Volume 25 (April 2015), 109–121

Herpetological Journal

FULL PAPER

Published by the British Herpetological Society

Niche differentiation of an anuran assemblage in temporary ponds in the Brazilian semiarid Caatinga: influence of ecological and historical factors

Arielson S. Protázio, Ralph L. Albuquerque, Laura M. Falkenberg & Daniel O. Mesquita

Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, Cidade Universitária, 58051-900, João Pessoa, Paraíba, Brazil

The investigation of historical factors which determine assemblage structure is largely based on the idea that closely-related species have similar ecological characteristics due to a shared evolutionary history. We used a Pseudocommunity Analysis (PA), Principal Component Analysis (PCA) and Canonical Phylogenetic Ordination (CPO) to evaluate the influence of phylogeny on microhabitat use, diet composition and morphology in an assemblage of 15 anuran species occupying temporary ponds in the semiarid Caatinga. Closely-related species used the same microhabitats, although at different proportions, and showed a high diet niche overlap. The PA showed that competition does not appear to regulate the assemblage. Closely-related species showed a high degree of morphological similarity, suggesting that body shape is a conservative trait. The CPO analysis revealed a historical influence on microhabitat use in the Hylidae and Leptodactyliformes dichotomy, and in the diet composition of the genus *Physalaemus* and Leiuperinae. Although resource use patterns reflect phylogenetic relationships among species, our results suggest that ecological factors such as competition further shaped the studied anuran assemblages.

Key words: assemblage structure; Canonical Phylogenetic Ordination, diet, ecological influence, microhabitat use, morphometry, phylogenetic influence

INTRODUCTION

An ecological community can be defined as the set of organisms coexisting in a specific geographic area (Menge, 1976; Connell, 1980). Traditionally, ecologists have always considered competition as the key mechanism to determine the dynamics of biological systems (Schoener, 1974; Seale, 1980; Tilman, 1982). Competition can induce differential resource use by species tending to minimise the negative effect of interaction and ensuring their coexistence (Pianka, 1973). Anurans have a complex life cycle that might favour interspecific competition. Individuals of different species often reproduce and forage synchronously in the same habitat (e.g., ponds, streams and lakes), which enhances the selection of specific phenotypic traits that can reduce niche overlap levels (Pfennig & Murphy, 2002; Relyea & Auld, 2005). Thus, competition in anuran assemblages can pervade temporal, spatial, trophic and acoustic niches (Vitt & Caldwell, 1994; Rossa-Feres & Jim, 2001; Bertoluci & Rodrigues, 2002).

Roughgarden & Diamond (1986) defined an ecological community based on spatial, trophic, morphological, and taxonomic dimensions, the latter highlighting the importance of evolutionary relationships in determining assemblage patterns. Recently, there has been an increase in the use of phylogenetic information to study ecological patterns (Losos, 1996; Webb et al., 2002; Wiens & Graham, 2005), sharing the idea that closely related species have similar characteristics determined by their common evolutionary history (Swenson et al., 2007; Losos, 2008; Wiens et al., 2010). This approach has been used to clarify many questions concerning variation in evolutionary patterns (Peterson et al., 1999; Wiens, 2004), and has proven useful in determining microevolutionary processes (Travis, 1983; Ryan, 1986; Richardson, 2001; Mesquita et al., 2006; Losos, 2008; Eterovick et al., 2010). In anurans, tadpoles from closely related species exhibit body shape and microhabitat use as the most conservative traits (Eterovick & Fernandes, 2001), whereas ecological traits in adults are more flexible (Eterovick et al., 2010). This highlights the need for a better understanding of how phylogeny influences organismal traits (Blomberg et al., 2003).

This study aimed to investigate the determinant factors of niche interactions in an anuran assemblage at temporary ponds in a Caatinga site in northeastern Brazil. Based on the hypothesis of phylogenetic niche conservatism, we predict that closely related species show high levels of overlap in spatial, dietary and morphological niches. To assess the interaction levels, we collected data on microhabitat use, diet and morphometry of 15 species. We aimed to answer whether species within assemblages exhibit differences

Correspondence: Daniel O. Mesquita (danmesq@dse.ufpb.br)

in resource use, and whether there are similarities in ecological traits among different species determined by their phylogenetic origin. Based on these questions, we attempted to identify which ecological or phylogenetic mechanisms regulate assemblage dynamics.

MATERIALS AND METHODS

Study area

This study was carried out in three temporary ponds located on Fazenda Junco, municipality of Cabaceiras, Paraíba state, Brazil (Table 1). The study site lies within the Caatinga biome and is located to the south of the ecoregion known as Depressão Sertaneja Setentrional and Cariri Paraibano. This region is characterised by the most common type of Caatinga, with low, dense and deciduous arboreal-shrubby vegetation (Velloso et al., 2002; Giulietti et al., 2007), and large areas of rocky outcrops (Sampaio, 2010). The climate is classified as hot semi-arid (BSh) according to the Köppen classification (Velloso et al., 2002). Caatinga areas have a high water deficit caused by irregular rainfall, soil with a low water-holding capacity and the presence of mountains and plateaux that intersect wet fronts (Sampaio, 2010). Cabaceiras is the municipality with the lowest precipitation rate in Brazil (Giulietti et al., 2007), with a mean of 350 mm per year, and frequently experiences severe and prolonged droughts (Velloso et al., 2002).

Ponds were visited monthly from May 2010 to August 2011, and sampled during three consecutive days, totalling 48 days of study. The ponds are located in a temporary stream along the streambed at approximately 100 m intervals. Anurans were captured manually through acoustic surveys around the temporary ponds between 1800 and 0000 hours. During the study period, the ponds showed little or no connection between them. However, the ponds showed a high physiognomic and geomorphological similarity, and the anuran fauna of all three ponds was thus considered a unique assemblage. Specimens were killed immediately with a xylocaine injection, preserved with 10% formalin and stored in 70% alcohol. No globally or locally endangered species (e.g., IUCN listed as threatened) were killed. Since the present study was part of a larger project involving reproduction, alternative techniques (such as stomach flushing for diet analysis) were not possible. We adhered to the ethical guidelines provided by American Society of Ichthyologists and Herpetologists (ASIH), The Herpetologists' League (HL) and the Society for the Study of Amphibians and Reptiles. All collected specimens are housed in the Herpetological Collection of the Universidade Federal da Paraíba.

Microhabitats

Eleven categories of microhabitats were identified: exposed soil, soil between vegetation, perched on herbaceous shrub, perched on shrub, perched on tree, perched on emergent vegetation, partially submerged, perched on rock, perched on bromeliad, perched on cactus and hole. The inverse of Simpson's Diversity Index (Simpson, 1949) was used to calculate the niche breadth based on microhabitat use (*B*):

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

where *p* is the proportion of microhabitat category *i*, and *n* is the total number of categories. The calculation of niche breadth from the inverse of Simpson's Diversity Index generated values ranging from 1 to 11, where 1 is the exclusive use of only one microhabitat (specialists) and 11 corresponds to the use of all categorised microhabitats (generalists). The overlap in the use of microhabitat was following Pianka (1986):

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

where *p* is the proportion of the microhabitat category *i*, *n* is the number of categories, and *j* and *k* represent the species being compared. The overlap index ranges from 0 to 1, where 0 represents no overlap and 1 represents complete overlap. Pianka's equation generates a matrix with niche overlap values among all species in the assemblage. A null model (pseudo community analysis - PA) was used to investigate the presence of non-random patterns in microhabitat use throughout the Niche Overlap Module of EcoSim (Gotelli & Graves, 1996). For this analysis, a data matrix was created with species corresponding to lines and microhabitat categories corresponding to columns, and values of each cell corresponding to the proportion of microhabitat use. The matrix was redesigned based on 1,000 randomisations to simulate random patterns. The existence of structure in the assemblage was verified by comparing observed and simulated niche overlaps (Gotelli & Graves, 1996). We used the randomisation algorithm 2 in the Module

Table 1. Temporary ponds sampled between May 2010 and August 2011 in Cabaceiras, PB, Brazil.

Pond	Coordinates	Elevation (m)	Maximum size (m^2)	Maximum depth (cm)	Months flooded
1	07°28'28.4"S, 38°20'39.3"W	444	13,561.0	146	11
2	07°28'81.2"S, 38°20'19.5"W	441	11,248.0	72	8
3	07°28'50.4"S, 38°20'20.1"W	441	7,313.4	50	6

of Niche Overlap of EcoSim (Gotelli & Entsminger, 2003). Since most individuals were reproductively active, we also investigated niche relations of reproductive males (Wells, 1988). We ran three sets of analysis, using only calling males, non-reproductive individuals, and all individuals combined. *Corythomantis greeningi*, *Leptodactylus caatingae*, *L. fuscus, L.* cf. *macrosternum*, and *Hypsiboas crepitans* were omitted from this analysis due to low calling activity.

Diet

Stomachs were analysed using a Leica® EZ4 stereomicroscope. Prey categories were identified to the taxonomic group of order, except for vertebrates and plant material. Ants (Formicidae) were considered as a separate category to non-ant Hymenoptera. A monophyletic Hemiptera group was also considered, comprising Heteroptera (bugs), Auchenorrhynca (cicadas) and Sternorrhynca aphids (Brusca & Brusca, 2007). The length and width of intact items were recorded using a Mitutoyo® digital caliper (0.01 mm) and the volume of each prey (*V*) was estimated using the ellipsoid formula

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

where *w* is prey width and *l* represents prey length. For volumetric analysis, only intact prey items were used to avoid volumetric under- or overestimation. The numerical and volumetric percentage of each prey category was also calculated, considering the pooled stomachs of all individuals of each species. Diet niche breadth (*B*) was calculated from the percentages of pooled stomach contents using the inverse of Simpson's Diversity Index (Simpson, 1949). Prey occurrence (*F*) was calculated from the ratio number of stomachs containing the prey *i*/total number of stomachs. To determine the relative contribution of each prey category, the Importance Index (*I*) for pooled stomachs was calculated using

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

where *F%* is the percentage of occurrence, *N%* is the numerical percentage and *V%* represents the volumetric percentage of prey *i*. We also estimate the resource availability and electivities dividing the volume of each category of prey by the total volume used in the assemblage. The overlap in diet was calculated using the equation suggested by Pianka (1973). A null model (PA) was again used to investigate the presence of non-random patterns in the diet composition. A Cluster Analysis (CA) was performed using the Euclidean Distance to assess the similarity in the diet of 12 anurans species (excluding species with low sample size), using the scores obtained from the Importance Index. In CA, our expectation is that groups based on diet similarity would include closely related species, reflecting the phylogenetic influence on resource use. For CA, we used the algorithm of paired groups (UPGMA) performed in PAST v.2.12 (Hammer et al., 2001).

Morphometry

Twelve morphometric variables were measured: snout-vent length (SVL), head length (HL), head width (HW), inter-orbital distance (IOD), eye-nostril distance (END) internarial distance (IND), thigh length (THL), tibia length (TL), foot length (FL), tympanum diameter (TD), eye diameter (ED) and inter-eye distance (IED), using a Mitutoyo® digital caliper (0.01 mm) and a Leica® EZ4 stereomicroscope. For morphometric analyses, we followed the terminology suggested by Napoli & Pimenta (2009).

All morphometric variables were log-transformed ($\log_{10}$) to fit requirements of normality (Zar, 1998). To partition the total morphometric variation between size and shape variation, we defined body size as an isometric size variable (Rohlf & Bookstein, 1987), following the procedure described by Somers (1986). This method is based on a Principal Component Analysis (PCA) and is useful to avoid using a one-dimensional body size variable such as SVL. We calculated an isometric eigenvector, defined *a priori* with values equal to $p^{-0.5}$, where *p* is the number of variables (Jolicoeur, 1963). We then obtained scores from this eigenvector, hereafter called body size, by post-multiplying the *n* by *p* matrix of log-transformed data, where *n* is the number of observations, by the *p* by 1 isometric eigenvector. To remove the effects of body size from the log-transformed variables, we used residuals of regression between body size and each shape variable to create a new matrix of adjusted variables, which we used in the PCA matrix.

PCA is an ordination technique that allows a simplified description of the variation among individuals, replacing the original variables by independent linear combinations (Principal Components, Zelditch et al., 2004). In the PCA, we used the covariance matrix, as suggested by Hammer et al. (2001) for data with the same unit. Simple regression and PCA were performed in the SYSTAT v.12 program for Windows.

Phylogenetic Influence

We used a Canonical Phylogenetic Ordination (CPO, Giannini, 2003) to analyse the influence of phylogeny on ecological traits. CPO is a phylogenetic comparison method based on Canonical Correspondence Analysis (Ter Braak, 1986). A *Y* matrix was created with microhabitat and diet and an *X* matrix was created containing monophyletic lineages of the 15 species, formed by a combination of binary indicators (0 and 1) that represent each monophyletic group (Fig. 1). A subset of intrinsic groups in the *X* matrix was created to best explain the data expressed in the *Y* matrix based on Monte Carlo permutations, assuming the null hypothesis of no phylogenetic conservation in diet and spatial niche. For microhabitat use, cells were composed by the proportion of use for each microhabitat category. We ran three sets of analysis, using only calling males, non-reroductive individuals, and all individuals. For the dietary data matrix, the cells corresponded to the Importance

Table 2. Frequency of microhabitat use of 15 anurans species in Cabaceiras, PB, Brazil. Values in parentheses are only of the number of calling males and niche breadth for microhabitat used by calling males. ES – exposed soil; SBV – soil between vegetation; HER – perched on herbaceous; SHR – perched on shrub; TRE – perched on tree; EV – perched on emergent vegetation; PS – partially submerged; RO – rock; HOL – hole; BRO – perched on bromeliad; CAC – perched on cactus.

Species	ES	SBV	HER	SHR	TRE	EV	PS	RO	HOL	BRO	CAC	*n*	Niche breadth
R. granulosa	28(16)	2(1)					5(1)	1(1)	3			39(19)	1.85(1.39)
R. jimi	11						16(5)					27(5)	1.93(1.00)
C. greeningi	1			1	1						1	4	4.00
H. crepitans							1(1)					1	1.00(1.00)
H. raniceps	1(1)		1(1)	3(2)		2	2	1				10(4)	5.00(2.67)
S. x-signatus	67(15)	35(13)	1	16(3)	12(6)	15(10)	5	4(1)	9(4)	2(2)	1	167(54)	4.31(5.21)
P. nordestina	17(1)		11(4)	18(9)	4(3)	4(3)				2(1)		56(21)	4.07(3.77)
L. caatingae	2											2	1.00
L. fuscus	2											2	1.00
L. cf. *macrosternum*	23	8					18	1	4			54	3.12
L. troglodytes	23	12(4)							2			37(4)	2.02(1.00)
P. albifrons	2						19(13)					21(13)	1.21(1.00)
P. cicada	22	9					55(39)	1	22			109(39)	2.92(1.00)
P. diplolister		6					5(5)					11(5)	1.98(1.00)
P. cristiceps		4(4)										4(4)	1.00(1.00)

Table 3. Niche overlap in microhabitat use (*italic*) and diet of the anuran assemblage in Cabaceiras, PB, Brazil. *R. g.* – *Rhinella granulosa*; *R. j.* – *Rhinella jimi*; *C. g.* – *Corythomantis greeningi*; *H. r.* – *Hypsiboas raniceps*; *S. x.* – *Scinax x-signatus*; *P. n.* – *Phyllomedusa nordestina*; *L. c.* – *Leptodactylus caatingae*; *L. f.* – *Leptodactylus fuscus*; *L.* cf. *m.* – *Leptodactylus* cf. *macrosternum*; *L. t.* – *Leptodactylus troglodytes*; *P. a.* – *Physalaemus albifrons*; *P. ci.* – *Physalaemus cicada*; *P. d.* – *Pleurodema diplolister*; *P. cr.* – *Proceratophrys cristiceps*.

Species	*R. g.*	*R. j.*	*C. g.*	*H. r.*	*S. x.*	*P. n.*	*L. c.*	*L. f.*	*L.* cf. *m.*	*L. t.*	*P. a.*	*P. ci.*	*P. d.*	*P. cr.*
R. granulosa		*0.696*	*0.488*	*0.304*	*0.868*	*0.599*	*0.976*	*0.976*	*0.870*	*0.903*	*0.275*	*0.533*	*0.165*	*0.069*
R. jimi	0.917		*0.283*	*0.495*	*0.523*	*0.347*	*0.566*	*0.566*	*0.911*	*0.500*	*0.879*	*0.905*	*0.528*	*0.000*
C. greeningi	0.342	0.525		*0.447*	*0.596*	*0.703*	*0.500*	*0.500*	*0.376*	*0.442*	*0.052*	*0.172*	*0.000*	*0.000*
H. raniceps	0.229	0.413	0.403		*0.445*	*0.725*	*0.224*	*0.224*	*0.439*	*0.198*	*0.468*	*0.466*	*0.286*	*0.000*
S. x-signatus	0.194	0.361	0.878	0.466		*0.695*	*0.834*	*0.834*	*0.795*	*0.946*	*0.149*	*0.442*	*0.374*	*0.435*
P. nordestina	0.277	0.421	0.484	0.529	0.635		*0.614*	*0.614*	*0.462*	*0.543*	*0.064*	*0.211*	*0.000*	*0.000*
L. caatingae	-	-	-	-	-	-		*1.000*	*0.753*	*0.884*	*0.104*	*0.345*	*0.000*	*0.000*
L. fuscus	-	-	-	-	-	-	-		*0.753*	*0.884*	*0.104*	*0.345*	*0.000*	*0.000*
L. cf. *macrosternum*	0.495	0.649	0.487	0.620	0.547	0.754	-	-		*0.796*	*0.664*	*0.849*	*0.578*	*0.262*
L. troglodytes	0.644	0.648	0.426	0.487	0.448	0.570	-	-	0.797		*0.092*	*0.396*	*0.354*	*0.461*
P. albifrons	0.732	0.635	0.203	0.128	0.124	0.157	-	-	0.367	0.551		*0.893*	*0.636*	*0.000*
P. cicada	0.464	0.541	0.441	0.279	0.402	0.498	-	-	0.526	0.418	0.345		*0.660*	*0.142*
P. diplolister	0.607	0.785	0.434	0.375	0.267	0.403	-	-	0.605	0.327	0.324	0.548		*0.768*
P. cristiceps	0.229	0.407	0.206	0.229	0.129	0.269	-	-	0.415	0.239	0.101	0.274	0.479	

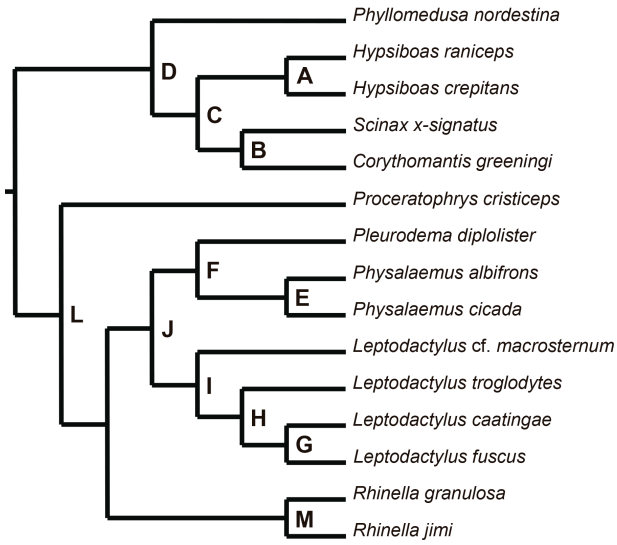

Fig. 1. Phylogeny of anurans used in Canonical Phylogenetic Ordination for microhabitat and diet data. Phylogenetic tree based in phylogenies of Nascimento et al. (2005); Ponssa (2008); Pyron and Wiens (2011). For microhabitat analysis, group A was removed because *H. crepitans* is represented by a single individual. For diet analysis, groups A, G and H were removed because *H. crepitans*, *L. caatingae* and *L. fuscus* did not present food items in the stomachs or had a small sample size.

Index for pooled stomachs of each prey category. CPO analyses were performed using the CANOCO v.4.5 program for Windows, using the following parameters: "symmetric scaling", "size in two-dimensional graphic", "downweighting for rare species", "manual selection of environmental variables", "9999 permutations", and "unrestricted permutations."

RESULTS

We recorded two bufonids (*Rhinella granulosa* and *R. jimi*), five hylids (*Corythomantis greeningi*, *Hypsiboas crepitans*, *H. raniceps*, *Phyllomedusa nordestina* and *Scinax x-signatus*), seven leptodactylids (*Leptodactylus caatingae*, *L. fuscus*, *L.* cf. *macrosternum*, *L. troglodytes*, *Physalaemus albifrons*, *P. cicada* and *Pleurodema diplolister*) and one odontophrynid (*Proceratophrys cristiceps*) in the assemblage. Most species (exceptions: *H. crepitans*, *L. caatingae*, *L. fuscus* and *P. cristiceps*) used more than one microhabitat (Table 2). Microhabitat categories at ground level were used by all species except *H. crepitans,* which was always found partially submerged. Leptodactylinae (*L. caatingae*, *L. fuscus*, *L.* cf. *mascrosternum* and *L. troglodytes*) were more associated with open ground, whereas Leiuperinae (*P. albifrons*, *P. cicada* and *P. diplolister*) were found mainly partially

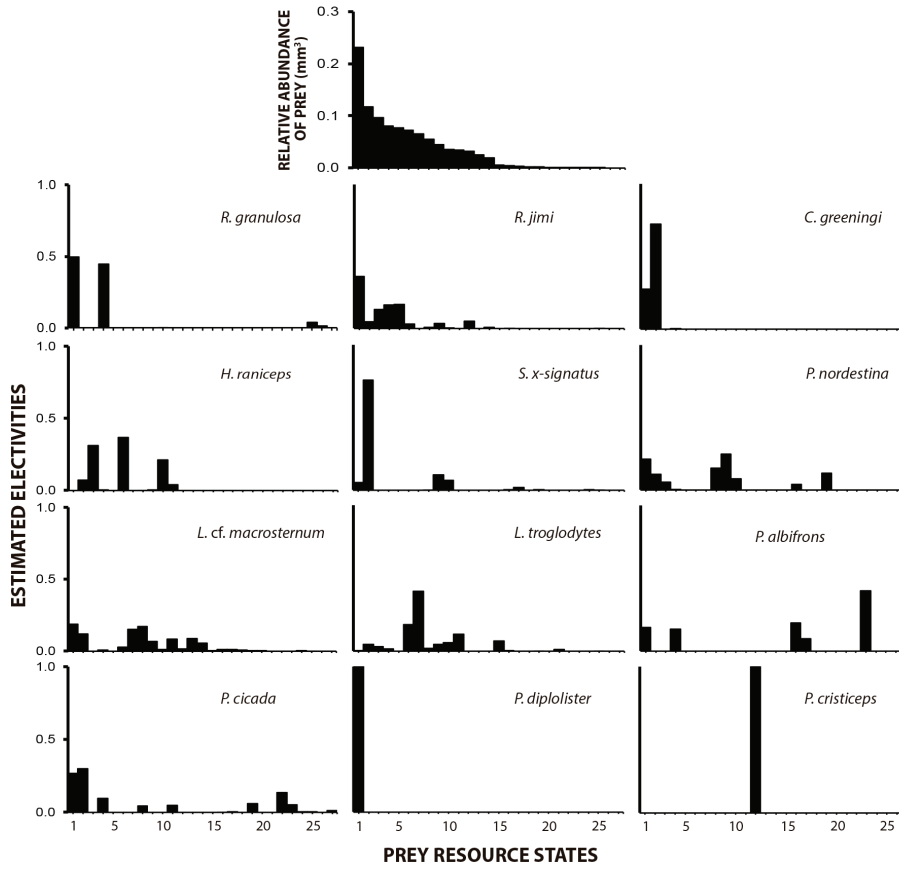

Fig. 2. Electivities of prey for 12 species in Cabaceiras assemblage. Prey categories: (1) Coleoptera; (2) Lepidoptera larvae; (3) Blattaria; (4) Formicidae; (5) Diplopoda; (6) Odonata; (7) Vertebrate; (8) Hemiptera; (9) Lepidoptera; (10) Aranae; (11) Orthoptera; (12) Scorpionida; (13) Annelida; (14) Dermaptera; (15) Gastropoda; (16) Insect larvae; (17) Non identified; (18) Phasmida; (19) Diptera; (20) Opiliones; (21) Isopoda; (22) Collembola; (23) Isoptera; (24) Non-ant Hymenoptera; (25) Acari; (26) Phtraptera; (27) Pseudoscorpiones.

Table 4. Diet importance index of 12 anuran species from Cabaceiras, PB, Brazil. For abbreviations of species see Table 3.

Prey categories	*R. g.*	*R. j.*	*C. g.*	*H. r.*	*S. x.*	*P. n.*	*L.*cf. *m.*	*L. t.*	*P. a.*	*P. ci.*	*P. d.*	*P. cr.*
Acari	4.12	1.62			2.06	8.57	3.67	3.04		2.85		
Aranae	1.48	6.59	25.75	16.02	9.13	17.02	11.13	8.29		1.03		
Non identified	19.09	7.27		4.72	12.44	11.92	11.65	9.10	11.69	12.50	10.48	
Blattaria		7.57		22.92	5.24	3.17		2.52			10.48	
Coleoptera	38.87	55.37	43.49	14.17	12.39	16.28	27.46	9.19	14.30	27.12	91.11	41.67
Collembola						1.98				39.82		
Lepidoptera		6.26		9.56	17.60	16.47	14.38	6.11		1.03		
Isoptera									43.01	3.89		
Scorpionida		4.94					1.19					61.11
Formicidae	71.10	55.03	17.26	3.17	1.84	1.38	9.77	24.12	48.55	10.93	13.81	
Orthoptera		4.85		7.56	1.84	9.73	12.09	11.42		2.91		41.67
Non-ant Hymenoptera					0.66		0.74			0.73		
Insect larvae		1.64			3.14	2.53	15.19	13.02	15.79	3.51		
Odonata		2.71		29.11			10.77	7.52				
Annelida							3.64					
Gastropoda							1.56	8.42				
Diptera					1.96	20.47	2.33	6.07		6.85		
Opiliones							0.78					
Lepidoptera larvae		10.11	76.09	9.62	46.01	11.75	9.21	9.42		12.03		
Phasmida							0.97					
Hemiptera		1.90		7.22	4.32	16.16	17.15	8.52		7.79		
Diplopoda		12.49					1.19					
Pseudoscorpiones										1.70		
Isopoda								3.68				
Dermaptera		1.90					6.23					
Plant material	45.23	50.71	47.54	43.35	31.88	40.76	45.70	26.34	75.42	14.99	44.89	17.09
Phthraptera	1.92											
Vertebrate							11.07	16.64				
Numeric niche breadth	1.39	2.24	1.13	6.35	6.23	6.31	7.53	6.03	2.04	1.23	1.77	3.00
Volumetric niche breadth	2.24	4.83	1.67	3.55	1.70	6.15	8.17	4.42	3.82	5.07	1.00	1.00
n	27	21	2	16	107	41	52	31	14	60	8	2

submerged. Five microhabitat categories were used by *R. granulosa* and a strong association with exposed soil was observed, whereas *R. jimi* used only two categories with most individuals found partially submerged. Among hylids, *S. x-signatus* used all identified categories, followed by *H. raniceps* and *P. nordestina* and *C. greeningi* (Six and four categories, respectively).

Hylid species showed high niche breadth values (highest for *H. raniceps*). Among all other species, only *L.* cf. *macrosternum* showed a niche breadth above 3. The lowest values were observed for *H. crepitans*, *L. caatingae*, *L. fuscus* and *P. cristiceps*. The highest overlaps in microhabitat use were observed between *L. caatingae* and *L. fuscus* (1.000), *B. granulosa* and *L. caatingae* (0.976), *B. granulosa* and *L. fuscus* (0.976), and *S. x-signatus* and *L. troglodytes* (0.946). When considering reproductive and non-reproductive individuals, there was no overlap between species from different families (Table 3). The PA showed an observed mean niche overlap of 0.46 and an expected mean of 0.38 (p=0.98 for the observed mean to be lower than the expected mean). When considering only calling males, the results were similar (Table 2, observed mean niche overlap: 0.27, expected mean: 0.30, p=0.09 for the observed mean to be lower than the expected mean). A further PA with non-reproductive individuals also indicate a lack of structure (p=1.0).

In total, 538 stomachs from 15 species were analysed, and 5,646 prey items distributed among 28 prey categories were identified (Table 4). The proportion of empty stomachs was 28.8% (n=155). *Hypsiboas crepitans*, *L. caatingae* and *L. fuscus* were not considered due to low sample size. Plants were the most consumed item for most species (Table 4). However, we consider the presence of plant material as accidental ingestion. Beetles were present in 40.6% of the stomachs, and were

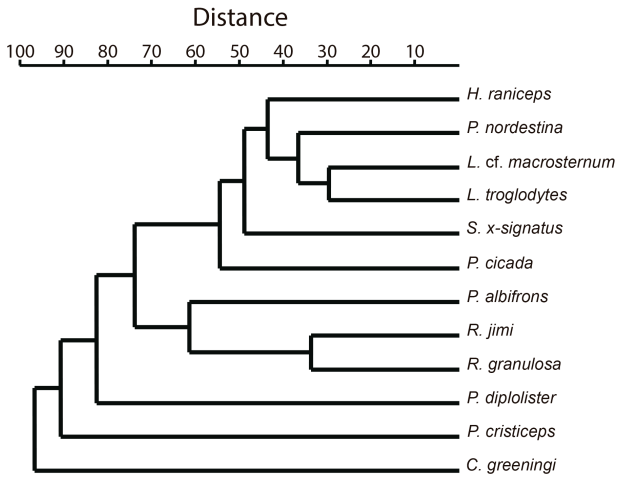

Fig. 3. Cluster analysis calculated with diet importance index among 12 anuran species.

the most important category (26.46%) followed by ants (19.55%) and collembola (12.69%). Ants was the most important category for *R. granulosa, P. albifrons* and *L. troglodytes*; beetles for *R. jimi*, *P. diplolister,* and *L.* cf. *macrosternum*; scorpions for *P. cristiceps*; lepidopteran larvae for *C. greeningi* and *S. x-signatus*; collembolans for *P. cicada*; dipterans for *P. nordestina*, and odonata for *H. raniceps*.

Leptodactylinae and Hylidae showed the highest niche breadths. *Leptodactylus* cf. *macrosternum* was the species with the highest value, followed by *H. raniceps* and *P. nordestina*; the lowest values were observed for *C. greeningi, P. cicada* and *R. granulosa*. The highest volumetric niche was observed for *L.* cf. *macrosternum*, followed by *P. nordestina* and *P. cicada*. The most abundant prey categories, such as beetles, butterfly larvae and ants, have the highest volumetrical contribuition to the diet of most species (Fig. 2). Only the diets of *P. albifrons* and *P. cristiceps* are characterised by high importance of less common prey categories (termites and scorpions, respectively).

Diet niche overlap varied between 0.101 (*P. albifrons* vs *P. cristiceps*) and 0.917 (*R. granulosa* vs. *R. jimi*, Table 3). High values were observed between *C. greeningi* and *S. x-signatus* (0.878), *L.* cf. *macrosternum* and *L. troglodytes* (0.797), as well as *R. jimi* and *P. diplolister* (0.785). The observed diet niche overlap mean was 0.44, comparing to an expected mean of 0.43, without significant differences (p=0.65).

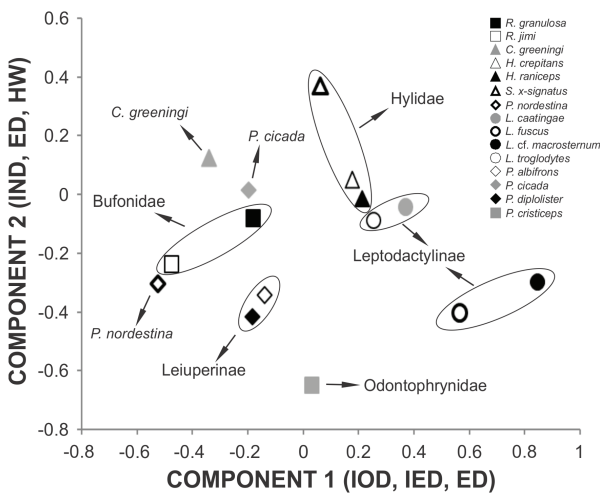

Fig. 4. Plot of mean of first two principal components of 12 morphometry variables of Cabaceiras anurans, based in adjusted data (see Materials and Methods).

The CA revealed two main groups: Bufonidae, and Hylidae + Leptodactylinae (Fig. 3). *Phyllomedusa nordestina*, *L.* cf. *macrosternum* and *L. troglodytes* showed the highest similarity within the second group. Leiuperines (*P. albifrons* and *P. cicada*) showed an intermediate diet composition among bufonids, hylids and leptodactylines. *Corythomantis greeningi* showed the most dissimilar diet composition compared to all other species, followed by *P. cristiceps* and *P. diplolister*.

Rhinella jimi showed the highest SVL and *P. cicada* was the smallest species (Online Appendix). The first and second factors of the PCA explained 54.26% of the total variation (Table 5). We observed a high morphological similarity between Bufonidae and Leiuperinae and among species of Leptodactylinae (Fig. 4). *Phyllomedusa nordestina* was segregated from the group formed by the other hylids. The inter-orbital distance was the most important variable for the first factor, and was inversely related to head length, eye-nostril distance, thigh length, tibia length, foot length and tympanum diameter. Internarial distance was the most important variable in the second PCA factor. An increase in internarinal distance was inversely related to a reduction in inter-orbital distance, eye-nostril distance, inter-eye distance, thigh length, tibia length and tympanum diameter.

Many ecological similarities were observed between closely related species (Fig. 5). Values for niche breadth were similar among hylids, and were the highest of all species. A similar result was found for Leptodactyliformes, which demonstrated a narrow microhabitat use niche (Fig. 5). This pattern of resource use and morphological adaptation the possession of adhesive discs in the Hylidae suggests a strong phylogenetic effect in microhabitat use operating early in the evolutionary history. Many pairs of closely related species also showed similarities in diet composition. *Scinax x-signatus* and *C. greeningi* preferred the same prey category (Fig. 5). The same was observed in the Bufonidae, in which beetles and ants were the most important categories. Leiuperinae species had a similar diet niche breadth. *Physalaemus albifrons* and *P. cicada* were the only species which consumed termites. Only *L.* cf. *macrosternum* and *L. troglodytes* contained gastropods and vertebrates in their diets and showed high niche breadth values.

The CPO revealed a strong phylogenetic influence in Hylidae and Leptodactyliformes, with the basal dichotomy explaining 29.34% of the total variation (Table 6). Significant historical effects were also found in Leiuperinae, Hylinae and Leptodactylidae (Table 6). The phylogenetic influence in diet composition in *Physalaemus* together with the Leiuperinae and Leptodactylinae explained more than half of the total variation (Table 6).

Table 5. Principal component analysis of 12 morphometry variables of Cabaceiras anurans, PB, Brazil.

Variables	Component I	Component II	Component III
Adjusted-SVL	0.021	0.090	0.117
Adjusted-HL	-0.171	0.012	-0.082
Adjusted-HW	0.011	0.250	-0.063
Adjusted-IOD	0.807	-0.434	-0.069
Adjusted-END	-0.167	-0.560	-0.098
Adjusted-IND	0.216	0.437	-0.139
Adjusted-IED	0.305	-0.008	0.122
Adjusted-THL	-0.046	-0.005	0.117
Adjusted-TL	-0.136	-0.098	0.091
Adjusted-FL	-0.087	0.113	0.113
Adjusted-TD	-0.269	-0.296	-0.691
Adjusted-ED	0.224	0.354	-0.631
Eigenvalue	0.1648	0.0989	0.0659
% variation explained	33.91	20.35	13.57

DISCUSSION

Microhabitat

In anuran assemblages, a broad niche breadth and the use of vertical microhabitats have previously been documented (Cardoso et al., 1989; Pombal Jr., 1997; Bertoluci & Rodrigues, 2002). The ability to use a variety of microhabitats is strongly linked with the morphology and size of species (e.g., Crump, 1971; Hödl, 1977; Bertoluci & Rodrigues, 2002), which enables segregation in space use and supposedly reduces competition (Rossa-Feres & Jim, 2001). In the Cabaceiras assemblage, phylogenetically closely related species used similar microhabitats although at different proportions. Bufonids were strongly associated with exposed soil, but *R. jimi* had more individuals using water bodies compared to the congeneric *R. granulosa*. Similarly, *P. albifrons*, *P. cicada* and *P. diplolister* were strongly associated with water, even though a large proportion of individuals of *P. cicada* used exposed soil and holes, whereas *P. diplolister* also used soil between vegetation, similar to in a previous study in Ilha Grande, Brazil (Almeida-Gomes et al., 2007). C*rossodactylus gaudichaudii* and *Hylodes phyllodes* used the same microhabitat categories, although in different proportions, with *C. gaudichaudii* being more associated with water and *H. phyllodes* with rocks (Almeida-Gomes et al., 2007). In the Cabaceiras assemblage, the the differences in proportions of microhabitat used between

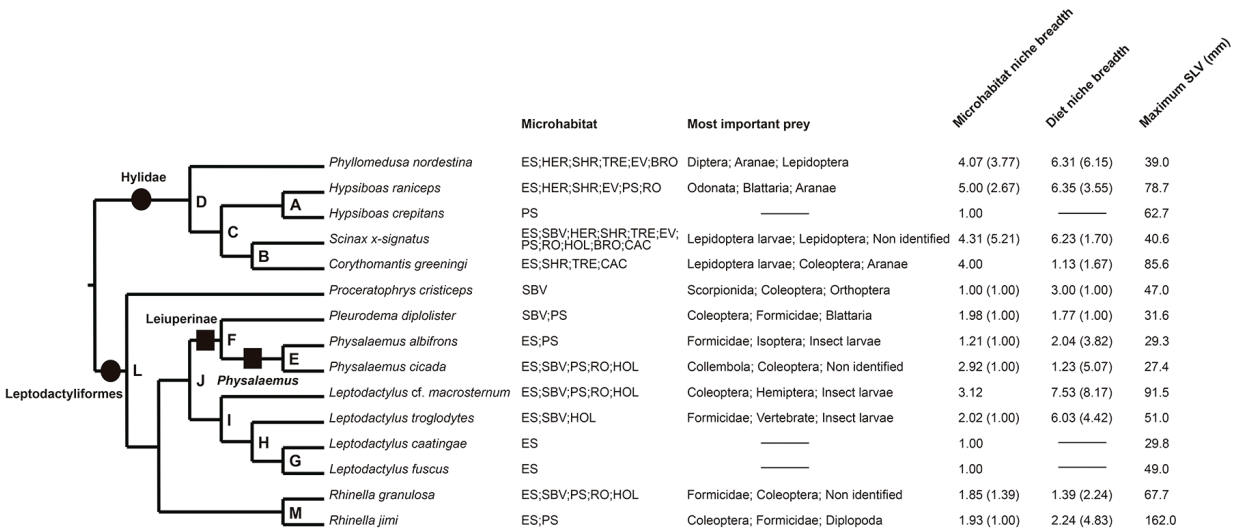

Fig. 5. Phylogeny coupled with ecological characteristics of 15 anuran species of Cabaceiras assemblage. For abbreviations of microhabitats see table 2. Microhabitat breadth values between parentheses represent calling microhabitat niche and outside microhabitat niche. Diet niche breadth values between parentheses represent volumetric niche and outside numeric niche. Symbols in phylogenetic tree represent nodes that showed significant *p*-value in CPO from microhabitat use (circle) and diet composition (square).

Table 6. Phylogenetic influence in ecology of anurans (microhabitat use and diet data) based on 9999 Monte Carlo randomisations. % represents percentage of the total variation found in each group. For identification of each group see Fig. 1.

Group	Variation	%	*F*	*p*
Microhabitat (all individuals)				
D/L (Hylidae/Leptodactyliformes)	0.424	29.343	3.645	0.0019
B (*Scinax*/*Corythomantis*)	0.267	18.478	2.076	0.0820
G (gr *fuscus*)	0.254	17.578	1.964	0.0922
C (Hylinae)	0.239	16.540	1.826	0.0890
I (Leptodactylinae)	0.225	15.571	1.706	0.1098
H (*L. troglodydes*/gr *fuscus*)	0.225	15.571	1.706	0.1087
J (Leptodactylidae)	0.209	14.464	1.574	0.1403
A (*Hypsiboas*)	0.190	13.149	1.417	0.2463
F (Leiuperinae)	0.160	11.073	1.168	0.3052
E (*Physalaemus*)	0.119	8.235	0.852	0.4894
M (Bufonidae)	0.056	3.875	0.386	0.8892
Microhabitat (Calling males)				
D/L (Hylidae/Leptodactyliformes)	0.652	36.404	3.231	0.0044
F (Leiuperinae)	0.627	35.008	3.059	0.0109
J (Leptodactylidae)	0.437	24.399	1.913	0.1037
E (*Physalaemus*)	0.374	20.882	1.582	0.1164
C (Hylinae)	0.296	16.527	1.200	0.4028
M (Bufonidae)	0.201	11.223	0.779	0.5617
Microhabitat (Non-reproductive individuals)				
D/L (Hylidae/Leptodactyliformes)	0.481	29.473	3.644	0.0015
C (Hylinae)	0.349	21.385	2.428	0.0160
J (Leptodactylidae)	0.288	17.647	1.926	0.0299
B (*Scinax*/*Corythomantis*)	0.271	16.605	1.792	0.1304
H (*L. troglodydes*/gr *fuscus*)	0.232	14.216	1.500	0.1556
G (gr *fuscus*)	0.227	13.909	1.463	0.2098
F (Leiuperinae)	0.205	12.561	1.306	0.2585
I (Leptodactylinae)	0.189	11.581	1.195	0.2970
E (*Physalaemus*)	0.127	7.782	0.771	0.5458
M (Bufonidae)	0.083	5.086	0.493	0.7676
Diet				
E (*Physalaemus*)	0.267	21.903	1.898	0.0544
F (Leiuperinae)	0.232	19.031	1.612	0.0495
I (Leptodactylinae)	0.204	16.735	1.388	0.1908
D/L (Hylidae/Leptodactyliformes)	0.179	14.684	1.200	0.2071
J (Leptodactylidae)	0.165	13.536	1.096	0.3147
C (Hylinae)	0.160	13.126	1.058	0.3878
B (*Scinax*/*Corythomantis*)	0.143	11.731	0.933	0.4692
M (Bufonidae)	0.125	10.254	0.809	0.5980

closely related species suggests that partitioning can occur on a fine scale.

Ecological factors might play an important role in microhabitat choice by anurans. Selective pressures related to predation and competition might induce the choice of a microhabitat that reduces these types of interaction and ensures survival (Eterovick & Sazima, 2000). This choice might also be related to physiological aspects which determine microhabitat use (Rittenhouse et al., 2008). Reproductive aspects related to phylogenetic restrictions can further determine habitat use (Zimmerman & Simberloff, 1996). Vieira et al. (2009) reviewed reproductive data for 44 anuran species from the Caatinga and showed a relationship with specific microhabitats. In the light of these findings, the microhabitat use of the Caatinga assemblage suggests that it is strongly related to reproductive aspects.

Diet Composition

Anurans are frequently considered opportunistic predators, with seasonal variation in diet composition according to prey availability (Toft, 1980b; Wells, 2007). However, diet patterns are frequently related to morphological and behavioural traits, which ensure specialisation in prey use (Toft, 1980a; Vitt & Caldwell, 1994), and diet specialisation might also be shaped by phylogeny (Toft, 1995). In the Cabaceiras assemblage, closely related species showed a large diet overlap, although overlap values were also high among phylogenetically distant species. The large overlap between *R. jimi* and *R. granulosa*, with ants and beetles being the main prey categories, is similar to that observed in other studies (Evans & Lampo, 1996; Vences et al., 1998; Sabagh & Carvalho e Silva, 2008; Duré et al., 2009). Bufonids are frequently considered

active foragers specialised on ants, suggesting a strong phylogenetic effect in the group (e.g., Vences et al., 1998; Isacch & Barg, 2002). However, the broader numeric and volumetric niche observed for *R. jimi* compared to *R. granulosa* might be explained by larger body size, which results in a broader spectrum of prey size (Vitt & Caldwell, 1994; Wells, 2007).

The high similarity in diet composition between Hylidae and Leptodactylidae might be related to their generalist lifestyle. A large similarity between the diet composition of *P. nordestina* and *P. azurea* as well as between *P. rohdei* and *P. burmeisteri* were previously observed; in the latter case the species preferred large prey with a lower concentration of chitin, such as insect larvae, lepidopterans, grasshoppers, spiders and beetles (Duré, 1999; Lima et al., 2010). Lepidopteran larvae and orthopterans had little importance in the diet of *P. nordestina* in Cabaceiras, but the presence of dipterans, beetles and spiders is consistent with what has been reported for other congeners (Duré, 1999; Lima et al., 2010).

The large overlap among non-phylogenetically closely related species might be caused by niche complementarity, which occurs when two species have a high overlap in one niche dimension but a low overlap in another niche (Pianka, 1973; Schoener, 1974). Alternatively, it can be due to prey availability not being a limiting factor (Pianka, 1973; Connor & Simberloff, 1979; Toft, 1980b; Winemiller & Pianka, 1990)

The presence of plant material in the anuran diet has been frequently considered accidental (Evans & Lampo, 1996), but also has been suggested to be an active strategy (Anderson et al., 1999; Santos et al., 2004; da Silva & de Britto-Pereira, 2006). In the Cabaceiras assemblage, all species had plant material in their stomachs. The extreme environmental conditions in the study area might have caused the high ingestion rate of plant material and might represent a strategy against dehydration (Anderson et al., 1999).

Morphometry

The morphological analysis of the anurans from Cabaceiras showed a high similarity among closely related species pairs. *Hypsiboas raniceps/H. crepitans*, *L. troglodytes/L. caatingae*, *P. albifrons/P. diplolister*, and *R. granulosa/R. jimi* were tightly clustered, indicating that body shape might be a conserved trait. However, some differences were also observed. *Phyllomedusa nordestina* and *C. greeningi* had different body shapes compared to the other species of the family (Trueb, 1970; Caramaschi & Cruz, 2002). Leiuperinae also occupied a different morphological space than the Leptodactylinae, and differed in body shape compared to the Leptodactylidae. Differences in body shape among phylogenetically closely related species might reflect specialisations in the use of specific prey or microhabitat towards better resource use (Toft, 1980a; Colli et al., 1992; Irschick et al., 1997). The segregation of Leiuperinae and Leptodactylinae in morphological space and microhabitat use thus largely reflects differences in body size and shape, which in turn reflects phylogeny.

Overall, head measurements were more relevant for the formation of groups than other variables, suggesting that body shape might be influenced by developmental patterns in temporary ponds. Many studies have revealed the effect of pond drying and density for anuran life history traits (e.g., Leips et al., 2000). Márquez-García et al. (2009) studied recently metamorphosed individuals of *R. spinulosa* in temporary ponds in the Chilean Andes and found that individuals from ponds that dried faster had reduced eye diameter, mouth-nose distance and hind-limb length. The low relevance of some morphological variables in this study might be a consequence of developmental patterns in rapidly-drying ponds, and an indication that environmental conditions affect body shape.

Phylogenetic Influence

The significant phylogenetic effect on microhabitat use in the Hylidae-Leptodactyliformes node and diet of *Physalaemus* is consistent with the ecological patterns observed in other assemblages (Moreira & Barreto, 1996; Rossa-Feres & Jim, 2001). The presence of adhesive discs in hylids allows the use of different microhabitats and the ability to explore new resources (Cardoso et al., 1989; Bertoluci & Rodrigues, 2002; Eterovick et al., 2010). However, bufonids, leptodactylids and odontophrynids remain limited to microhabitats in soil and water (particularly for breeding), which reflects a more basal pattern of microhabitat use (Cardoso et al., 1989; Eterovick & Sazima, 2000; Prado & Pombal Jr., 2005).

Although significant phylogenetic effects were observed in *Physalaemus*, similar effects were also observed in Leiuperinae and could be related to a historical influence on the diet composition of this group. Ants and termites are important prey types for leiuperines (Vitt & Caldwell, 1994; Moreira & Barreto, 1996; Santos et al., 2003). In other parts of Brazil *P. cicada* is a termite specialist (Santana & Juncá, 2007), whereas in Cabaceiras termites were not important. However, the presence of termites only in *P. cicada* and *P. albifrons* stomachs still suggests a possible phylogenetic influence to the diet of *Physalaemus*. Similarly, *P. diplolister* consumed a large proportion of ants and beetles as confirmed from other localities (Santos et al., 2003), demonstrating the importance of historical factors. A large proportion of termites might be related to seasonal variation in prey availability (Santos et al., 2003). Rosa et al. (2002) studied a population of *P. gracilis* in Uruguay, and also did not find termites as a relevant prey category for the species. Indeed, the lack of anuran natural history studies in the Caatinga makes it difficult to compare populations.

Investigations concerning phylogenetic influence have provided relevant information about ecological interactions in assemblages. However, detecting phylogenetic influences in anurans might be difficult, because individuals show a remarkable plasticity in resource use (Vitt & Caldwell, 1994; Eterovick & Fernandes, 2001; Eterovick et al., 2010). In general, both ecological and phylogenetic components should influence assemblage dynamics. However, frogs from studied assemblage appear to be more shaped by historical factors.

ACKNOWLEDGEMENTS

The authors thank S. Pombo and R. Pombo for allowing entry to the Junco ranch and for all their support; to P.C. Eterovick and F.G.R. França for their valuable suggestions on the manuscript; to A. Protázio, Anselmo, L. Cavalcante and S. Carvalho for help with fieldwork and suggestions. We also thank CAPES and Reuni for financial support to A.S. Protázio and CNPq for financial support to R.L. Albuquerque and D.O. Mesquita. We thank ICMbio for permission to sample animals (n° 30122-1), and University of Texas and Eric Pianka for providing the DOM conditions to finalise this manuscript.

REFERENCES

Almeida-Gomes, M., Hatano, F.H., Van Sluys, M. & Rocha, C.F.D. (2007). Diet and microhabitat use by two Hylodinae species (Anura, Cycloramphidae) living in sympatry and syntopy in a Brazilian Atlantic Rainforest area. *Iheringia, Série Zoologia* 97, 27–30.

Anderson, A.M., Haukos, D.A. & Anderson, J.T. (1999). Diet composition of three anurans from the playa wetlands of northwest Texas. *Copeia* 515–520.

Bertoluci, J. & Rodrigues, M.T. (2002). Seasonal patterns of breeding activity of Atlantic Rainforest anurans at Boraceia, Southeastern Brazil. *Amphibia-Reptilia* 23, 161–167.

Blomberg, S.P., Garland, T. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57, 717–745.

Brusca, R.C. & Brusca, G.J. (2007). *Invertebrados*. Rio de Janeiro, RJ: Editora Guanabara Koogan S.A.

Caramaschi, U. & Cruz, C.A.G. (2002). *Phyllomedusa*: posição taxonômixa, hábitos e biologia (Amphibia, Anura, Hylidae). *Phyllomedusa* 1, 5–10.

Cardoso, A.J., Andrade, G.V. & Haddad, C.F.B. (1989). Distribuição espacial em comunidades de anfíbios (Anura) no sudeste do Brasil. *Revista Brasileira de Biologia* 49, 241–249.

Colli, G.R., Araújo, A.F.B., da Silveira, R. & Roma, F. (1992). Niche partitioning and morphology of two syntopic *Tropidurus* (Sauria: Tropiduridae) in Mato Grosso, Brazil. *Journal of Herpetology* 26, 66–69.

Connell, J.H. (1980). Diversity and coevolution of competitors, or the ghost of competition past. *Oikos* 35, 131–138.

Connor, E.F. & Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology* 60, 1132–1140.

Crump, M.L. (1971). Quantitative analysis of the ecological distribution of a tropical herpetofauna. *Occasional Papers of the Museum of Natural History of University of Kansas*, 3, 1–62.

da Silva, H.R. & de Britto-Pereira, M.C. (2006). How much fruit do fruit-eating frogs eat? An investigation on the diet of *Xenohyla truncata* (Lissamphibia: Anura: Hylidae). *Journal of Zoology* 270, 692–698.

Duré, M.I. (1999). *Phyllomedusa hypochondrialis*: diet. *Herpetological Review* 30, 92–92.

Duré, M.I., Kehr, A.I. & Schaefer, E.F. (2009). Niche overlap and resource partitioning among five sympatric bufonids (Anura, Bufonidae) from northeastern Argentina. *Phyllomedusa* 8, 29–39.

Eterovick, P.C. & Sazima, I. (2000). Structure of an anuran community in a montane meadow in southeastern Brazil: effects of seasonality, habitat, and predation. *Amphibia-Reptilia* 21, 439–461.

Eterovick, P.C. & Fernandes, G.W. (2001). Tadpole distribution within montane meadow streams at the Serra do Cipo, southeastern Brazil: ecological or phylogenetic constraints? *Journal of Tropical Ecology* 17, 683–693.

Eterovick, P.C., Rievers, C.R., Kopp, K., Wachlevski, M., et al. (2010). Lack of phylogenetic signal in the variation in anuran microhabitat use in southeastern Brazil. *Evolutionary Ecology* 24, 1–24.

Evans, M. & Lampo, M. (1996). Diet of *Bufo marinus* in Venezuela. *Journal of Herpetology* 30, 73–76.

Giannini, N.P. (2003). Canonical phylogenetic ordination. *Systematic Biology* 52, 684–695.

Giulietti, A.M., Bocage Neta, A.L., Castro, A.A.J.F., Gamarra-Rojas, C.F.L., et al. (2007). Diagnóstico da vegetação nativa do bioma Caatinga In *Biodiversidade da Caatinga: Área e Ações Prioritárias para Conservação*, 47–90. Silva, J.M.C., Tabarelli, M., Fonseca, M.T.d. and Lins, L.V. (Eds).Brasilia, DF:Ministério do Meio Ambiente.

Gotelli, N.J. & Graves, G.R. (1996). *Null Models in Ecology*. Washington, USA: Smithsonian Institution Press.

Gotelli, N.J. & Entsminger, G.L. (2003). EcoSim: Null Models software for ecology, Acquired Intelligence Inc & Kesey-Bear, Jericho, VT 05465, Available from: <http://garyentsminger.com/ecosim/index.htm>.

Hammer, Ø.; Harper, D.A.T., Ryan, P.D. (2001). Past: Paleontological Statistics software package for education and data analysis [Internet]. Available from: <http://folk.uio.no/ohammer/past/>.

Hödl W. (1977). Call differences and calling site segregation in anuran species from central Amazonian floating meadows. *Oecologia*. 28, 351–363.

Irschick, D.J., Vitt, L.J., Zani, P.A. & Losos, J.B. (1997). A comparison of evolutionary radiations in mainland and Caribbean *Anolis* lizards. *Ecology* 78, 2191–2203.

Isacch, J.P. & Barg, M. (2002). Are bufonid toads specialized ant-feeders? A case test from the Argentinian flooding pampa. *Journal of Natural History* 36, 2005–2012.

Jolicoeur, P. (1963). The multivariate generalization of the allometry equation. *Biometrics* 19, 497–499

Leips, J., McManus, M.G. & Travis, J. (2000). Response of treefrog larvae to drying ponds: comparing temporary and permanent pond breeders. *Ecology* 81, 2997–3008.

Lima, J.E.D., Rodder, D. & Sole, M. (2010). Diet of two sympatric *Phyllomedusa* (Anura: Hylidae) species from a cacao plantation in southern Bahia, Brazil. *North-Western Journal of Zoology* 6, 13–24.

Losos, J.B. (1996). Phylogenetic perspectives on community ecology. *Ecology* 77, 1344–1354.

Losos, J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* 11, 995–1003.

Márquez-Garcia, M., Correa-Solis, M., Sallaberry, M. & Mendez, M.A. (2009). Effects of pond drying on morphological and life-history traits in the anuran *Rhinella spinulosa* (Anura: Bufonidae). *Evolutionary Ecology Research* 11, 803–815

Menge, B.A. (1976). Organization of New England rocky

intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* 46, 355–393.

Mesquita, D.O., Colli, G.R., França, F.G.R. & Vitt, L.J. (2006). Ecology of a Cerrado lizard assemblage in the Jalapão region of Brazil. *Copeia* 2006, 460–471.

Moreira, G. & Barreto, L. (1996). Alimentação e variação sazonal na frequência de capturas de anuros em duas localidades do Brasil cental. *Revista Brasileira de Zoologia* 13, 313–320.

Napoli, M.F. & Pimenta, B.V.S. (2009). A new species of the *Bokermannohyla circumdata* group (Anura: Hylidae) from the coastal forests of Bahia, northeastern Brazil. *Copeia* 2009, 674–683.

Nascimento, L.B., Caramaschi, U. & Cruz, C.A.G. (2005). Taxonomic review of the species groups of the genus *Physalaemus* Fitzinger, 1826 with revalidation of the genera *Engystomops* Jiménez-De-La-Espada, 1872 and *Eupemphix* Steindachner, 1863 (Amphibia, Anura, Leptodactylidae). *Arquivos do Museu Nacional, Rio de Janeiro* 63, 297–320

Peterson, A.T., Soberon, J. & Sanchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. *Science* 285, 1265–1267.

Pfennig, D.W. & Murphy, P.J. (2002). How fluctuating competition and phenotypic plasticity mediate species divergence. *Evolution* 56, 1217–1228.

Pianka, E.R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics* 4, 53–74

Pianka, E. R. (1986). *Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure*. Princeton, New Jersey: Princeton University. Press.

Pombal Jr., J.P. (1997). Distribuição espacial e temporal de anuros (Amphibia) em uma poça temporária na serra de Paranapiacaba, sudeste do Brasil. *Revista Brasileira de Biologia* 57, 583–594.

Ponssa, M.L. (2008). Cladistic analysis and osteological descriptions of the frog species in the *Leptodactylus fuscus* species group (Anura, Leptodactylidae). *Journal of Zoological Systematics and Evolutionary Research* 46, 249–266.

Prado, G.M. & Pombal Jr., J.P. (2005). Distribuição espacial e temporal dos anuros em um brejo da Reserva Biológica de Duas Bocas, Sudeste do Brasil. *Arquivos do Museu Nacional, Rio de Janeiro* 63, 685–705.

Pyron, R.A. & Wiens, J.J. (2011). A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution* 61, 543–583.

Relyea, R. A. & Auld, J.R. (2005). Predator- and competitor-induced plasticity: how changes in foraging morphology affect phenotypic trade-offs. *Ecology* 86, 1723–1729.

Richardson, J.M.L. (2001). The relative roles of adaptation and phylogeny in determination of larval traits in diversifying anuran lineages. *American Naturalist* 157, 282–299.

Rittenhouse, T.A.G., Harper, E.B., Rehard, L.R. & Semlitsch, R.D. (2008). The role of microhabitats in the desiccation and survival of anurans in recently harvested oak-hickory forest. *Copeia* 807–814.

Rohlf, F.J. & Bookstein, F.L. (1987). A comment on shearing as a method for "size correction". *Systematic Zoology* 36, 356–367

Rosa, I., Canavero, A., Maneyro, R., Naya, D.E. & Camargo, A. (2002). Diet of four sympatric anuran species in a temperate environment. *Boletín de la Sociedad Zoologica del Uruguay* 13, 12–20.

Rossa-Feres, D.C. & Jim, J. (2001). Similaridade do sítio de vocalização em uma comunidade de anfíbios anuros na região noroeste do Estado de São Paulo, Brasil. *Revista Brasileira de Zoologia* 18, 439–454.

Roughgarden, J. & Diamond, J.M. (1986). Overview: The role of species interactions in community ecology In *Community Ecology*, 333–343. Diamond, J. and Case, T.J. (Eds).New York, NY:Harper & Row, Publishers, Inc.

Ryan, M.J. (1986). Factors influencing the evolution of acoustic communication: biological constraints. *Brain Behavior and Evolution* 28, 70–82.

Sabagh, L.T. & Carvalho e Silva, A.M.P.T. (2008). Feeding overlap in two sympatric species of *Rhinella* (Anura : Bufonidae) of the Atlantic Rain Forest. *Revista Brasileira de Zoologia* 25, 247–253.

Sampaio, E.V.S.B. (2010). Características e potencialidades In *Uso Sustentável e Conservação dos Recursos Florestais da Caatinga*, 29–48. Gariglio, M.A., Sampaio, E.V.S.B., Cestaro, L.A. and Kageyama, P.Y. (Eds). Brasília, DF:Serviço Florestal Brasileiro.

Santana, A.S. & Juncá, F.A. (2007). Diet of *Physalaemus cf. cicada* (Leptodactylidae) and *Bufo granulosus* (Bufonidae) in a semideciduous forest. *Brazilian Journal of Biology* 67, 125–131.

Santos, E.M., Almeida, A.V. & Vasconcelos, S.D. (2004). Feeding habits of six anuran (Amphibia: Anura) species in a rainforest fragment in Northeastern Brazil. *Iheringia* 94, 433–438.

Santos, J.W.A., Damasceno, R.P. & Rocha, P.L.B. (2003). Feeding habits of the frog *Pleurodema diplolistris* (Anura, Leptodactylidae) in Quaternary sand dunes of the Middle Rio São Francisco, Bahia, Brazil. *Phyllomedusa* 2, 83–92

Schoener, T.W. (1974). Resource partitioning in ecological communities. *Science* 185, 27–39.

Seale, D.B. (1980). Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. *Ecology* 61, 1531–1550.

Simpson, E.H. (1949). Measurement of diversity. *Nature* 163, 688.

Somers, K.M. (1986). Multivariate allometry and removal of size with principal component analysis. *Systematic Zoology* 35, 359–368.

Swenson, N.G., Enquist, B.J., Thompson, J. & Zimmerman, J.K. (2007). The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* 88, 1770–1780.

Ter Braak, C.J.F. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167–1179.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press.

Toft, C.A. (1980a). Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia* 45, 131–141.

Toft, C.A. (1980b). Seasonal variation in populations of Panamanian litter frogs and their prey: a comparison of wetter and drier sites. *Oecologia* 47, 34–38.

Toft, C.A. (1995). Evolution of diet specialization in poison-dart

frogs (Dendrobatidae). *Herpetologica* 51, 202–216

Travis, J. (1983). Variation in growth and survival of *Hyla gratiosa* larvae in experimental enclosures. *Copeia* 232–237

Trueb, L. (1970). Evolutionary relationships of casque-headed tree frogs with co-ossified skulls (family Hylidae). *University of Kansas Publications Museum of Natural History* 18, 547–716.

Velloso, A.L., Sampaio, E.V.S.B. & Pareyn, F.G.C. (2002). *Ecorregiões propostas para o Bioma Caatinga*. Recife: Associação Plantas do Nordeste - Instituto de Conservação Ambiental - The Nature Conservancy do Brasil.

Vences, M., Glaw, F. & Bohme, W. (1998). Evolutionary correlates of microphagy in alkaloid-containing frogs (Amphibia: Anura). *Zoologischer Anzeiger* 236, 217–230.

Vieira, W.L.D., Santana, G.G. & Arzabe, C. (2009). Diversity of reproductive modes in anurans communities in the Caatinga (dryland) of northeastern Brazil. *Biodiversity and Conservation* 18, 55–66.

Vitt, L.J. & Caldwell, J.P. (1994). Resources utilization and guild structure of small vertebrates in the Amazon forest leaf litter. *Journal of Zoology (London)* 234, 463–476.

Vitt, L.J. & Pianka, E.R. (2005). Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Science* 102, 7877–7881.

Webb, C.O., Ackerley, D.D., McPeek, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33, 475–505.

Wells, K.D. (1988). The effect of social interactions on anuran vocal behavior In *The evolution of the amphibian auditory system*, 433–454. Fritzsch, B., Ryan, M.J., Wilczynski, W., Hetherington, T.E. and Walkowiak, W. (Eds).New York, NY:John Wiley and Sons.

Wells, K.D. (2007). *The ecology and behavior of amphibians*. Chicago, IL: The Uninversity of Chicago Press.

Wiens, J.J. (2004). Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution* 58, 193–197.

Wiens, J.J. & Graham, C.H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology Evolution and Systematics* 36, 519–539.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., et al. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13, 1310–1324.

Winemiller, K.O. & Pianka, E.R. (1990). Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60, 27–55.

Zar, J.H. (1998). *Biostatistical Analysis*. Englewood Cliffs, New Jersey: Prentice-Hall, Inc.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D. & Fink, W.L. (2004). *Geometric Morphometrics for Biologists: A Primer*. San Diego, CA, USA: Elsevier Academy Press.

Zimmerman, B.L. & Simberloff, D. (1996). An historical interpretation of habitat use by frogs in a central Amazonian forest. *Journal of Biogeography* 23, 27–46.

Accepted: 11 August 2014