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Structure of a Caatinga anuran assemblage in Northeastern Brazil

Estrutura de uma Taxocenose de Anuros no Nordeste do Brasil

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Abstract

Based on data on diet and microhabitat use, we investigated the importance of current (ecological) and historical factors (phylogenetic) in the organization of an anuran assemblage in temporary ponds in a Caatinga area in Northeastern Brazil. The objective of this study was to verify how diet and microhabitat use influence the community structure, and their determinants. Niche breadth based on microhabitat use was relatively low for all species; thus, we also observed a spatial segregation between Hylidae and other families. The closely related species exhibit a more similar diet; the main prey categories used by Caatinga anurans were Coleoptera, insect larvae and Formicidae. The pseudo-community analysis based on diet and microhabitat use revealed that the observed niche overlap did not differ statistically from random, indicating a lack of detectable competition for these resources. The Canonical Phylogenetic Ordination (CPO) analyses revealed no significant phylogenetic effect on the assemblage, neither for diet nor for microhabitat use. Results suggest that predation and hydroperiod may be the most important factors in determining assemblage patterns, but more studies are needed to support this hypothesis.

Keywords: community, Amphibia, ecological factors, historical factors.

Resumo

Com base em dados da dieta e uso de microhabitat, investigamos os fatores atuais (ecológicos) e históricos (filogenéticos) na organização de uma taxocenose de anuros de poças temporárias em uma área de Caatinga no Brasil. O objetivo desse estudo consistiu em verificar como a dieta e o uso de microhabitat influenciam a estrutura da comunidade, assim como suas determinantes. A amplitude de nicho no uso de microhabitat foi relativamente baixa para todas as espécies. Todavia, observou-se uma segregação espacial entre a família Hylidae e as demais. As principais categorias alimentares foram Coleoptera, larvas de Insecta e Formicidae. Espécies filogeneticamente próximas apresentaram dieta similar. A análise de pseudocomunidades revelou que as diferenças para os valores de dieta e uso de microhabitat não são significativas, indicando ausência de competição por esses recursos. A análise de ordenação canônica não detectou efeito significativo da filogenia para dieta e uso de microhabitat. Os resultados sugerem que o hidroperíodo e a predação podem ser os fatores mais importantes na determinação dos padrões da taxocenose, porém, mais estudos são necessários para sustentar essa hipótese.

Palavras-chave: comunidade, Amphibia, fatores ecológicos, fatores históricos.

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Introduction

Assemblage structure can be defined as a non-randomized use of resources by coexisting individuals (Begon *et al.*, 2007; Ricklefs, 2010; Ricklefs and Miller, 1999). The knowledge of resource use patterns by coexisting species is vital for understanding ecological systems, once it provides information about competitive interactions among species (Pianka, 1986; Winemiller and Pianka, 1990). Previously, competition was considered as a primary structuring assemblage mechanism (MacArthur *et al.*, 1972). Physical disturbance, predation and parasitism were also considered important (Diamond and Case, 1986; Hudson and Greenman, 1998). More recently, special attention has been given to the evolutionary history of species, supposing that many characteristics of the current species are simply the result of phylogenetic conservatism (Cavender-Bares *et al.*, 2009; Ernst *et al.*, 2012; Losos 2008). Finally, ecological and phylogenetic factors may be important for determining the current patterns of assemblages (Cavender-Bares *et al.*, 2009; Ernst *et al.*, 2012; Eterovick *et al.*, 2010; Losos, 2008; Mesquita *et al.*, 2006; Mesquita *et al.*, 2007; Webb *et al.*, 2002; Wiens *et al.*, 2011).

Some studies with anuran assemblages have been performed in the Neotropical region in the last 30 years. Toft (1980, 1981) conducted pioneering studies on anuran assemblages in tropical forests from Panama and Peru, investigating diet patterns and foraging mode, suggesting that these species could be classified as ant specialists, not-ant specialists and generalists. Santos *et al.* (2004), studying the feeding habits of six frog species in an Atlantic Forest fragment, identified that most species behave as generalists and there was a slightly greater niche breadth in the rainy season. López *et al.* (2005) evaluated the diet niche overlap among nine Leptodactylidae species in western Argentina, finding a positive correlation among prey and body size and anuran mouth width. In an anuran assemblage in the Cerrado of central Brazil, a significant relationship was found between phylogeny and interspecific synchrony (Bini *et al.*, 2003). However, the vast majority of studies did not take into account the influence of the evolutionary history of species.

The Caatinga Biome comprises a decidual dry environment (see Leal *et al.*, 2005), covering an area of 734,478 km² (MMA, 2002) and harbours a great diversity of environments with its typical vegetation type located in the "Depressão Sertaneja" (Velloso *et al.*, 2002). The Cariri region from Paraíba State is considered one of the driest Brazilian areas, with annual average temperatures around 25 °C with unequally distributed average rainfall of 350 mm per year (Cabral, 1997). Most studies on the Caatinga herpetofauna are restricted to checklists or species descriptions. Arzabe (1999) studied two anuran assemblages in different altitude areas, observing how environmental characteristics promote differences in assemblage organization. Vieira *et al.* (2007) examined the spatial and temporal distribution of an anuran assemblage associated with temporary ponds in Cariri from Paraíba State, and noticed that environment heterogeneity and hydroperiod affect the assemblage dynamics, and Protázio *et al.* (2015) has recently found historical influence on microhabitat use for hylids and Leptodactyliformes in temporary ponds in Caatinga, although their results suggest that ecological factors such as competition are more apparent in anuran assemblages. In order to increase the knowledge about the amphibian ecology and natural history in the Caatinga, the objective of this study was to verify how the diet and microhabitat use influence the community structure, and their determinants. We also test for Phylogenetic effects in anuran assemblage from the Cariri region, Paraíba State, Brazil.

Material and methods

Study site

Field surveys were conducted from March 2008 to April 2010 at the Estação Experimental de São João do Cariri – EESJC (07° 25' S, 36° 30' W), and at Fazenda Olho D'água (07° 22' S, 36° 31' W), near São João do Cariri municipality, in the central part of Paraíba state. The altitude ranges between 450 and 550 m above sea level and the mean temperature from 28° to 35° C. Both sites have a shallow and rocky soil with many rocky outcrops. Soils are composed mainly by sand or clay, having moderate permeation capacity and water retention. Vegetation is composed of dispersed shrubs with some evenly distributed trees, which can reach ten meters height. There is a high density of cacti and bromeliads, as well as temporary ponds, during the rainy season (Vieira *et al.*, 2007).

Sampling methods

Based on a previous study (see Vieira, 2006), we chose five temporary ponds as sampling sites; in each site, we measured size and maximum depth (Table 1). Monthly samplings were carried out from March 2008 to April 2010, however, we only registered anuran activity during the rainy season (March to June 2008; January to April 2009 and 2010), when ponds keep surface water and males were calling, totalizing 58 hours of search. The amphibians were sampled throughout visual transects and auditory search procedures (Crump and Scott Jr, 1994) between 19h and 24h. Visual surveys consisted of walking a complete lap along the shore of the pond, searching for potential microhabitats used by anurans at a distance about five meters from the pond, during approximately 30 to 50 minutes in each pond. On each field trip, the sequence of the sampled ponds was randomized and all the individuals collected were registered. The individuals were

Table 1. Characterization of temporary ponds during the survey period in São João do Cariri, Paraíba State, northeastern Brazil.

Ponds	Coordinates	Area (m²)	Max. Profundity (cm)
1	07°22'53"S, 36°31'50"W	3,000	26
2	07°22'52"S, 36°31'51"W	3,693.6	28.4
3	07°22'50"S, 36°31'49"W	15,622	75
4	07°22'49"S, 36°31'46"W	11,345.7	36
5	07°22'45"S, 36°31'50"W	113.0	44.5

captured by hand and transported to the laboratory, where they were euthanized with an injection of lidocaine and preserved with 10% formalin. All animals were housed at the "Coleção Herpetológica da Universidade Federal da Paraíba".

Microhabitat

We recorded microhabitat use for each individual captured, considering the substrate and the perching height, divided into twelve categories (water's edge, water, grass, bare soil, crevice, trunk, rocks, aquatic vegetation, herbaceous vegetation, shrubs, fallen trunk and leaf litter), and niche breadth was calculated using the inverse of Simpson's index (Simpson, 1949):

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2}$$

where p_i is the proportion of individuals using the resource *i* and *n* is the total number of categories. Values ranged from 1 (use only one microhabitat) to 12 (use equally all microhabitats). The niche overlap was evaluated using Pianka's index (1973), which can vary from 0 (no overlap) to 1 (complete overlap). The index is represented by the following equation:

$$O_{jk} = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}}$$

where p_{ij} is the proportion of resource *i* used by the species *j*; p_{ik} is the proportion of resource *i* used by the species *k*; *n* is the number of categories used. Niche overlap between all species pairs was calculated using EcoSim (Gotelli and Entsminger, 2003).

Diet

In the lab, all stomach contents were removed, analyzed under a stereomicroscope and identified mainly at the taxonomic level of order, except Formicidae and vertebrates. The width and length of intact preys were measured with digital calipers (to the nearest 0.01 mm) and the volume was estimated using an ellipsoid formula (Vitt, 1991):

$$V = \frac{4}{3}\pi \left(\frac{w}{2}\right)^2 \left(\frac{l}{2}\right)$$

where *w* is prey width and *l* is prey length.

Diet niche breadth was calculated for prey number and volume, using Simpson's index (1949), described above. To determine the importance of each prey category in species diet, we calculated the importance index for pooled stomachs using the following equation:

$$I = \frac{F\% + N\% + V\%}{3}$$

where *F*% is the percentage of occurrence, *N*% is the numeric percentage and *V*% is the volumetric percentage. Diet niche overlap was calculated using Pianka index (1973), described above.

To test how diet varies between prey selection and random food availability in the environment, we used the four most abundant anurans (*P. cicada*, *P. albifrons*, *L. fuscus* and *P. nordestina*). To evaluate food availability in the environment, we used 10 pitfalls (300 ml plastic cups) and 2 window traps disposed randomly, near to the ponds, covering all microhabitats. The traps were revised daily, during the field trips. The invertebrates collected were preserved in ethanol 70%. The identification was performed under a stereoscopic microscope using adequate literature (Barnes *et al.*, 1993; Brusca and Brusca, 2007); experts were consulted when necessary.

Statistical analyses

To verify the presence of non-random patterns in diet and microhabitat, we used EcoSim niche overlap module (Gotelli and Entsminger, 2003). The species were arranged in rows, while microhabitat and diet categories were arranged in columns. The matrix is randomized in order to reproduce random patterns that would be expected with the lack of ecological or historical factors. The options used in EcoSim was Pianka index and randomization algorithm two, which replaces the original categories in the matrix by random numbers between zero and one, but retains the zero structure of the original resource matrix (Winemiller and Pianka, 1990).

To check whether species diets represent random samples of food availability, we also used EcoSim module in a similar way as for diet and microhabitat analysis. For this, several analyses were performed comparing each species and prey availability. If non-random patterns were detected, the diet of the species was considered to represent a non-random sample of food availability. In these analyses, we used only species represented by 20 individuals in the samplings.

To evaluate the influence of evolutionary history of species, we used a Canonical Phylogenetic Ordination-CPO (Giannini, 2003), which is a modification of a Canonical Correspondence Analysis-CCA (Ter Braak, 1986), a method that promotes the ordination of a group of variables (X) in a way that the relationship with a second group (Y) of variables is maximized. In this work, one of the matrices (Y) presents the data obtained from the anuran assemblage (diet and microhabitat), while the other matrix (X) is a tree matrix that contains all of the monophyletic groups of the assemblage, extracted from most recent phylogenies (Ponssa, 2008; Pyron and Wiens, 2011), each one encoded as a binary variable. Thus, the analysis consists of the search for subsets (columns of X) that best explain the variation in Y, using correspondence analysis combined with Monte Carlo permutations. The analysis was performed in the program CANOCO 4.5 for Windows using the following settings: “symmetric scaling”, “bi-plot scaling”, “downweighting of rare species”, “manual selection of environmental variables” (monophyletic groups), “9.999 permutations”, and “unrestricted permutations”.

Results

Species composition

We observed a total of 13 species of adult anurans distributed in five families. Leptodactylidae was the most representative family, with 6 species [(*Leptodactylus caatingae* Heyer & Juncá, 2003, *Leptodactylus fuscus* (Schneider, 1799), *Leptodactylus macrosternum* Miranda-Ribeiro, 1926, *Leptodactylus troglodytes* Lutz, 1926, *Physalaemus albifrons* (Spix, 1824) and *Physalaemus cicada* Bokermann, 1966)], followed by Hylidae, with 3 species [*Hypsiboas raniceps* Cope, 1862, *Phyllomedusa nordestina* Caramaschi, 2006, *Scinax x-signatus* (Spix, 1824)] and Bufonidae, with 2 species [*Rhinella jimi* (Stevaux, 2002) and *Rhinella granulosa* (Spix, 1824)]. Odontophrynidae and Microhylidae were represented only by one species, *Proceratophrys cristiceps* (Müller, 1883) and *Dermatonotus muelleri* (Boettger, 1885), respectively.

Microhabitat

Most anurans were found in the shore area of temporary ponds. *Physalae-*

Table 2. Frequency of microhabitat use (percentage in parenthesis) of an anuran assemblage in São João do Cariri, Paraíba State, northeastern Brazil.

Categories	*P.c*	*L.f*	*P.a*	*Ph.n*	*L.m*	*S.x*	*H.r*	*R.g*	*Pr.c*	*L.c*	*R.j*	*L.t*	*D.m*
Water’s edge	6 (15.4)	8 (23.5)	17 (54.8)	-	8 (42.1)	5 (35.7)	-	6 (75)	-	3 (50)	1 (20)	1 (25)	-
Water	31 (79.5)	-	10 (32.25)	-	3 (15.8)	-	4 (44.4)	-	-	-	-	-	-
Grass	-	22 (64.7)	4 (12.95)	-	-	-	3 (33.3)	-	-	-	2 (40)	-	-
Bare Soil	1 (2.55)	1 (2.9)	-	-	-	-	-	1 (12.5)	-	-	-	-	-
Crevice	1 (2.55)	-	-	-	1 (5.3)	-	-	-	-	-	-	-	-
Trunk	-	-	-	5 (25)	1 (5.3)	1 (7.2)	-	1 (12.5)	-	-	-	3 (75)	-
Rocks	-	3 (8.9)	-	7 (35)	5 (26.2)	6 (42.8)	2 (22.3)	-	-	2 (33.3)	2 (40)	-	1 (100)
Aquatic Veg.	-	-	-	1 (5)	1 (5.3)	-	-	-	-	-	-	-	-
Herb. Veg.	-	-	-	5 (25)	-	-	-	-	-	-	-	-	-
Shrubs	-	-	-	1 (5)	-	2 (14.3)	-	-	-	-	-	-	-
Fallen Trunk	-	-	-	1 (5)	-	-	-	-	-	1 (16.7)	-	-	-
Leaf Litter	-	-	-	-	-	-	-	-	8 (100)	-	-	-	-
N	39	34	31	20	19	14	9	8	8	6	5	4	1
L_n	1.52	2.07	2.37	3.92	3.57	2.96	2.79	1.68	1	2.57	2.77	1.6	1

Notes: Aquatic Veg. – Aquatic Vegetation, Herb. Veg. – Herbaceous Vegetation, *N* – Number of collected individuals, L_n – Numeric niche breadth, *D.m – Dermatonotus muelleri*, *H.r – Hypsiboas raniceps*, *L.c – Leptodactylus caatingae*, *L.f – Leptodactylus fuscus*, *L.m – Leptodactylys macrosternum*, *L.t – Leptodactylus troglodytes*, *P.a – Physalaemus albifrons*, *P.c – Physalaemus cicada*, *Ph.n – Phyllomedusa nordestina*, *Pr.c – Proceratophrys cristiceps*, *R.g – Rhinella granulosa*, *R.j – Rhinella jimi*, *S.x – Scinax x-signatus.*

mus albifrons and *P. cicada* were more common in the water's edge and inside the water, as well as other Leptodactilydae, even though they also often occupied dry areas, such as bare and rocky soils (*L. fuscus*, *L. caatingae* and *L. macrosternum*), crevices in the ground, and associated with tree trunks or aquatic vegetation (*L. troglodytes* and *L. macrosternum*). Most Hylidae were observed on rocks or associated with herbaceous vegetation or shrubs, except *H. raniceps*, which was more frequently found in the aquatic environment and on the grass. *Rhinella jimi* and *R. granulosa* were mostly found bordering aquatic environments (water's edge), although they were also recorded in dry places (e.g., bare soil, grass and rocks). Finally, *Proceratophrys cristiceps* was found only on leaf litter and *Dermatonotus muelleri* on rocks (Table 2).

Phyllomedusa nordestina shows the highest niche breadth (3.92). Microhabitat niche overlap varied from zero to 0.90 (Table 3). The species that present greatest niche overlaps were *L. macrosternum* and *S. x-signatus*, while the species with less overlap were *P. nordestina* and *L. fuscus*. The pseudo-community analysis indicated that the probability of observing, by chance, a mean niche overlap of 0.284 (simulated mean) or less is 0.059, indicating lack of assemblage structure.

Diet

We analyzed the stomach contents of 203 individuals, totaling 1,004 preys of 20 categories. According to the importance index, the most important category for the assemblage was Coleoptera, followed by insect larvae and Formicidae (Table 4). However, we also found sand particles in 35.96% of the stomachs as well as plant fragments (26.61%) and amorphous material (46.30%).

Diet niche overlap ranged from zero (*D. muelleri* vs. *L. fuscus*, *L. macrosternum*, *S. x-signatus*, *P. cristiceps*, *L. caatingae*, *R. jimi* and *L. troglodytes*) to 0.99 (*L. caatingae* vs. *R. granulosa*). The overlap was also high among the species of the genus *Physalaemus* and *Rhinella. Scinax x-signatus* showed high overlap only with *P. nordestina.* The pseudo-community analysis indicated that the probability of observing, by chance, a mean niche overlap of 0.39 (simulated mean) or less is 0.41, indicating lack of assemblage structure.

A total of 6,462 potential prey recorded in the environment belonged to 15 categories: Collembola, Diptera, Homoptera, Coleoptera, Hymenoptera, Acari, insect larvae, Araneae, Orthoptera, Thysanura, Lepidoptera, Hemiptera, Odonata, Thysanoptera and small vertebrates, mostly froglets. From four "pseudo-community" analyzes between species and prey availability, the occurrence of prey selection was indicated only for *L. fuscus*, in relation to insect larvae (Table 5).

Historical factors

The two canonical ordination analyses explained 55.62% of the total variation in the diet composition of

Table 3. Microhabitat (bold) and diet niche overlap of an anuran assemblage from São João do Cariri, Paraíba State, northeastern Brazil.

	P.c	***L.f***	***P.a***	***Ph.n***	***L.m***	***S.x***	***H.r***	***B.g***	***Pr.c***	***L.c***	***B.j***	***L.t***	***D.m***
P.c	-	0.49	0.96	0.36	0.53	0.39	0.50	0.88	0.73	0.90	0.82	0.44	0.006
L.f	**0.065**	-	0.40	0.16	0.23	0.16	0.59	0.18	0.13	0.26	0.16	0.33	0
P.a	**0.647**	**0.471**	-	0.37	0.57	0.40	0.45	0.94	0.75	0.97	0.90	0.37	0.004
Ph.n	**0**	**0.088**	**0**	-	0.31	0.83	0.17	0.36	0.26	0.37	0.35	0.24	0
L.m	**0.447**	**0.33**	**0.82**	**0.40**	-	0.32	0.30	0.60	0.45	0.60	0.57	0.18	0
S.x	**0.116**	**0.30**	**0.52**	**0.59**	**0.86**	-	0.22	0.40	0.30	0.41	0.39	0.21	0
H.r	**0.728**	**0.566**	**0.48**	**0.258**	**0.407**	**0.275**	-	0.48	0.34	0.47	0.45	0.14	0
B.g	**0.19**	**0.336**	**0.821**	**0.08**	**0.79**	**0.619**	**0**	-	0.73	0.99	0.95	0.29	0.0001
Pr.c	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	-	0.72	0.69	0.21	0
L.c	**0.152**	**0.339**	**0.677**	**0.39**	**0.90**	**0.88**	**0.199**	**0.78**	**0**	-	0.94	0.32	0
B.j	**0.063**	**0.819**	**0.414**	**0.462**	**0.59**	**0.69**	**0.62**	**0.324**	**0**	**0.62**	-	0.27	0
L.t	**0.06**	**0.106**	**0.26**	**0.469**	**0.346**	**0.31**	**0**	**0.46**	**0**	**0.253**	**0.105**	-	0
D.m	**0**	**0.13**	**0**	**0.693**	**0.497**	**0.738**	**0.372**	**0**	**0**	**0.534**	**0.66**	**0**	-

Notes: *D.m – Dermatonotus muelleri, H.r – Hypsiboas raniceps*, *L.c – Leptodactylus caatingae*, *L.f – Leptodactylus fuscus*, *L.m – Leptodactylys macrosternum*, *L.t – Leptodactylus troglodytes*, *P.a – Physalaemus albifrons*, *P.c – Physalaemus cicada*, *Ph.n – Phyllomedusa nordestina*, *Pr.c – Proceratophrys cristiceps*, *R.g – Rhinella granulosa*, *R.j – Rhinella jimi*, *S.x – Scinax x-signatus*.

Table 4. Diet importance index of an anuran assemblage from São João do Cariri, Paraíba State, northeastern Brazil.

Categories	*P.c*	*L.f*	*P.a*	*Ph.n*	*L.m*	*S.x*	*H.r*	*B.g*	*Pr.c*	*L.c*	*B.j*	*L.t*	*D.m*
Coleoptera	28.39	16.43	48.45	16.7	40.66	24.04	26.73	78.43	28.13	61.51	76.87	22.67	-
Blattaria	-	1.1	-	-	-	-	2.3	-	-	-	0.53	-	-
Formicidae	26.90	6.27	19.34	5.68	5.35	2.48	-	40.9	19.53	10.06	38	17.70	-
Scorpiones	-	2.2	-	-	0.7	-	-	-	2.17	-	-	-	-
Araneae	6.83	-	6.68	7.07	4.41	13.06	9.38	-	-	-	7.39	-	-
Lepidoptera	3.17	2.38	-	24.48	18.53	21.13	-	-	-	-	7.27	-	-
Insect larvae	17.08	40.75	19.07	14.23	12.57	8.69	23.21	13.10	-	12.72	13.74	24.17	-
Orthoptera	3.74	14.19	-	-	4.51	-	53.52	4.36	-	-	-	-	-
Odonata	3.17	-	-	-	4.71	22.33	-	-	-	-	-	-	-
Collembola	19.35	-	17.33	2.73	2.12	-	-	-	-	9.66	-	-	-
Isoptera	2.21	-	3.17	-	-	-	-	4.34	-	-	-	-	100
Chillopoda	-	-	-	-	-	-	-	-	2.17	-	-	-	-
Diptera	2.64	-	2.51	9.53	10.61	-	-	8.70	-	-	6.86	-	-
Hemiptera	6.41	1.88	6.28	-	2.22	-	-	-	13.27	-	-	-	-
Acari	2.18	-	3.98	2.73	-	-	-	4.34	-	-	-	-	-
Diplopoda	-	-	2.87	-	-	-	-	-	-	-	23	-	-
Gastropoda	-	-	-	-	8.38	-	-	-	21.07	-	-	-	-
Vertebrates	-	4.1	-	-	23.80	-	-	-	-	-	-	-	-
Homoptera	7.86	-	1.27	1.5	2.12	5.35	-	-	-	-	-	35.47	-
Pseudoescorpiones	-	-	1.27	-	-	-	-	-	-	-	-	-	-
N	39	34	31	20	19	14	9	8	8	6	5	4	1
Numeric niche breadth	4.63	3.06	4.51	5.88	5.22	5.34	3.48	2.10	3.77	2.28	2.30	4	1
Volumetric niche breadth	4.06	3.04	2.15	2.57	2.50	3.97	1.90	1.15	2.90	1.26	1.64	2.49	1

Notes: *N* – number of collected individuals, *D.m* – *Dermatonotus muelleri*, *H.r* – *Hypsiboas raniceps*, *L.c* – *Leptodactylus caatingae*, *L.f* – *Leptodactylus fuscus*, *L.m* – *Leptodactylys macrosternum*, *L.t* – *Leptodactylus troglodytes*, *P.a* – *Physalaemus albifrons*, *P.c* – *Physalaemus cicada*, *Ph.n* – *Phyllomedusa nordestina*, *Pr.c* – *Proceratophrys cristiceps*, *R.g* – *Rhinella granulosa*, *R.j* – *Rhinella jimi*, *S.x* – *Scinax x-signatus*.

the anuran assemblage (Table 6; Figure 1). The Monte-Carlo test showed that the diet of *D. muelleri* explaining 43.79% of the variation (group C – Figure 1) and Hylidae vary 11.83% from others families (group J – Figure 1); however this result was not significant (*P*=0.0643) and (*P*=0.3017), respectively. For microhabitat use, the Monte-Carlo test showed differences to *P. cristiceps* (14.90%) and between Hylidae and Leptodactylidae (12.52%), but they were not significant (*P*=0.072 and *P*=0.2703, respectively).

Discussion

Species composition

Our study site, in the Caatinga domain of Paraíba State, comprises about 24 amphibian species, being 23 anuran and one Gymnophiona (Cascon, 1987; Arzabe, 1999; Arzabe *et al*., 2005; Vieira *et al*., 2007; Protázio *et al.*, 2015). In the Cariri region studied, in five temporary ponds, we recorded 13 anuran species over two years. A previous study in the same area, obtained three additional species *Pleurodema diplolistris* (Peters, 1870), *Trachycephalus atlas* Bokermann, 1966 and *Corythomantis greeningi* Boulenger, 1896 (Vieira *et al.,* 2007). This difference may be caused by regional differences on microhabitats and microclimate or even by the explosive reproductive behaviour of these species (Arzabe, 1999; Vieira *et al*., 2009; Wells, 2007). All species in this study are widely distributed, even throughout other biomes, although some species, such as *H. raniceps*, *S. x-signatus* and *L. macrosternum*, may represent species complexes (Caldwell and Araújo, 2005; Frost, 2010; Maragno and Cechin, 2009).

Microhabitat

The Caatinga biome shows low floristic diversity and vast dry areas without a well-pronounced rainy season (Vieira, 2006). These characteristics result in a restricted availability of microhabitats and reproductive sites. In general, species occurred near temporary ponds, especially Leptodactylidae and Bufonidae, which show the greatest microhabitat use overlap, which is typical of the biology of anuran from dry environments (Stebbins and Cohen, 1995; Wells, 2007). In addition, the low heterogeneity in open environments can also exert influence, usually because microhabitat categories are less numerous than species richness (Bernarde *et al*., 1999; Cardoso *et al*., 1989).

Species of Hylidae and Leptodactylidae were more generalists, using most available microhabitat categories

Table 5. Pseudo-community analysis based on the diet of each species of an anuran assemblage in São João do Cariri, northeastern Brazil, vs. prey availability. P = Probability of the observed niche being less than or equal to the simulated niche.

Species	Observed mean	Simulated mean	Overlap	*P*
Physalaemus cicada	0.74	0.69	0.74	0.67
Leptodactylus fuscus	0.05	0.49	0.05	< 0.001
Physalaemus albifrons	0.50	0.54	0.50	0.34
Phyllomedusa nordestina	0.27	0.63	0.28	0.68

Table 6. Historical effects on the diet and microhabitat use of Caatinga anurans from São João do Cariri, Paraíba State, northeastern Brazil. Results of Monte Carlo permutation tests of individual groups (defined as in Figure 1). Percentage of the variation explained (relative to total unconstrained variation); F- and P-values for each variable are given (9999 permutations) for each main matrix.

Group(s)	Variation	Variation %	F	P
		Diet		
C	0.733	43.79	6.109	0.0643
J	0.198	11.83	1.175	0.3017
B	0.168	10.04	0.983	0.3215
A	0.152	9.08	0.877	0.4650
E	0.144	8.60	0.827	0.7201
H	0.127	7.58	0.728	0.7468
D	0.126	7.53	0.718	0.5307
I	0.119	7.11	0.677	0.9845
G	0.107	6.39	0.607	0.7902
K	0.100	5.97	0.565	0.7185
F	0.080	4.78	0.445	0.8576
		Microhabitat		
E	0.357	14.90	1.491	0.0724
J	0.300	12.52	1.230	0.2703
K	0.289	12.06	1.178	0.2403
C	0.233	9.72	0.932	0.3810
I	0.225	9.39	0.894	0.6135
A	0.218	9.10	0.867	0.4921
F	0.161	6.72	0.628	0.6847
G	0.157	6.56	0.609	0.7952
H	0.129	5.39	0.497	0.9326
D	0.117	4.89	0.446	0.8781
B	0.101	4.22	0.386	0.9321

(Cascon, 1987; Vieira *et al.*, 2007). However, in other biomes, Leptodactylidae species were more conservative on microhabitat use (Kopp and Eterovick, 2006; Santana *et al.*, 2008). Hylidae were more associated with herbaceous strata, trees and shrubs, and more commonly found in rocks, indicating strong historical influence on resource use patterns of these species, as found by Eterovick and Sazima (2000); Machado and Bernarde (2002) and Santana *et al.* (2008). The high plasticity in microhabitat use can be explained by their morphology, the distinct shape of limbs with adhesive toes, allowing the vertical use of different substrates (Pombal Jr., 1997).

Species of Leptodactylidae were more related with wetlands, occurring mainly on pond border, as observed for other closely related species from Atlantic Rainforest (Eterovick and Sazima, 2000; Santana *et al.*, 2008). However, some species studied herein were also found associated with rocky formations, such as *L. fuscus*, *L. macrosternum* and *L. caatingae*, in contrast to closely related species in other environments (Conte and Machado, 2005; Heyer and Juncá, 2003). Species of Bufonidae were more frequent in flooding areas, similarly to studies conducted in northeastern Argentina, in which the association of *R. granulosa* with flooded environments, as well as of other species with dry rock outcrops was observed (Duré *et al.*, 2009), indicating a strong historical influence. *Proceratophrys cristiceps* used a unique microhabitat (litter) and showed a non-sharing spatial niche with any other species. The association with the litter, as well as with dry sites, was also observed for other close related species, such as *Odontophrynus americanus* (Duméril & Bibron, 1841), *Proceratophrys cururu* Eterovick & Sazima, 1998 (Eterovick and Sazima, 2000) and *Proceratophrys boiei* (Wied-Neuwied, 1825) (Teixeira *et al.*, 2002).

The lack of structure assemblage found in the pseudo-community analysis indicates that there are no sufficiently strong competitive forces acting among species, suggesting that microhabitat use is not a limiting resource (Connor and Simberloff, 1979). This result may be explained by the unpredictability of the hydroperiod (Vieira *et al.*, 2009), and a possible pressure by predators that keeps the resource below the carrying capacity (Kopp and Eterovick, 2006; Mesquita *et al.*, 2006).

Diet

Usually, diet from most anurans is generalist and consists mainly of ar-

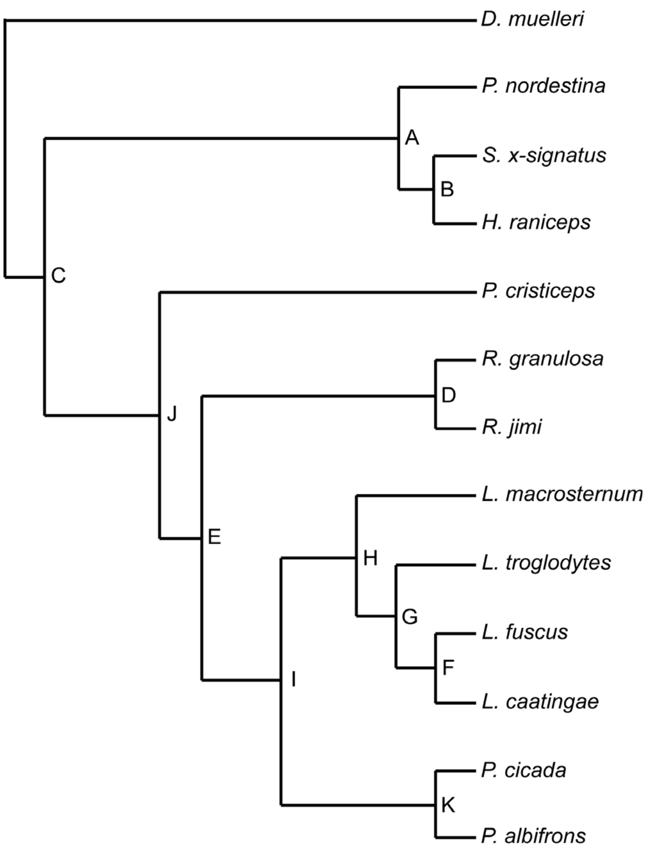

Figure 1. Phylogeny used in Canonical Phylogenetic Ordenation for microhabitat and diet based on Ponssa (2008) and Pyron and Wiens (2011).

thropods and other small invertebrates (Toft, 1980, 1981; Wells, 2007). Despite the fact that the assemblage shows a diverse diet composition, most species presents high preference for Coleoptera, similarly to other neotropical frog assemblages (Parmelee, 1999; Toft, 1981). The presence of sand grains, as well as plant material, should be due to an accidental ingestion (Santana and Juncá, 2007), although sand grains can help in mechanical digestion (Evans and Lampo, 1996), and vegetation fragments may be important in mineral and water complement (Anderson *et al.*, 1999).

Rhinella jimi and *R. granulosa* present typical dietary items, especially ants and beetles (Duré *et al.*, 2009; Sabagh and Carvalho-e-Silva, 2008; Santana and Juncá, 2007). *Dermatonotus muelleri* fed mainly on termites, which, even based on a single record, may suggest a specialization, since this type of specialization in fossorial anurans seems to be common (Nomura *et al.*, 2009; Wells, 2007).

Physalaemus spp. fed mainly on beetles, ants and collembolans, in contrast to close related Atlantic Rainforest frogs, where termites are the main prey category (Santana and Juncá, 2007; Santos *et al.*, 2004). In addition, *P. nordestina* fed mainly on Homoptera and Lepidoptera, differently from *Phyllomedusa* aff. *hypocondrialis* (Daudin, 1800) (possibly *P. nordestina*, Caramaschi, 2006), which has arachnids as the most important prey category in a study performed in a Atlantic Rainforest fragment in Pernambuco State (Santos *et al.*, 2004). Wells (2007), in a frog assemblage review, showed differences in structuring forces between savannas and tropical forests. However, the diet difference presented herein could be due to environmental pressures, which may affect prey availability.

All species behaved as generalists in the present study. Leptodactylidae in general showed the widest diet prey diversity, similarly to other studies (Parmelee, 1999). Hylidae also present a large niche breadth, with *P. nordestina* showing the largest niche breadth in the assemblage. On the other side, Bufonidae showed the smallest niche breadths. Some authors argue that Bufonidae exhibit similar diets among them, consisting mostly of beetles and ants (Clarke, 1974; Parmelee, 1999; Toft, 1981), the low niche breadth of *R. jimi* and *R. granulosa* could be simply a result of phylogenetic conservatism.

The major food niche overlap was observed between Leptodactylidae and Bufonidae. *Leptodactylus caatingae* and *R. granulosa* showed the highest diet niche overlap, mainly due to high consumption of Coleoptera. However, they fed in different habitats (Vieira *et al.*, 2007), characterizing a niche complementarity event (Pianka, 1974, 1986). In addition, we must consider prey size also as a segregating factor (MacArthur and Levins, 1967; Wilson, 1975). The low overlap among *D. muelleri* and other species simply reflect sample size, since only one specimen was captured. However, several studies set the Microhylidae as termite and ant specialists (Parmelee, 1999; Solé *et al.*, 2002), reflecting a conservative diet, justifying the low overlap.

The lack of structure assemblage found in the pseudo-community analysis indicates that there are no sufficiently strong competitive forces acting among species, suggesting that the resources are not limiting (Connor and Simberloff, 1979). Studies in African Savanna revealed that prey availability is not a limiting resource, being the assemblage organization dictated mainly by water availability (Barbault, 1974). This pattern was also found in the present study, which was corroborated by the positive correlation between species activity and hydroperiod (Bertoluci and Rodrigues, 2002), as well as pond depth (Vieira *et al.*, 2007).

The diet analysis, taking into account prey availability, reveals a strong relationship between prey availability and stomach contents. We observed that important diet categories (e.g., Coleoptera and Formicidae) were also listed among the most abundant prey available in the environment, highlighting the opportunist nature of the species in accordance with food availability (Hirai and Matsui, 1999; Labanick, 1976). Only *L. fuscus* had the diet as a by-product of non-random sample of prey availability, which may be due to high importance of insect larvae in its diet, which were not abundant in the samplings, possibly due to a sampling problem (Ozanne, 2005; Woodcock, 2005). In addition, some studies show the importance of insect larvae in frog diet, which may be due to their abundance in the rainy season (Araújo *et al.*, 2007; De-Carvalho *et al.*, 2008; Guimarães *et al.*, 2011).

Historical factors

Based on CPO results, we did not found a historical basis on the diet of anuran assemblage in São João do Cariri region. Despite the CPO results, the species of Hyloidea clade (C group – Hylidae, Bufonidae, Leptodactylidae and Odontophrynidae – Figure 1), in general, consume similar prey in other locations (Parmelee, 1999; Santana and Juncá, 2007; Toft, 1980, 1981) and *D. muelleri* (Ranoidea clade) consumed mainly termites, corroborating the idea that most Microhylidae has a highly conservative diet (Parmelee, 1999; Simon and Toft, 1991; Solé *et al.,* 2002) – it could be some important phylogenetic influence in the diet of this assemblage, but it was not detectable by CPO. Nevertheless, the hydroperiod appeared to be the major structuring factor in dry environments, and not prey availability, which does not appear to be a limiting factor (Barbault, 1974; Vieira *et al.*, 2009; Vieira *et al.*, 2007), allowing the Caatinga anurans to have a conservative diet. However, further studies involving anuran assemblages to test the influence of ecological and historical factors are essential to confirm this trend.

Although we do not identify a significant historical effect for microhabitat use, we can observe a discrepancy between Hylidae and other species, which were more restricted to horizontal portions of the environment. This pattern was also observed in tropical forests (Parmelee, 1999; Vitt and Caldwell, 1994) and in dry environments of open areas (Eterovick and Sazima, 2000; Vieira *et al.*, 2007). The absence of historical effects in microhabitat use could be related to environmental disturbances that the study area suffers constantly (Vieira *et al.*, 2009). Eterovick *et al.* (2010), in a study performed with some frog assemblages from Atlantic rainforest, found a weak relationship between "conservatism" and microhabitat use, with *Dendropsophus minutus* (Peters, 1872) populations differing in microhabitat use among assemblages, indicating that the ecological pressures, such as predation (Kopp and Eterovick, 2006), or water availability (Vieira *et al.*, 2007), could be more important than historical factors.

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