejected. None of the four Moran's I-coefficients calculated for the data set (community composition; 1 variable vs. 4 distance classes) is significant, nor is the overall correlogram ($p > 0.15$). Therefore, the distribution pattern of the anuran community (NMS axis) is not related to the spatial distribution of SUs in the area investigated.

Discussion

Overview of Anuran Species Composition

In a qualitative analysis, the anuran species richness of the Sete Passagens State Park (PESP) (15 species) resembles those of other mountain regions in the Caatinga Domain (12–18 species; Arzabe 1999, Borges-Nojosa and Cascon 2005, Vieira *et al.* 2007). However, the species richness is noticeably less than that of the overall Chapada Diamantina Ecoregion (44 species; Juncá 2005), which comprises more distinct landscapes (e.g., Caatinga, Campo Rupestre, Cerrado, and Deciduous and Semideciduous Forests) and total area.

The Chapada Diamantina Ecoregion is one of the five biogeographic subregions of endemism proposed by Galindo-Leal and Câmara (2005) for the Tropical Atlantic Forest (based on birds, primates, and butterflies). The PESP is located in the Bahia's northwestern limit of the original Tropical Atlantic Forest cover, but its anuran composition is related to a mixture of distinct phytophysiognomies. *Scinax pachycrus* and *Hypsiboas crepitans* are common in xeric environments of the Caatinga Domain. *Bokermannohyla circumdata*, *Hypsiboas faber*, *Ischnocnema paulodutraii*, *Phyllomedusa bahiana*, *Scinax* sp. 2 (*S. catharinae* Group), *S. eurydice*, and *Rhinella crucifer* usually are associated with the Atlantic Forest Domain. *Bokermannohyla oxente*, *Strabo-*

mantis aramunha, *Scinax* sp. 1 (*S. ruber* Group), and *Proceratophrys* sp. nov. (*P. cristiceps* Group) are common inhabitants of ecosystems closely associated to the Campo Rupestre. One particular record deserves mention. The record of *Bokermannohyla circumdata* represents the northernmost limit of the *B. circumdata* Group, which is distributed mainly in mountain stream habitats in the Tropical Atlantic Forests above 350 m elevation (Napoli and Caramaschi 2004). Species of this group also inhabit riparian forests in high elevation fields in the Caatinga, Cerrado, and Tropical Atlantic Forest domains (e.g., *B. diamantina*, *B. circumdata*, *B. feioi*, *B. ibitipoca*, *B. nanuzae*, *B. ravida*, and *B. sazimai*; Napoli and Juncá 2006). To date, *B. diamantina* was the single species in this group known for the Brazilian semi-arid (type-locality Serra do Barbado, Chapada Diamantina, Bahia State). The occurrence of *B. circumdata* at the Serra de Jacobina Mountain Range is an important observation for biogeography and conservation, because it suggests that this area is a relict of the original Atlantic Forest, and represents the northern limits of the *B. circumdata* Group. Napoli and Juncá (2006) concluded that species of the *B. circumdata* Group occur in the Cerrado and Caatinga domains because riparian forests are present and these provide, to some degree, environmental conditions similar to those of the Atlantic Tropical Forests from coastal Brazil; these authors observed that these species should not be considered as characteristic taxa of Cerrado and Caatinga biomes.

The spatial distribution of the anuran species among the main phytophysiognomies of the PESP largely agrees with their known ecological requirements. The brachycephalid frog *Ischnocnema paulodutraei* was observed in all environments in which anurans occurred and *Ischnocnema* sp. nov. in almost all, but primarily in those lacking bodies of water bodies and having low humidity (Table 1). As with other Terrarana and the closely allied *I. paulodutraei*, these species probably undergo direct development and terrestrial breeding (Hedges *et al.*

2008, Napoli *et al.* 2009). This reproductive mode allows these species to breed in environments lacking bodies of water, and may explain, in part, the simultaneous occupation of distinct types of environments. A similar, widespread distribution was observed by Bastazini *et al.* (2007) for *I. paulodutraei* in a Restinga environment of northern Bahia State, Brazil, where this taxon occurred in all phytophysiognomies recognized by them and inhabited both high- and low-humidity environments.

The presence of *Scinax pachycrus* in the PESP may be accidental, because this species usually is found in the xeric Caatinga plant cover of lowland areas surrounding the park (Rodrigues 2003)—an environment that is absent from the montane region of the PESP. Indeed, the only two specimens encountered were in P16, an area mostly open (80%), covered by Campo Rupestre, and marked by sparse treelets, shallow soil, and no bodies of water. Phytophysiognomically, this environment is more similar to the Caatinga plant cover than it is to other open habitats and forested areas of the PESP.

The treefrogs *Hypsiboas crepitans*, *H. faber*, and *Phyllomedusa bahiana* are common inhabitants of forest edges and adjacent open habitats; they use lakes, ponds, water reservoirs, and other similar lentic environments to breed (Lutz 1954 [*H. faber* and *Phyllomedusa burmeisteri*]; Caldwell 1992 [*H. crepitans*]; Martins 1993a, b; Martins *et al.* 1998 [*H. faber*]). In the PESP, these species occur in habitats with mixed features of open areas and edges of riparian forests, and always are adjacent to bodies of water.

Bokermannohyla circumdata, *Rhinella crucifer*, and *Scinax* sp. 2 (*S. catharinae* Group) are restricted to the densest forest patches of the PESP (Environments 5 and 6, Figure 2, Table 1). This spatial distribution pattern largely agrees with the ecological constraints known for these species, including forested areas with lotic and/or lentic water bodies in which their larvae develop. The treefrog *Bokermannohyla*

circumdata always inhabits stream habitats in the Atlantic Rain Forest (Napoli 2005), where the species uses the herbaceous vegetation to breed, and its tadpoles develop in the small rivulets and flooded adjacent areas (Napoli 2000). Species of the *Scinax catharinae* Group typically are forest dwellers (Pombal *et al.* 2010); thus, it is not surprising *Scinax* sp. 2, a member of this species group, is restricted to the densest forest patches of the PESP with lotic environments. Toads of the *Rhinella crucifer* Group usually inhabit forested areas of the Atlantic Forest Domain (Baldissera *et al.* 2004). As a terrestrial species, its absence in other forest patches in the PESP (Environments 3 and 4, Figure 2, Table 1) may be related to its vulnerability to different degrees of deforestation (including burning the understory) that have occurred in the more accessible areas during the last 20 years. However, the presence of the terrestrial frogs *Ischnocnema paulodutraei*, *Ischnocnema* sp. nov., *Proceratophrys* sp. nov., and *Strabomantis aramunha* in Environments 3 and/or 4 does not support this explanation. For additional natural history information on *S. aramunha*, including specimens from the PESP, see Napoli *et al.* (2010).

Treefrogs of the genus *Trachycephalus* are placed among the casque-headed hylids, mainly characterized by their co-ossified skulls and phragmotic behavior (using the head to plug burrows) related to their microhabitat usage of bromeliads and tree holes (Pimenta *et al.* 2009). In the PESP, *Trachycephalus mesophaeus* was captured in forest patches with the highest density of epiphytic bromeliads, which may explain its preference for these forest patches.

The two species of the *Scinax ruber* Group (*sensu* Pombal 1995) observed in the PESP occupy different environments, with *Scinax* sp. 1 in mostly in patches of forest that are not dense, whereas *S. eurydice* inhabits edges of denser forest patches. Both species follow the general ecological requirements related to the *S. ruber* Group, mainly for inhabiting forest edges and usually breeding in open areas.

Bokermannohyla oxente belongs to the *B. pseudopseudis* Group (Lugli and Haddad 2006), and like other species in this group, lives close to permanent streams, bordered by riparian vegetation, as was observed for the PESP's population of *B. oxente*.

The anuran species composition of the PESP, when compared to the anuran fauna of the surrounding open area covered by xeric vegetation (Caatinga plant cover) (Table 1), identifies the PESP as almost a forest island in the Caatinga landscape; see Vanzolini 1981 for a discussion of the current mesic enclaves found in northeastern Brazil. Almost all anuran species from the surrounding open area are inhabitants of permanent and temporary ponds; they sometimes invade forest edges, whereas anurans from the PESP usually are associated with forests. The only five species common to both areas—*Bokermannohyla oxente*, *Hypsiboas crepitans*, *H. faber*, *Phyllomedusa bahiana*, and *Scinax pachycrus*—are found in open or transitional areas with or without lentic environments. *Corythomantis greeningi*, a hylid treefrog widespread in the Caatinga Domain, was only found in a patch of forest outside the park. These dry forest patches differ physiognomically from the mountain forests in the PESP, and they are not protected, as is usually the case for non-montane landscapes in the Caatinga Domain. The PESP should not be understood as an isolated unit, but instead as being ecologically and historically related to the adjacent Caatinga plant cover, lowland areas, and dry forests. This underscores the importance of including these different, but contiguous, phytophysiognomic areas within new environmental protection areas in the Brazilian Semi-arid.

Environmental Variables Determining Community Structure

The spatial distribution of anuran species in the Sete Passagens State Park (PESP) is strongly determined by the vegetation structure, as evidenced by an environmental gradient from open areas of Campo Rupestre to forested areas.

Within this gradient, forest patches have greater species richness than areas with direct sunlight; this probably reflects the structural complexity of forests, which provide more predictable (Colwell 1974), complex (Putman 1996), and heterogeneous habitats than shrubby environments. (See Tews *et al.* 2004 for a brief review on the relation between species diversity and habitat heterogeneity.) Vegetation structure is known to influence amphibian species composition both on regional (e.g., Parris 2004, Bastazini *et al.* 2007) and local scales (e.g., Afonso and Eterovick 2007). Similar results of positive association between structural complexity and richness, diversity or species composition in anuran communities were found by other studies (e.g., Atauri and Lucio 2001; Krishnamurthy 2003).

Areas having a different conservation status have different anuran species compositions (Dixo and Verdade 2006). Gillespie *et al.* (2005) found species richness too much higher in minimally disturbed forest and forest habitats with only moderate disturbance levels than in highly modified or disturbed habitats, such as secondary forests, plantations, and villages. Some studies conducted in small scale and disturbed environments did not find association between anuran species richness and habitat heterogeneity. Vasconcelos and Rossa-Feres (2005) studied an anuran community from a human-modified area originally covered by seasonal forests in the State of São Paulo, and reported an association between anuran species richness and air temperature and moisture. Santos *et al.* (2007), who analyzed an area similar to that of Vasconcelos and Rossa-Feres (2005), stated that the hydro-period was the environmental variable that best explained the anuran species richness. These studies were carried out in highly disturbed habitats; moreover, the environmental variables used to describe the habitat heterogeneity were only associated with bodies of water, as inner vegetation, marginal vegetation, and vegetation surrounding bodies of water, clearly denoted the lack of complex forest stratification (e.g., litter, herb, shrub, understory, and canopy layers).


In the Campo Rupestre, almost all anurans were captured in terrestrial bromeliads, and in sample units without bromeliads and/or shrub vegetation, they were absent. Bromeliads are considered to be important microhabitats for several species, as they provide moisture, shelter, and breeding sites, especially in environments with high air temperatures, low soil and air moistures, and absence of bodies of water (Dejean and Olmsted 1997, Richardson 1999, Schneider and Teixeira 2001, Teixeira *et al.* 2002). However, PC3, associated with the number of terrestrial bromeliads, was not able to explain the anurans spatial distribution in the area studied. Bastazini *et al.* (2007) studied an anuran community in a Restinga environment (characterized by Suguio and Tessler 1984), and terrestrial bromeliads were among the environmental variables that best explained the changes in anuran composition. This may have resulted from the clear gradient in the distribution of numbers of bromeliads along the SUs—something that is lacking in PESP.

Most investigations of anuran communities are limited to bodies of water, such as breeding ponds and streams (e.g., Arzabe *et al.* 1998, Arzabe 1999, Borges and Juliano 2007, Zina *et al.* 2007), mainly because water is conventionally considered the most important factor in shaping the spatial distribution of the anuran fauna. Nevertheless, this relation has been scarcely tested (e.g., Zimmerman and Bierregaard 1986, Eterovick 2003, Afonso and Eterovick 2007, Bastazini *et al.* 2007). In the present study, variables associated with bodies of water (e.g., PC2) are not significantly correlated with the spatial distribution of the anuran fauna. Despite the dependence of anurans on water, primarily for breeding sites, environments with more complex stratification of the vegetation have a lower incidence of direct sunlight, many available microhabitats, and wet soils with high accumulations of organic materials; together, these ensure appropriate moisture and temperatures to support a large diversity of adult anurans. Parris and McCarthy (1999), Vallan (2002),

Krishnamurthy (2003), and Parris (2004) observed the importance of vegetation structure in sculpting species community composition. These authors reported positive associations between the structural complexity of vegetation and species richness, species diversity and/or species composition. In Brazil, Bastazini *et al.* (2007) found a strong environmental gradient structuring the anuran community of a Restinga habitat, also determined by changes in plant communities.

In the present study, plant cover was the most important environmental factor determining the structure of the anuran community in an area characterized mainly by montane riparian forests associated to open areas of rocky fields. Other anuran communities of different phytophysiognomies should be tested to reveal the environmental variables responsible for their spatial distributions, and whether plant communities also are the main determinant of their structures.

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