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The role of bromeliad architecture and abiotic factors in occupation by anurans

O papel da arquitetura das bromélias e fatores abióticos na ocupação por anuros

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Abstract

Bromeliads are excellent models for the study of biological communities, as their structural complexity simulates highly heterogeneous environments. The present study explored the effect of the structural complexity of terrestrial bromeliads as a refuge site, as well as the influence of macro-spatial variables on the abundance of anurans in the Caatinga biome. This study was carried out in the municipality of Paulo Afonso, state of Bahia, northeast of Brazil, where two sites with a high abundance of bromeliads of the species *Aechmea aquilega* were selected. The sites were visited twice a month, in a total of 15 visits. The survey of the presence and abundance of anurans in the interior of the plants was performed visually. Bromeliads with anurans inside had their height, leaf number and internal temperature (intrinsic variables) measured. Air temperature, air humidity and precipitation (extrinsic variables) were also measured. Principal Component Analysis and Multiple Regression Model were used to identify the influence of these variables on the abundance of anurans in the interior of the plants. A total of 147 anurans, distributed among the Bufonidae and Hylidae families, were found, with an average of 1.3 individuals per bromeliad and 9.8 individuals per visit. The internal temperature of the bromeliads was 1.6ºC lower than air temperature, however, the intrinsic and extrinsic variables did not have an effect on the abundance of anurans. Anurans preferably used large bromeliads, with 78.2% of individuals using bromeliads taller than 60 cm. The results suggested that the biotic and abiotic factors discussed did not significantly influence the use of bromeliads by anurans. Additional studies addressing other aspects of the structural complexity of bromeliads and environmental factors are necessary to better understand the use of these plants by anurans in the Caatinga biome.

Key words*:* amphibians, community structure, refuge site, semi-arid, intrinsic and extrinsic variables, hydric stress.

Resumo

Bromélias são excelentes modelos para estudo de estrutura de comunidades biológicas, já que sua complexidade estrutural simula ambientes altamente heterogêneos. Este trabalho investigou o efeito da complexidade estrutural de bromélias terrícolas, como sítio de refúgio, e das variáveis macro-espaciais na abundância de anuros na Caatinga. O estudo foi realizado no município de Paulo Afonso, Estado da Bahia, Nordeste do Brasil, onde foram selecionados dois sítios que apresentaram alta abundância de bromélias da espécie *Aechmea aquilega*. Os sítios foram visitados duas vezes ao mês, totalizando 15 visitas. A investigação da presença e da abundância de anuros no interior dos vegetais se

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deu por meio de busca visual. Bromélias com anuros em seu interior tiveram registradas sua altura, seu número de folhas e sua temperatura interna (variáveis intrínsecas), além de temperatura do ar, umidade do ar e precipitação (variáveis extrínsecas). Análise dos Componentes Principais e modelo de Regressão Múltipla foram utilizados para identificar a influência destas variáveis na abundância de anuros no interior dos vegetais. Foram encontrados 147 anuros distribuídos entre as famílias Bufonidae e Hylidae, com média de 1,3 indivíduos por bromélia e 9,8 indivíduos por visita. Temperaturas internas das bromélias mostraram-se 1,6ºC mais baixas que as temperaturas do ar, no entanto, as variáveis intrínsecas e extrínsecas não tiveram efeito na abundância de anuros. Anuros utilizaram predominantemente bromélias grandes, com 78,2% dos indivíduos utilizando bromélias acima de 60 cm de altura. Os resultados sugerem que os fatores bióticos e abióticos investigados não apresentam influência significativa no uso de bromélias pelos anuros. Estudos adicionais que abordem outros aspectos da complexidade estrutural das bromélias e fatores ambientais são necessários para melhor compreensão do uso dessas plantas por anuros na Caatinga.

Palavras-chave: anfíbios, estrutura de comunidade, sítio de refúgio, semiárido, variáveis intrínsecas e extrínsecas, estresse hídrico.

Introduction

Habitat heterogeneity is important to the population dynamics of assemblages, since it reduces competition and negative interaction through niche segregation, and thus enables the coexistence of different species (MacArthur, 1972). Considering these inherent aspects in assemblage dynamics, bromeliads are excellent models for investigating diversity and structure patterns of biological communities (Armbruster *et al.*, 2002). The structural complexity of the plants, especially in terms of number of rosettes and size (Srivastava, 2006), simulates highly heterogeneous environments (Albertim *et al.*, 2010; Gonçalves-Souza *et al.*, 2011) with a complexity level comparable to some larger systems (*e.g.*, ecosystems) (Srivastava *et al.*, 2004), with features that make them attractive environments for several zoological groups (Richardson, 1999; Kitching, 2004). Ecological patterns concerning animal/bromeliad interaction found a strong association between groups of beetles, for example, and species of Neotropical bromeliads (Balke *et al.*, 2008), suggesting the existence of a complex speciation process generated from species-specific interaction. Moreover, bromeliads are also considered of great importance for local diversity expansion, significantly influencing diversity patterns (Richardson, 1999; Gonçalves-Souza *et al.*, 2010).

In general, the ecological importance of bromeliads is related to the structural complexity of these plants (Srivastava, 2006) and by the ability to store water inside their rosettes (Frank and Lounibos, 1987; Teixeira *et al.*, 1997; Cogliatti-Carvalho *et al.*, 2010). Thus, bromeliads are able to create a highly heterogeneous environment (Albertim *et al.*, 2010; Gonçalves-Souza *et al.*, 2011), with abiotic characteristics different from the surrounding environment, conducive to permanence and the survival of many aquatic or terrestrial species (Maguire Jr., 1971; Richardson, 1999; Kitching, 2004). Although the mechanisms involved in the association between fauna and phytotelma are not yet clearly defined (Balke *et al.*, 2008), it can be inferred that environmental constraints are likely to be determinant factors for the use of bromeliads by fauna. This becomes evident in regions with severe hydric stress, although it depends on the physical and biotic aspects related to phytotelma, as well as the ecological characteristics of each species (Duellman, 1970; Wells, 2007).

There are aspects of the life history of amphibians that are strongly associated with environmental complexity, such as richness patterns (Bastazini *et al.*, 2007; Xavier and Napoli, 2011), call site usage (Ryan *et al.*, 2009), and site of spawning and refuge (Seebacher and Alford, 2002). These ecological attributes are dependent on specific environmental components and closely related to physiological constraints (Duellman and Trueb, 1994). Considering the ecological aspects of anurans, bromeliads appear to be favorable environments for the survival and coexistence of many species, as their architectural structure provides a large number of niches, with their own physical and chemical characteristics (Laessle, 1961).

Anurans may use the bromeliads in several niche dimensions, such as nutritive dimension (Mesquita *et al.*, 2004), reproductive dimension (Krügel and Richter, 1995, Schineider and Teixeira, 2001), and refuge dimension (Schineider and Teixeira, 2001), suggesting that different species use this resource in different ways. In general, studies involving anuran/bromeliad association are often simple descriptions or records of plant usage by some species, but do not investigate the environmental factors involved in the association.

The objective of the present study was to investigate the effect of the structural complexity of bromeliads of the species *Aechmea aquilega* (Salisbury) Grisebach, 1864 and of the abiotic variables on the abundance of anurans using the plant as a refuge site. The following question was asked: “Is the abundance of anurans in the interior of *Aechmea aquilega* related to the structural complexity of the plant as well as to air temperature, relative air humidity, and precipitation?"

Material and methods

Study area

This study was carried out in the municipality of Paulo Afonso, in the state of Bahia, in the northeast of Brazil, which is contained within the São Francisco River Basin, in the Caatinga biome. The Caatinga is a biome that has limited availability of water resources, resulting in a complex rain formation system (Sampaio, 2010), with annual periods of drought and the development of xerophytic vegetation adapted to these conditions. The Municipality of Paulo Afonso has a semi-arid tropical climate, with an average air temperature of 29ºC and annual rainfall of 907 mm (Reis, 2004).

For this study, two sites with a high abundance of bromeliads of the species *Aechmea aquilega* (Salisbury) Grisebach, 1864 were selected: (i) O Touro and A Sucuri Balneary (09°23'50, 3"S and 30º12'46, 6"W) in Paulo Afonso Island, at the edges of the artificial lake of the same name, characterized by shrubs, trees, and grasses, with mostly exposed soil, or with shallow litter; (ii) Urubu Island (09°23'30, 5"S and 38°12'00, 1"W), an area with a large number of streams, permanent ponds, and waterfalls, characterized by homogeneous and dense arbustive-arboreous stratum, with thickly littered soil.

Data collection

A total of 15 surveys were performed, between September 2007 and May 2008, with the exception of April. Two surveys were performed every month, except for September and May (one visit each) and December (three visits). To facilitate data gathering, the O Touro and Sucuri Balneary site was divided into two plots (10 x 2 m) and the Urubu Island site was divided into three plots (30 x 4 m). Although bromeliads are distributed in isolation, difference in plot size and quantity are related to density difference between *A. aquilega* abundance in each site. During each survey, a plot from each site was sampled, and the bromeliads were verified. The biotic aspects of those bromeliads that had anurans inside, as well as abiotic aspects, were measured. The investigation of anurans present in the bromeliads occurred between 7:00h and 12:00h, in order to increase the chance of finding individuals using *A. aquilega* as refuge site. The search was based on the visual encounter method (Crump and Scott, 1994), moving leaves of bromeliads manually to expose the animals. Abundance of anurans was taken to be the total number of individuals found in the interior of the plants.

To evaluate the relationship between anuran abundance and biotic factors, two morphometric variables were measured that summarize the structural complexity of the plant: bromeliad height (from ground to the apex of the largest leaf) and number of leaves. In addition, an abiotic factor, the temperature inside the plant (precision thermometer of 0.5°C), was considered, together with the biotic factors, as "intrinsic variables", following suggestion of Gonçalves-Souza *et al.* (2011). In this analysis, each bromeliad corresponded to one sampling unit. Bromeliads were divided into five categorical classes according to height: (i) 20-40 cm, (ii) 41-60 cm, (iii) 61-80 cm, (iv) 81-110 cm, and (v) >110 cm, based on Stuckert *et al.* (2009). This categorization allowed a relationship between size and usage proportion of bromeliad by anurans to be established, facilitating the identification of possible preferences for morphometric variables of plants.

The influence of abiotic factors on anuran abundance was assessed based on the variables of air temperature (outside the plant), relative air humidity, and precipitation, henceforth "extrinsic variables". For this analysis, each visit day was considered to be a sample unit, and the effect of variables was evaluated in relation to accumulated anuran abundance per day. The average air temperature per visit day was obtained by measuring the external temperature of each selected bromeliad (thermometer accurate to 0.5°C). The mean values of relative air humidity and the total accumulated precipitation were taken daily, compatible with each visit day, both measured from a macro-scale space at the Meteorological Station of Paulo Afonso and the database of the Real Time Monitoring Program, Northeast Region – Proclima (www.cptec.impe.br/Proclima), respectively.

Statistical analysis

The identification of differences between the internal temperature of *Aechmea aquilega* and air temperature was performed using the Mann-Whitney test. The effect of intrinsic variables (bromeliad height, number of leaves, and internal temperature) for anuran abundance in each bromeliad (response variable) and extrinsic variables (air temperature, relative air humidity, and rainfall) for accumulated abundance of anurans in bromeliads during each visit (response variable) was checked using Multiple Regression (Zar, 1999). For statistical purposes, measured data from the two sites were merged and treated together. Data normality was verified using the D'Agostino-Pearson test for intrinsic variables and the Shapiro-Wilk test for extrinsic variables. The level of significance was set at 0.05 for all statistical analysis and Past 2.06 (Hammer *et al.*, 2001) and BioEstat 5.0 (Ayres *et al.*, 2007) software was used.

Reduction of multicollinearity

One of the limitations of using Multiple Regression is the assumption of the absence of correlation between predictor variables (multicollinearity) (Tabachnick and Fidell, 2007). Using this model, it is expected that each predictor variable contributes only to predicting the dependent variable, otherwise the real relationship among dependent and predictor variables in the data set can be masked (Graham, 2003). The presence of multicollinearity among predictor variables was verified using Spearman Correlation. Subsequently, Principal Components Analysis (correlation matrix) was carried out to reduce multicollinearity in the data set, showing the variables with the highest contribution to each component (loadings). Scores generated by PCA were used in a Stepwise Regression (forward) and, from the estimate of the partial regression coefficients (R^2), the component that best explained the dependent variable was selected. Variables with higher loadings for a selected component were used in the Multiple Regression model, with those with values above 0.5 being considered relevant (Gatz, 1984). The two predictor variables with the highest values were selected in situations in which loadings were relevant for all, in an attempt to assign a conservative character to the Multiple Regression model (more details can be found in Abdul-Wahab *et al.*, 2005; Tabachnick and Fidell, 2007). Data of intrinsic and extrinsic variables was treated separately, considering number of individuals per bromeliad and number of individual visits per day as dependent variables, respectively, for all regressions. For PCA and Multiple Regressions, data was log-transformed (Log_{10}) to obtain normality.

Results

A total of 147 anurans was found inside 112 bromeliads, distributed among six species and two families (Table 1). *Rhinella granulosa* Spix, 1894 was the species with the largest number of individuals, followed by *Scinax x-signatus* Spix, 1824 and *Scinax pachycrus* Miranda-Ribeiro, 1937, with *Hypsiboas raniceps* Cope, 1862 having the lowest number of individuals. One or two individuals (mean = 1.3 individuals; *SD* = 0.63) were found in each bromeliad and between nine and 10 individuals (mean = 9.8 individuals; *SD* = 5.1) per visit day. The temperature inside the plants (28.13°C ± 3.17) was 1.6°C lower than the air temperature (29.73°C ± 2.94). Comparison of these temperatures indicated a significant difference ($U = 4440.00$; $p = 0.0002$).

There was strong correlation between predictor variables, demonstrating multicollinearity in the data set (Table 2 and Table 3). For intrinsic variables, Stepwise Regression based on PCA scores showed that component 3 provided a better account for variation between predictor variables (Table 4), when the higher number of leaves and bromeliad size best explained the variation of the number of individuals. For extrinsic variables, Stepwise Regression showed that component 1 best explained the variation of abundance of anurans inside the bromeliads per visit day (Table 4). Observation of the loadings of component 1 showed that air temperature and humidity were those that best explained variation of the data set.

The abundance of anurans that used *A. aquilega* was not significantly related to intrinsic ($p = 0.619$; $R^2 = 0.018$) or extrinsic ($p = 0.312$; $R^2 = 0.176$) variables. However, variation in the number of leaves was the intrinsic variable that best explained the presence of anurans in bromeliads. Humidity was the extrinsic variable that best explained the accumulated abundance of anurans per visit day (Table 5). Analysis of proportion of anurans by height category of *A. aquilega* showed that anurans mainly used bromeliads (78.2% of individuals) that were taller than 60 cm (Figure 1).

Discussion

The influence of biotic and abiotic factors on animal communities that use bromeliads has been comprehensively explained (Frank and Lounibos, 1987; Richardson, 1999; Armbruster *et al.*, 2002), and these are considered determinant factors for their organization. For amphibians, the structural complexity of bromeliads has allowed a description of communities functioning from several niche dimensions (Mesquita *et al.*, 2004; Oliveira and Navas, 2004; Silva and Britto-Pereira, 2006; Albertim *et al.*, 2010; Silva *et al.*, 2011) and has shown that their intrinsic characteristics may influence various aspects of the life history of many species. The species richness registered in the present study corresponds to 43% of the species recorded for the region (Protázio *et al.*, 2010), suggesting the importance of bromeliads for maintaining the local diversity of the anurans. The greater presence of hylids found in the interior of *A. aquilega* is similar to other studies of

Table 1. Anuran amphibians registered between September 2007 and May 2008 in the bromeliad *Aechmea aquilega*, in the municipality of Paulo Afonso, state of Bahia, Brazil.

Taxon	Number of individuals
Bufonidae	
Rhinella granulosa Spix, 1894	56
Rhinella jimi (Stevaux, 2002)	6
Hylidae	
Corythomanthis greeningi Boulenger, 1896	4
Hypsiboas raniceps Cope, 1862	1
Scinax pachycrus Miranda-Ribeiro, 1937	30
Scinax x-signatus Spix, 1824	50
Total	147

Table 2. Spearman correlation for intrinsic variables. Values in parentheses represent *p-value* and values in bold represent significant *p-value*.

Intrinsic variables	Number of individuals	Internal temperature	Number of leaves	Height
Number of individuals	1.000	0.122 (0.199)	0.109 (0.251)	-0.064 (0.501)
Internal temperature (ºC)			-0.225 **(0.017)**	-0.224 **(0.018)**
Number of leaves				0.262 **(0.005)**
Height (cm)				1.000

Table 3. Spearman correlation for extrinsic variables. Values in parentheses represent *p-value* and values in bold represent significant *p-value*.

Extrinsic variables	Number of individuals	Air temperature	Humidity	Rainfall
Number of individuals	1.000	0.222 (0.426)	-0.208 (0.457)	-0.422 (0.117)
Air temperature (ºC)			-0.508 **(0.053)**	-0.627 **(0.012)**
Humidity (%)				0.502 (0.056)
Rainfall (mm)				1.000

Table 4. Loadings of Principal Component Analysis. Values in bold represent variables used in Multiple Regression models.

	Component1	Component2	Component3
Intrinsic variables			
Internal temperature (ºC)	-0.500	-0.852	0.155
Number of leaves	0.627	-0.232	**0.744**
Height (cm)	0.598	-0.469	**-0.650**
Eigenvalue	1.511	0.836	0.653
% variance	50.35	27.87	21.78
Stepwise Regression % variation R^2	0.01	1.43	2.03
Extrinsic variables			
Air temperature (ºC)	**-0.609**	-0.301	-0.734
Humidity (%)	**0.596**	0.438	-0.673
Rainfall (mm)	0.524	-0.848	-0.087
Eigenvalue	1.909	0.659	0.432
% variance	63.66	21.96	14.39
Stepwise Regression % variation R^2	11.33	4.55	2.21

Table 5. Biotic and abiotic characteristics and Multiple Regressions used to evaluate the influence on the abundance of anurans.

	Number of samples	Mean ± SD	R^2 partial	t-value	*p-value*
Intrinsic variables					
Multiple Regression R^2=0.018, p=0.619					
Height (cm)	112	76.96 ± 21.59	-0.080	-0.359	0.721
Number of leaves	112	13.09 ± 4.74	0.145	1.387	0.168
Internal temperature (ºC)	112	28.13 ± 3.17	----	----	----
Extrinsic variables					
Multiple Regression R^2=1.176, p=0.312					
Air temperature (ºC)	15	29.54 ± 2.57	0.300	0.122	0.905
Humidity (%)	15	67.57 ± 9.39	-2.029	-1.249	0.236
Rainfall (mm)	15	0.19 ± 0.45	----	----	----

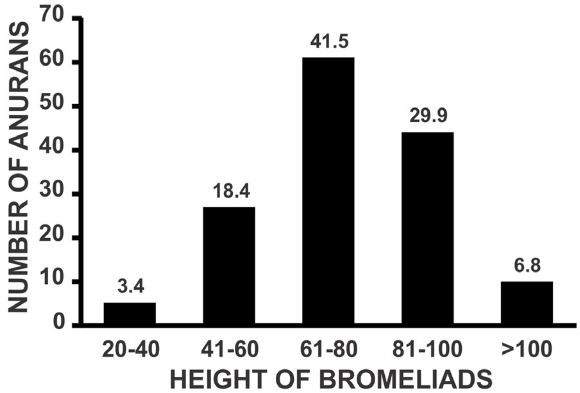

Figure 1. Anuran abundance by bromeliad height (cm). Values on bars represent relative abundance (%).

the association between anurans and bromeliads (Schineider and Teixeira, 2001; Albertim *et al.*, 2010) and may be associated with the presence of adhesive discs, which allow access to new niches (Cardoso *et al.*, 1989).

Although the present study revealed a significant difference between the internal and external temperature of the bromeliad, the abundance of anurans that used *A. aquilega* was not explained by any of the intrinsic or the extrinsic variables discussed. The lack of significance in variables suggests the existence of other more determinant factors in the association between anurans and *A. aquilega* in the Caatinga biome, which may be revealed through analysis of the bromeliads without anurans inside them (see Silva *et al.*, 2011). The lack of influence of biotic and abiotic factors was also found by other studies about the association between animals and bromeliads. Romero and Vasconcellos-Neto (2005) found that there was no relationship between the abundance of *Psecas chapoda* (Peckham and Peckham, 1894) spiders and bromeliad size in forested areas. These authors suggested that this relationship might be dependent on the dry leaves accumulated in the rosettes of bromeliads, which made the use of the microhabitat difficult for the spiders. Oliveira and Navas (2004) also found no significant difference between the numbers of bromeliad leaves with or without *Scinax perpusillus* (A. Lutz & B. Lutz, 1939), indicating that this variable is not decisive in the microhabitat selection of the species. However, in this same study the authors found significant difference in a series of other variables for the presence of male individuals, such as height above ground, tank width, bromeliad radius, density and the pH of the water of the bromeliads.The absence of a relationship between abundance of anurans in bromeliads and precipitation was also described in the "restinga" environment in the state of Rio de Janeiro, in the southeast of Brazil, contradicting the notion that the use of bromeliads is an adaptation against water stress (Silva *et al.*, 2011). In fact, the lack of association between anuran abundance in *A. aquilega* and abiotic variables in the present study is in accordance with studies of Silva *et al.* (2011), suggesting that this relationship may not be associated with hydric stress.

It was noted that anurans mainly used bromeliads that were 61-110 cm tall, similarly to the results by Stuckert *et al.* (2009), Mesquita *et al.* (2004) and Oliveira and Navas (2004), which suggest that anurans avoid intra or interspecific encounters. Higher bromeliads have more leaves (unpublished data), which creates the possibility of different niches in their axils (Maguire, 1971). In addition, the increased size of *A. aquilega* is also accompanied by a decrease in temperature inside the plants (unpublished data), making these bromeliads possibly more attractive microhabitats for anurans.

In the present study, the influence of various biotic and abiotic factors could not be detected regarding the use of *Aechmea aquilega* by anurans. Therefore, it may be assumed that the selection of bromeliads is dependent on other structural and environmental factors, such as number of leaves, bromeliad height and external humidity. This consideration is based on the evidence of other variables that influence the use of these plants by fauna, such as the amount of stored water and detritus mass (Armbruster *et al.*, 2002), pH of stored water (Oliveira and Navas, 2004), presence of inflorescence (Romero and Vasconcellos-Neto, 2005), relation between anuran body size and bromeliad size (Mesquita *et al.*, 2004), and food availability (Silva and Britto-Pereira, 2006). Additional studies addressing other aspects of the structural complexity of bromeliads and environmental factors are necessary to better understand the use of these plants by anurans in the Caatinga biome.

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