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Acoustic ecology of an anuran assemblage in the arid Caatinga of northeastern Brazil

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Differences in advertisement calls and calling sites are important mechanisms that regulate interactions in anuran assemblages. Individuals might have preferences for ranges of acoustic parameters and calling sites that reduce overlap and ensure coexistence. Herein, acoustic and ecological data were used to investigate the relationships among 12 anurans that co-occur in temporary ponds in the Caatinga, Cabaceiras municipality, Paraíba state, Brazil. Anurans exhibited calling activity correlated with rainfall, but were also spatially dispersed. High overlap levels in calling microhabitats and acoustic parameters were observed, especially among pairs of closely related species. Analysis of null models showed a lack of structure in the spatial and acoustic niche, indicating the lack of detected competition. Results suggest that the calling activity of the species is strongly influenced by rainfall, moreover, the temporal partition appears to ensure coexistence. Finally, strong historical effects were detected in Leiuperinae, Leptodactylidae and in the partition Hylidae–Leptodactyliformes.

Keywords: semi-arid; calling activity; calling microhabitat; null models; ecological factors; historical factors

Introduction

Several factors are considered important for the maintenance of the dynamics and relationships among species in assemblages. Trophic attributes (Péfaur and Duellman 1980; Toft 1980a, 1980b), morphological characteristics (Losos 1990; Leips et al. 2000; Vitt et al. 2000), and position in space (Rossa-Feres and Jim 2001) are often used as tools to evaluate the interaction levels among individuals and are useful in identifying the presence of structure in some dimensions of ecological niches (Hutchinson 1957; Pianka 1973).

In anuran assemblages, specific differences in advertisement calls, combined with the partition in calling sites are considered important mechanisms that regulate the interactions among individuals (Hödl 1977). The ability to vocalize has allowed the development of a complex social system in which the physical and spectral characteristics of calls promote reproductive isolation among species (Wells and Schwartz 1984; Gerhardt and Huber 2002), as well as being useful in the selection of reproductive partners with better skills (Wells and Schwartz 1984; Gerhardt 1991; Baugh and Ryan 2010). Individuals from different species might also show a preference for

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specific calling sites that enhance the chances of spreading sound and reduce acoustic interference (Hödl 1977; Ryan 1988; Santos and Rossa-Feres 2007).

Investigations into acoustic and behavioural aspects of anurans often demonstrate the influence of habitat structure on acoustic parameters and use of calling sites (Kime et al. 2000; Preininger et al. 2007; Boeckle et al. 2009). In addition, spectral and temporal characteristics of advertisement show variation in the intensity and degradation levels strongly correlated with habitat complexity (Ryan 1988; Boeckle et al. 2009). Moreover, less heterogeneous environments might provide a lower availability of breeding sites and tend to increase overlap levels (Vasconcelos and Rossa-Feres 2008). In general, it can be expected that assemblages from less heterogeneous environments will show a high overlap in calling microhabitat use and higher acoustic partition (Hödl 1977; Martins and Jim 2003). In contrast, assemblages from more heterogeneous environments might show a greater segregation in calling microhabitat and a higher acoustic overlap (Cardoso et al. 1989; Bernarde and Anjos 1999).

According to Santos and Rossa-Feres (2007), anuran assemblages might have levels of interactions that involve several niche dimensions. Hence, species that overlap in one niche dimension tend not to share another dimension, revealing the existence of niche complementarity (Schoener 1974; Santos and Rossa-Feres 2007; Silva et al. 2008). In this study, acoustic and ecological data are combined to investigate the niche relationships in an anuran assemblage from the Caatinga region of northeastern Brazil. The aim was to test the hypothesis that non-random patterns in the anuran assemblage of temporary ponds in the Caatinga can be attributed to acoustic partitioning. We addressed the following questions. (1) Does the anuran assemblage of temporary ponds show non-random patterns in calling activity, calling microhabitat use, and acoustic parameters? (2) Do closely related species have a high overlap in resource use due to their phylogenetic proximity? (3) Do species with a high overlap in one niche dimension show niche partitioning in another dimension? (4) Does the level of historical effects vary among clades?

Materials and methods

Study area

This study was carried out from May 2010 to September 2011, on the Junco ranch (07° 29' S; 36°20' W; elevation 462 m), in Cabaceiras municipality, Paraíba state, northeastern Brazil. Located in Caatinga, Cabaceiras is situated in an ecoregion called Depressão Sertaneja Setentrional, also known as Cariri Paraibano, featuring semiarid climate of the BSh type (Velloso et al. 2002). The vegetation in the region is characterized as shrubby Caatinga, with a predominance of low vegetation with dense thorns (Andrade-Lima 1981; Velloso et al. 2002). Cabaceiras is the municipality with the lowest precipitation rate of Brazil (Giulietti et al. 2007), with an annual mean of up to 350 mm of rainfall (Velloso et al. 2002). Due to a variety of geomorphological characteristics such as the presence of mountains and soils with low water holding capacity, severe and prolonged droughts are common in this region (Sampaio 2010).

To collect data, we performed 15 excursions on three consecutive days in each month, totalling 45 days of study. We investigated three adjoining temporary ponds that are in the creek bed of a temporary stream known as ‘Riacho Junco’. As a result of the environmental characteristics, only three temporary ponds maintained sufficient water levels to guarantee the anurans' reproduction. In periods of intense rainfall, ponds are interconnected by narrow waterways. However, as the region is characterized by a short hydroperiod, the ponds were isolated during most of the study period, and dried out completely in June, August and September 2010. Because the temporary ponds from which the records of all investigated species came shared physiognomic and geomorphological similarities, and (during the study) they were a maximum of 20 m distant from each other, we considered the anurans from the ponds to be a single assemblage.

Calling activity

To describe the temporal niche, the species richness of the Cabaceiras assemblage was determined, based on records of calling males (see Zimmerman 1994; Bertoluci 1998). The existence of a relationship among species richness in calling activity on the day of each visit (variable response) and environmental variables was verified through a Spearman correlation, using as environmental variables: (1) air temperature (°C); (2) soil temperature (°C); (3) water temperature (°C); (4) cumulative daily rainfall (mm); (5) accumulated rainfall on the previous day (mm); (6) accumulated rainfall in the previous 2 days; and (7) accumulated rainfall in the 3 days before each visit. The use of the correlation coefficient might reveal abiotic aspects that can create ideal conditions for reproduction, measuring the number of species in vocalization activity on each visit day.

Data for air temperature at breast height, water and soil temperature were measured in the field using a DeltaTrak® thermometer with 0.2°C accuracy. Temperature values used for the Spearman correlation coefficient were obtained by calculating the arithmetic mean of the microhabitat temperatures used by different species, which were or were not in calling activity. Precipitation data were obtained on a macro-spatial scale from the database of *Programa de Monitoramento em Tempo Real da Região Nordeste – Proclima* (www.cptec.inpe.br/proclima).

For the correlation analysis involving water temperature, we used data only from the days when the ponds had water and allowed the measurement of the variable. The Spearman correlation coefficient was performed in the BioEstat 5.0 program (Ayres et al. 2007), with a 0.05 significance level.

Microhabitat of calling frogs

Anurans were identified by actively searching around the temporary ponds from 18:00 h to 00:00 h. For individuals performing vocalization activity, the microhabitat, air temperature at breast height and substrate temperature were recorded, as well as the advertisement call when possible. For analyses of spatial niche, 10 calling microhabitat categories were created: exposed soil, soil between vegetation, grass, shrub, tree, emergent vegetation, partially submerged vegetation, on rock, in hole, and bromeliad. The inverse of the Simpson Diversity Index (Simpson 1949) was used to calculate the niche-breadth of the calling microhabitat (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 the Simpson Diversity Index generated values ranging from 1 to 10, in which 1 corresponded to the exclusive use of only one microhabitat (specialists) and 10 corresponded to the use of all microhabitats in the same proportion (generalists). The overlap in the use of the call sites was calculated by the equation suggested by Pianka (1973):

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

where p represents the proportion of call-site category i, n is the number of categories, and j and k represent the species being compared. Overlap scores range from 0 (no overlap) to 1 (complete overlap). The null model was used to investigate the presence of non-random patterns in the use of call sites (i.e. microhabitat categories) through the Niche Overlap Module of EcoSim (Gotelli and Entsminger 2003). For the Niche Overlap Module, a data matrix was created with species corresponding to lines, microhabitat categories corresponding to columns, and values of each cell representing the use proportion of each microhabitat category. The matrix was subjected to 1000 randomizations to simulate random patterns that would be expected in the absence of an assemblage structure. In the null model, significant values show structure in the assemblage based on the existence of detectible competition and/or phylogenetic conservatism. In contrast, no significant values indicate a lack of competition and the consequent lack of structure in resource use (Gotelli and Graves 1996). Parameters used in the Niche Overlap Module of EcoSim were the 'niche overlap index of Pianka' and 'randomization algorithm two'.

To answer whether closely related species have a high overlap in resource use (microhabitat) due to their phylogenetic proximity, we used a Mantel test using microhabitat and calling parameters overlap and phylogenetic distance, based on a recently published phylogeny (Pyron et al. 2013). In addition, to evaluate whether the level of historical effects varied among clades, we used a Canonical Phylogenetic Ordination (CPO) (Giannini 2003), which analysed the influence of phylogeny on the ecological traits of the anuran species. CPO is a phylogenetic comparison method based on Canonical Correspondence Analysis (Ter Braak 1986). For the CPO, a Y matrix was created with ecological data (microhabitat) and an X matrix was created, containing data of the monophyletic lineages of 11 anuran species (Figure 1). The X matrix is formed by a combination of binary indicators (0 and 1) that represent each monophyletic group. Analyses consisted of creating a subset of intrinsic groups in the X matrix that best explained the data obtained and were expressed in the Y matrix based on the permutations of Monte Carlo and from the null hypothesis of no phylogenetic conservation of spatial niche in the assemblage. CPO analyses were performed using the CANOCO 4.5 program for Windows, using the following parameters: 'Symmetric scaling', 'size in two-dimensional graphic', 'downwieghting for rare species', 'manual selection of environmental variables', '9999 permutations', and 'unrestricted permutations.'

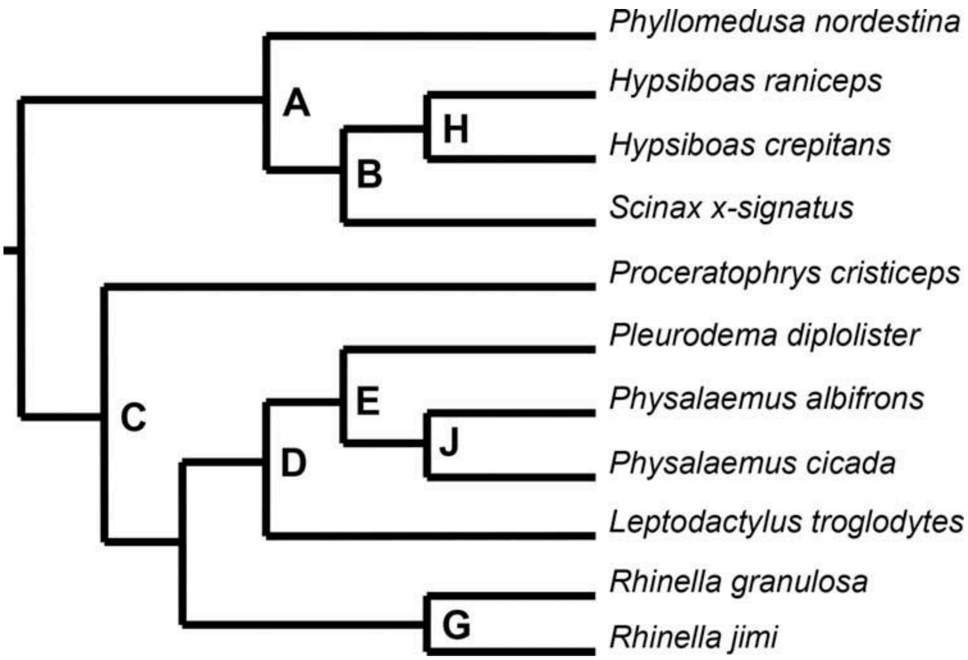

Figure 1. Phylogeny of anurans used in canonical phylogenetic ordination for microhabitat and diet data. Phylogenetic tree based in phylogenies of Nascimento et al. (2005), Ponssa (2008), Pyron and Wiens (2011).

Acoustic analysis

Advertisement calls were recorded with a Marantz PMD660 Professional recorder coupled to a Sennheiser ME66 unidirectional microphone, with an attendance rate of 44 100 Hz and 16-bit resolution in mono standard. For each calling individual, a track of 4 minutes of the advertisement call at a distance of about 1 m was recorded. The terminology used in the acoustic analysis followed the suggestions of Wells (1988), Littlejohn (2001) and Gerhardt and Huber (2002), from the definitions: (1) song –sound unit emitted at regular intervals and might contain one or multiple notes; (2) note–subunit of the call formed after a short period of silence; (3) pulse – smallest unit of acoustic signal.

Calls were digitized and analysed according to their spectral and temporal aspects using Raven Pro 1.3 program. The spectral parameters were obtained using the Discrete Fourier Transformation algorithm and filter with a band of 248 Hz. The temporal parameters were measured from the direct analysis of oscillograms. The following acoustic variables were measured: dominant frequency (Hz); number of notes per call; note duration (ms); call duration (ms); call repetition rate (min^{-1}); inter-call interval (ms); and number of pulses per note. When possible, we tried to collect up to three call series per species, and later calculated the mean and standard deviation and minimum and maximum variation of each acoustic variable to use in the analysis (Appendix 1). The acoustic records were housed in the acoustic collection of the Coleção Herpetológica da Universidade Federal da Paraíba (CHUFPB).

The null model was used to verify the existence of non-random patterns in the use of acoustic space using the Niche Overlap Module of EcoSim (Gotelli and Entsminger 2003), using a data matrix with species corresponding to lines, acoustic variables corresponding to columns, and values of each matrix cell corresponding to the arithmetic mean of each acoustic variable (see Bourne and York 2001). The matrix was reshuffled based on 1000 randomizations, to simulate random patterns that would be expected in the absence of assemblage structure. The existence of structure in the acoustic space is verified by comparison between the mean of the observed overlap and the mean of the simulated overlap, in which a significant p-value indicates the presence of competition regulating the resource use (Gotelli and Graves 1996). The parameters used in the Niche Overlap Module of EcoSim, was the 'niche overlap index of Pianka' and 'randomization algorithm two'.

To answer whether closely related species have a high overlap in resource use (acoustic variables) due to their phylogenetic proximity, we used a Mantel test using calling parameter overlap and phylogenetic distance, based on a recently published phylogeny (Pyron et al. 2013). Additionally, we performed a partial Mantel test between microhabitat and acoustic niche overlap while holding phylogenetic distance constant, based on a recently published phylogeny (Pyron et al. 2013). This approach would test for correlation between two niche matrices while controlling for phylogeny.

Furthermore, to evaluate whether the level of historical effects varied among clades, we used CPO (Giannini 2003), as described for microhabitat use from calling frogs. Since body size could influence the call from frogs, we used snout–vent length (SVL) as a co-variate in the CPO. In addition, to answer whether species with a high overlap in one niche dimension (microhabitat of calling frogs) show niche partitioning in another dimension (acoustic space), we performed a Mantel test with the three niche overlap matrices generated by the Niche Overlap Module of EcoSim (Gotelli and Entsminger 2003), calling site overlap, based on microhabitat used, temporal niche, based on time of year of calling activity and acoustic parameters.

Subsequently, the influence of body size (independent variable) in the dominant frequency of the advertisement call of each species was verified by simple regression analysis using log-transformed data (Log_{10}). Also, cluster analysis was performed using the Euclidean distance to check similarity levels in acoustic parameters among 11 anuran species. In cluster analysis, our expectation was that closely related species would form concise groups, due to the existence of possible phylogenetic influences on the advertisement call. For cluster analysis, the paired groups algorithm (UPGMA) was used in the PAST 2.12 program (Hammer et al. 2001) with log-transformed data (Log_{10}). Simple regression analysis was performed in the BioEstat 5.0 program (Ayres et al. 2007), at the 0.05 significance level.

Results

Temporal niche

Twelve anuran species were registered calling: two bufonids (*Rhinella granulosa* and *Rhinella jimi*); four hylids (*Hypsiboas crepitans*, *Hypsiboas raniceps*, *Phyllomedusa nordestina* and *Scinax x-signatus*), five leptodactylids (*Leptodactylus* cf. *macrosternum*, *Leptodactylus troglodytes*, *Physalaemus albifrons*, *Physalaemus cicada* and *Pleurodema diplolister*) and one odontophrynid (*Proceratophrys cristiceps*). Two

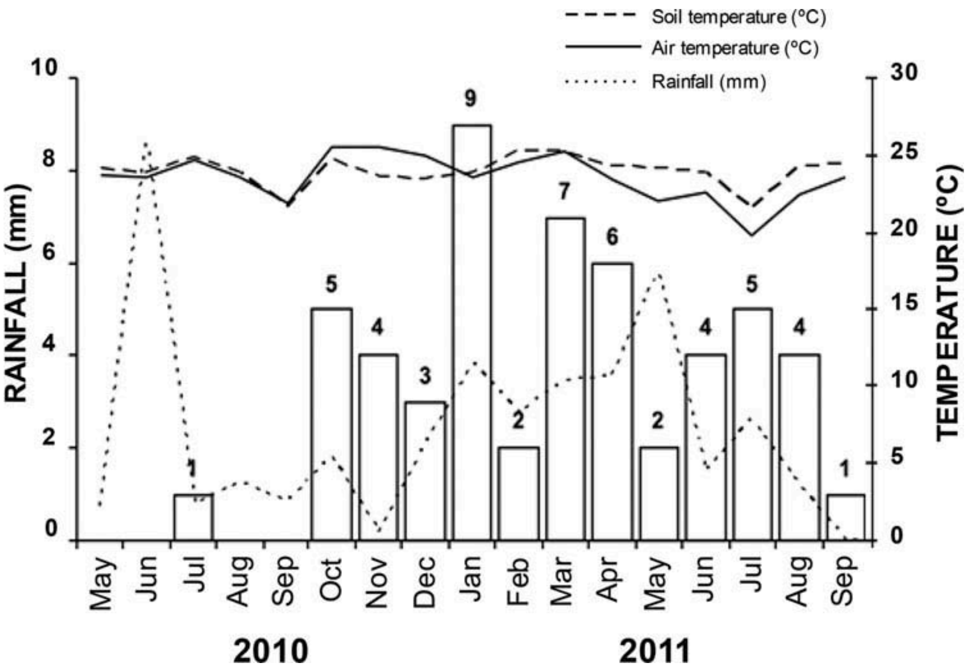

Figure 2. Richness of anuran species and abiotic variables in Cabaceiras assemblage between May 2010 and November 2011. Values above bars represent number of species in calling activity.

other leptodactylids (*Leptodactylus caatingae* and *Leptodactylus fuscus*) and one hylid (*Corythomantis greeningi*) were also registered, but showed no calling activity during our observations. Hence, their calls were not considered in further analyses.

All species initiated their calling activity together with an increase in rainfall (Figure 2), with January being the month with the highest species richness (Table 1). *Scinax x-signatus* and *Phyllomedusa nordestina* had the longest calling activity, calling in eleven and eight consecutive months, respectively. *Pleurodema diplolister* demonstrated the shortest period, calling only during two nights in January, in accordance with its explosive reproduction pattern. *Physalaemus albifrons* and *Physalaemus cicada* had a high overlap in the calling period, with males calling at the same time of the year and forming large reproductive aggregates. *Rhinella granulosa* and *R. jimi* had a partial temporal overlap and called in spaced months, not consecutively.

The richness of calling of active species was correlated with precipitation either on the same day, or one or two days preceding the capture of the frog and the correlation was higher with precipitation on the same day of capture (Table 2), showing that an increase in rainfall is immediately followed by an increase in the number of species vocalizing.

Spatial niche

The calling frogs were found in 10 microhabitats, but most of them showed specialized behaviour (Table 3). Hylids displayed generalist behaviour, with *S. x-signatus* being the species with the broadest niche, followed by *Phyllomedusa nordestina* and

Table 1. Calling activity of 12 anuran species in temporary ponds of Cabaceiras, Paraíba, Brazil.

Species	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Rhinella granulosa						X	X		X			X					
Rhinella jimi						X		X	X		X						X
Hypsiboas crepitans															X	X	
Hyspiboas raniceps												X		X	X	X	
Scinax x-signatus			X			X	X	X	X	X	X	X	X	X	X	X	
Phyllomedusa nordestina									X	X	X	X	X	X	X	X	
Leptodactylus cf. *macrosternum*									X					X	X		
Leptodactylus troglodytes								X	X		X	X					
Physalaemus albifrons						X	X		X		X						
Physalaemus cicada						X	X		X		X						
Pleurodema diplolister									X								
Proceratophrys cristiceps											X	X					

Table 2. Spearman coefficient between species richness in calling activity and abiotic variables.

	No. samples	Coefficient	*T*	*p*
Accumulated rainfall (mm)				
Day of visit	41	0.4827	3.4422	**0.0014**
1 day before the visit	41	0.4210	2.8985	**0.0061**
2 days before the visit	41	0.3356	2.2245	**0.0319**
3 days before the visit	41	0.0417	0.2606	0.7958
Air temperature (ºC)	41	0.0276	0.1725	0.8639
Soil temperature (ºC)	41	0.2386	1.5342	0.1330
Water temperature (ºC)	31	0.3172	1.8010	0.0820

Note: Boldface values represent significant *p*-value ($p < 0.05$).

H. raniceps. Except for hylids, only *R. granulosa* used more than one microhabitat, even so, most of the individuals were on exposed ground. Leptodactylids were very similar in space use, calling when partially submerged, except *L. troglodytes,* which called only on soil among vegetation.

Analysis revealed that type of overlap varied from complete overlap to no overlap among species (Table 4). Calling bufonids showed no overlap in microhabitat. Hylids also showed low values, with higher overlaps between *H. raniceps* and *S. x-signatus* and *H. raniceps* and *Phyllomedusa nordestina*. However, *H. raniceps* called at the end of the rainy season, showing a tendency to partition temporally with the other hylids.

Most leptodactylids had a complete overlap, calling when partially submerged, except *L. troglodytes,* which had a complete overlap with *Proceratophrys cristiceps*. Considering the acoustic and temporal niche, some segregation appears to exist among leptodactylids, with *L.* cf. *macrosternum* calling at a different time period from the other group members. The null model analysis indicated a lack of structure in the assemblage. The observed and expected mean overlaps were 0.33 and 0.32, respectively, and the chance that the observed mean was significantly lower than the expected mean was 0.64.

A Mantel test between the niche overlap matrix based on microhabitat used by calling frogs and phylogenetic distance revealed a non-significant relationship ($r = 0.09905$, $p = 0.301$), indicating that closely related species do not necessarily have a high overlap in microhabitat, corroborating the lack of structure in this frog assemblage. In addition, a CPO based on 9999 Monte Carlo permutations revealed a strong phylogenetic influence in Leiuperinae and the partition between Hylidae and Leptodactyliformes, with the former explaining 28.60% of the total variation and the basal dichotomy (Hylidae and Leptodactyliformes) explaining 24.89% of the total variation (Table 5). This shows that the level of historical effects varies among clades, with some clades more affected by phylogenetic history than others.

Acoustic niche

Anuran advertisement calls were classified into three groups: (1) simple-structured, composed of a single note, formed by *S. x-signatus*, *Physalaemus albifrons*, *Proceratophrys cristiceps* and *L. troglodytes*; (2) intermediate between simple and trill, composed of up to two notes with different spectral characteristics, formed by

Table 3. Abundance by calling microhabitat for 12 anuran species from temporary ponds in Cabaceiras, Paraíba, Brazil.

Species	ES	SBV	HER	SHR	TRE	EV	PS	ROC	HOL	BRO	WCS
Rhinella granulosa	12	4						1			1.80
Rhinella jimi							4				1.00
Hypsiboas crepitans							1				1.00
Hypsiboas raniceps	1	1		2							2.67
Scinax x-signatus	14	13		3	6	7		1	4	2	5.21
Phyllomedusa nordestina	1		5	9	3				1		3.09
Leptodactylus cf. *macrosternum*							3				1.0
Leptodactylus troglodytes		3									1.0
Physalaemus albifrons							15				1.0
Physalaemus cicada							36				1.0
Pleurodema diplolister							4				1.0
Proceratophrys cristiceps		4									1.0

Note: ES, exposed soil; SBV, soil between vegetation; HER, herbacea; SHR, shrub; TRE, tree; EV, emergent vegetation; PS, partially submerged; RO, rock; HOL, hole; BRO, bromeliad; WCS, width of the calling microhabitat.

Table 4. Overlap in calling sites for 12 frog species from temporary ponds in Cabaceiras, Paraíba, Brazil.

Species	*R. j.*	*H. c.*	*H. r.*	*S. x.*	*P. n.*	*L.* cf. *m.*	*L. t.*	*Ph. a.*	*Ph. ci.*	*Pl. d.*	*Pr. cr.*
R. granulosa	0.00	0.00	0.515	0.795	0.088	0.00	0.315	0.00	0.00	0.00	0.315
R. jimi		1.00	0.00	0.00	0.00	1.00	0.00	1.00	1.00	1.00	0.00
*H. crepitans**			0.00	0.00	0.00	1.00	0.00	1.00	1.00	1.00	0.00
H. raniceps				0.615	0.717	0.00	0.408	0.00	0.00	0.00	0.408
S. x-signatus					0.258	0.00	0.593	0.00	0.00	0.00	0.593
P. nordestina						0.00	0.00	0.00	0.00	0.00	0.00
L. cf. *macrosternum*							0.00	1.00	1.00	1.00	0.00
L. troglodytes								0.00	0.00	0.00	1.00
Ph. albifrons									1.00	1.00	0.00
Ph. cicada										1.00	0.00
Pl. diplolister											0.00

Notes: *R. g.*, *Rhinella granulosa*; *R. j.*, *Rhinella jimi*; *H. c.*, *Hypsiboas creptans*; *H. r.*, *Hypsiboas raniceps*; *S. x.*, *Scinax x-signatus*; *P. n.*, *Phyllomedusa nordestina*; *L.* cf. *m.*, *Leptodactylus* cf. *macrosternum*; *L. t.*, *Leptodactylus troglodytes*; *Ph. a.*, *Physalaemus albifrons*; *Ph. ci.*, *Physalaemus cicada*; *Pl. d.*, *Pleurodema diplolister*; *Pr. cr.*, *Proceratophrys cristiceps*. *Species with a single record.

Table 5. Phylogenetic influence in ecology of anurans (microhabitat use of calling frogs and acoustic variables) based in 9999 Monte Carlo randomization.

Group	Variation	%	*F*	*p*
Microhabitat use of calling frogs				
E (Leiuperinae)	0.500	28.60	2.580	0.0345
A/C (Hylidae/Leptodactyliformes)	0.435	24.89	2.169	0.0581
D (Leptodactylidae)	0.347	19.85	1.647	0.0829
J (*Physalaemus*)	0.307	17.56	1.430	0.2078
F (Leptodactylinae)	0.235	13.44	1.054	0.3860
B (Hylinae)	0.178	10.18	0.7740	0.4426
G (Bufonidae)	0.149	8.52	0.6390	0.5994
H (*Hypsiboas*)	0.093	5.32	0.3880	0.8410
Calling variables				
E (Leiuperinae)	0.768	39.43	4.299	0.0020
D (Leptodactylidae)	0.558	28.64	2.723	0.0315
A/C (Hylidae/Leptodactyliformes)	0.433	22.23	1.963	0.0714
J (*Physalaemus*)	0.428	21.97	1.937	0.1180
B (Hylinae)	0.188	9.65	0.7490	0.5295
G (Bufonidae)	0.188	9.650	0.7510	0.6311
H (*Hypsiboas*)	0.077	3.95	0.2910	0.9275

Notes: % represents percentage of the total variation found in each group. For identification of each group see Figure 1.

H. crepitans, *H. raniceps* and *Phyllomedusa nordestina*; and (3) long trill, composed of many similar notes repeated regularly, formed by *R. granulosa*, *R. jimi*, *Physalaemus cicada*, and *Pleurodema diplolister*.

Most species called in frequencies between 1000 and 3000 Hz, showing spectral overlap (Appendix 1). *Physalaemus cicada* had the highest dominant frequency, followed by *L. troglodytes* and *R. granulosa*. *Rhinella jimi* and *H. crepitans* had the lowest dominant frequency. *Physalaemus albifrons* had the highest number of pulses per note and *Phyllomedusa nordestina* the lowest.

Anurans had a strong acoustic differentiation in temporal parameters. *Physalaemus cicada* had the longest call and shortest note, whereas *Physalaemus albifrons* had one of the longest notes. *Phyllomedusa nordestina* produced the shortest note and *H. raniceps* the longest. The null model analysis in acoustic parameters showed a lack of competition, with an observed mean overlap of 0.93 and an expected mean of 0.73, with a probability that the observed mean was lower than the expected mean of 1.0.

A CPO based on 9999 Monte Carlo permutations revealed a strong phylogenetic influence in Leiuperinae and Leptodactylidae, with Leiuperinae explaining 39.43% of the total variation, and Leptodactylidae explaining 28.64% (Table 5). In addition, a Mantel test between the niche overlap matrix based on microhabitat used by calling frogs and acoustic parameters revealed a non-significant relationship (r = – 0.1138, p = 0.835), indicating that species with a high overlap in acoustic niche do not show niche partitioning in microhabitat use for calling, corroborating the lack of structure in this frog assemblage. Furthermore, Mantel tests between the niche overlap matrix based on calling site overlap and acoustic parameters and temporal niche revealed non-significant relationships (calling site versus calling period: $r = 0.1205$, $p = 0.162$; acoustic parameters versus calling period: $r = -0.2122$, $p = 0.913$), indicating that species with a high overlap in acoustic niche and microhabitat do not show niche partitioning in calling period, corroborating the lack of structure in this frog assemblage. Additionally, a Mantel test between acoustic niche overlap and phylogenetic distance revealed a non-significant relationship ($r = -0.080$, $p = 0.718$), indicating that closely related species do not necessarily have a high acoustic overlap, corroborating the lack of structure in this frog assemblage. Finally, the partial Mantel test between microhabitat and acoustic niche overlap while holding phylogenetic distance constant revealed a non-significant relationship ($r = 0.0891$, $p = 0.313$), indicating that when controlling for phylogeny effects, species do not necessarily have a high acoustic and microhabitat overlap, again corroborating the lack of structure in this frog assemblage.

Body size had a significant relationship to the dominant frequency ($F = 7.7985$, $p = 0.0202$), suggesting that restrictions in the dominant frequency are influenced by body size. Despite this, *R. granulosa* and *L. troglodytes* diverged from this pattern, showing an intermediate body size and a high frequency call (Figure 3). Cluster analysis based on Euclidian distances for the seven acoustic variables formed two major groups: (1) containing bufonids and *Physalaemus cicada* with long trill calls; and (2) formed by hylids, the other leptodactylids and the odontophrynid, with single notes and intermediate calls, except for *Pleurodema diplolister*, which was the unique species in this group with long trill calls (Figure 4).

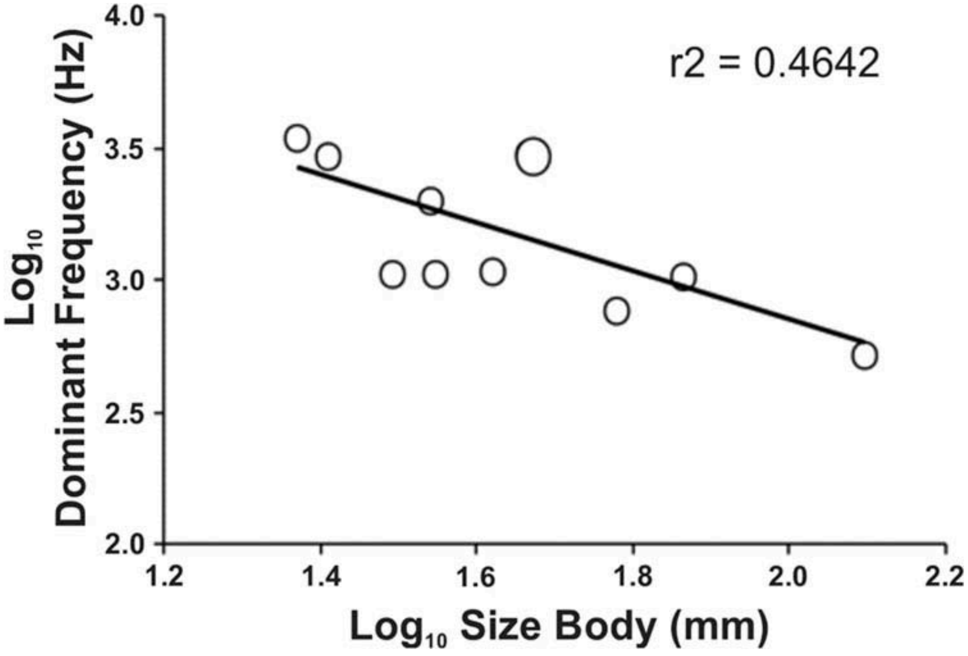

Figure 3. Relations of body size and dominant frequency of 11 anuran species. Small circles represent one species and a big circle represents two species.

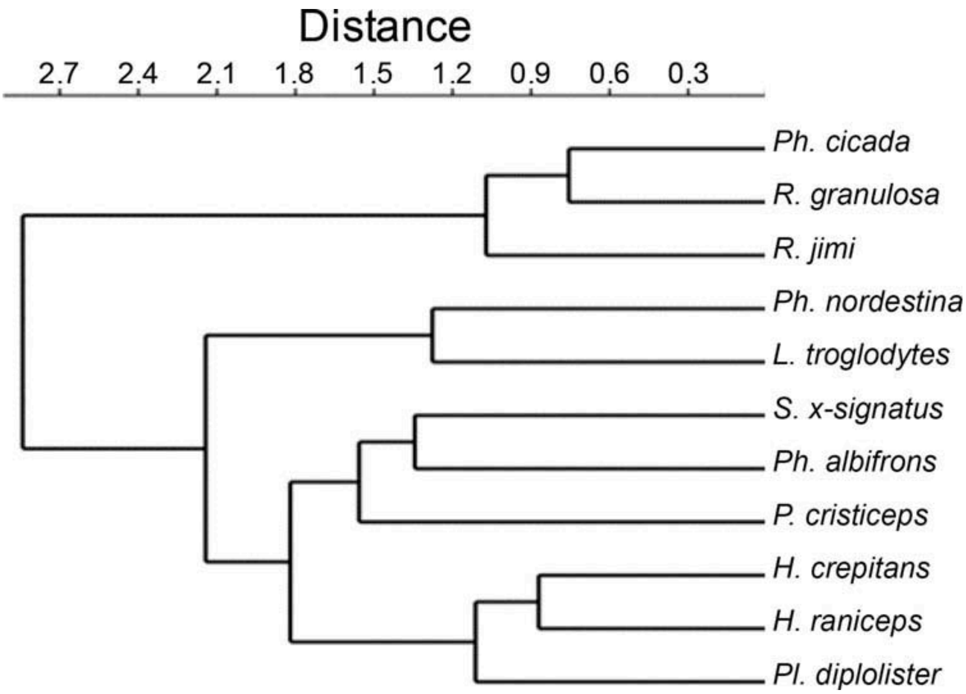

Figure 4. Cluster analysis based in Euclidean distance calculated from mean of seven call parameters of 11 anuran species.

Discussion

Temporal niche

The anuran assemblage of Cabaceiras demonstrated a calling activity similar to that of other tropical assemblages, showing a strong effect of abiotic factors in reproduction (Arzabe 1999; Bertoluci and Rodrigues 2002; Prado et al. 2005). Abiotic factors determine food availability (Toft 1980b), and allow the formation of water bodies with optimum characteristics (Árzabe et al. 1998; Gottsberger and Gruber 2004). In the semi-arid frog assemblages, rainfall effects appear to be greater (Arzabe 1999; Vieira et al. 2007). The lack of correlation between the number of species calling and water and air temperatures in the Cabaceiras assemblage, indicates a secondary effect of these abiotic variables. However, it should be considered that some species might respond differently to variations in temperature (Stebbins and Cohen 1995; Navas et al. 2010). Except for *Phyllomedusa nordestina* and *Scinax x-signatus*, which call for many consecutive months, many species from the Cabaceiras assemblage call intermittently. This behaviour might be associated with an adaptation to avoid interspecific competition among tadpoles by temporal segregation (Bertoluci and Rodrigues 2002). Prado and Pombal (2005) also observed an intermittent vocalization period in a population of *Rhinella ornata* in the Reserva Biológica de Duas Bocas, southeast Brazil, and concluded that it might be a common behaviour in bufonids, and related to historical factors. However, the Cabaceiras assemblage is composed of many phylogenetically distant species, suggesting that this calling behaviour is more related to ecological factors.

Species with a high overlap in calling microhabitat tend to segregate within a temporal niche. This is a clear pattern in the leptodactylids and hylids. Temporal niche partitioning is considered a secondary effect in the structure of anuran assemblages (Pombal 1997; Prado and Pombal 2005; Santos et al. 2007). However, some assemblages appear to have a temporal segregation in reproductive period and avoid competition for reproductive space (Bertoluci and Rodrigues 2002; Gottsberger and Gruber 2004; Prado et al. 2005). In the Cabaceiras assemblage, the calling activity pattern suggests that temporal partition might play an important role in species coexistence.

Spatial niche

Anurans in the Cabaceiras assemblage showed a strong specificity in the use of call sites. Most species made specialized use of this resource, except hylids. The generalist behaviour shown by hylids and the specialized behaviour shown by bufonids, leptodactylids and odontofrynids has been frequently reported in other assemblages (Cardoso et al. 1989; Rossa-Feres and Jim 2001; Prado and Pombal 2005). The plasticity shown by hylids is often associated with morphological aspects of the group (adhesive pads), which allows a vertical stratification that reduces competition with nearby males (Cardoso et al. 1989; Pombal 1997). This pattern is consistent with CPO results, where basal dichotomy between Hylidae and Leptodactyliformes counted for most variation in our data, indicating a historical phylogenetic signal, which appears to be associated with morphology.

Overall, overlap among species in an assemblage might be related to habitat complexity, such as vegetation height and type (Vasconcelos and Rossa-Feres 2008). Heterogeneous habitats (forested areas) provide plenty of niche options and tend to reduce overlap (Cardoso et al. 1989). Consequently, less complex environments (open areas) should show greater overlap in calling microhabitats (Cardoso et al. 1989; Bernarde and Anjos 1999). In addition, spatial niche partitioning also could be related to species richness and abundance of calling males (Cardoso et al. 1989; Santos et al. 2007), which could promote an increase or decrease of intra- or interspecific competition (Wells 1988). According to Santos et al. (2007), abundance fluctuations of calling males during the reproductive period can help to explain high microhabitat niche overlap and should be a common pattern in dry and seasonal areas. This pattern was also found in our study; however, accurate abundance estimates are necessary to solve this issue.

Even though we assume that the Cabaceiras assemblage has a low habitat complexity, since it is located in an open area (see Cardoso et al. 1989), and the short hydroperiod of the temporary ponds limits the number of specific reproductive sites (see Árzabe et al. 1998), the observed behaviour in microhabitat use, coupled with evidence for the lack of structure in the use of call sites, suggest that this resource is not a limiting factor. In addition, restrictions in microhabitat use shown by bufonids, leptodactylids and odontofrynids, might be more associated with restrictions in the evolution of spawning strategies than to adaptations to reproductive isolation (Zimmerman and Simberloff 1996). This is particularly evident in Leiuperidae, where males called partially submersed, a behaviour that is strongly associated with reproduction using foam nests (Vieira et al. 2009), suggesting a strong historical influence.

Acoustic niche

The high acoustic overlap, coupled with the lack of assemblage structure, suggests an absence of competition regulating the use of acoustic space in the Cabaceiras assemblage. However, species with similar acoustic parameters tend to vocalize in different periods of the year and species with different acoustic parameters tend to overlap in their temporal and/or spatial niches, suggesting adaptation to avoid acoustic interference (Schwartz and Wells 1983). Sympatric species can show differences in acoustic parameters to ensure communication (Martins and Jim 2003), an effect that is more evident in assemblages in open areas, which are usually affected by habitat structure (Cardoso et al. 1989; Santos and Rossa-Feres 2007).

The similarity in the advertisement call of *H. crepitans* with *H. raniceps* and of *R. granulosa* with *R. jimi* suggests that the advertisement call is very conservative. As expected, the advertisement call of bufonids was frequently a trill and finished abruptly (Salas et al. 1998; Tárano 2010; Guerra et al. 2011). *Hypsiboas* also produced an intermediate call in the central Amazon (Hödl 1977), suggesting an historical influence. Conversely, the CPO revealed a significant historical effect in Leiuperinae and Leptodactylidae, with a decrease of explained variation by the CPO in the most derived clades in the tree. This could indicate possible character displacement in advertisement calls, which promotes the recognition of males by conspecific females and also allows coexistence (Brown and Wilson 1956; Gerhardt 1994). However, an analysis of other sympatric and allopatric populations is essential for a more precise interpretation of this trend. The anurans that called synchronically also tended to demonstrate regularly timed calls, possibly to avoid overlap. Males changed the call timing in an attempt to minimize acoustic interference with close conspecifics and heterospecifics (Schwartz and Wells 1983; Wells 1988), which increased sound propagation and recognition by females (Ryan 1988).

As stated in many studies (Duellman and Pyles 1983; Ryan 1986), call frequencies are highly influenced by body size. Large frogs have modifications in the larynx that promote low frequency calls (Ryan 1988), showing a strong effect of morphology on the advertisement call structure in most assemblages. However, noises caused by other males or the environment might induce advertisement calls with dominant frequencies that reduce acoustic interference (Preininger et al. 2007; Boeckle et al. 2009). This might explain why some species in the assemblage had dominant frequencies of approximately 2000 Hz.

In anurans, females are frequently more receptive to advertisement calls with lower dominant frequencies and higher numbers of pulses and harmonics (Gerhardt 1994; Bernal et al. 2009). Considering sympatric species, the interference of heterospecific acoustic signals appears to exert different effects on a female’s recognition, varying among species (Marshall et al. 2006). In addition, the recognition can be also associated with the overlap level of the acoustic signal, in other words, the lower the acoustic overlap among species, the greater are the chances of signal recognition within species (Marshall et al. 2006). These factors could explain the absence of a clear acoustic structure in our study.

Many studies have been performed with frog assemblages (Hödl 1977; Salas et al. 1998; Bourne and York 2001; Martins and Jim 2003; Santos and Rossa-Feres 2007) and evidence of acoustic partitioning has been frequently observed. However, few studies tested hypotheses based on null models, which increases the risk of type I error in the data sets (Chek et al. 2003). We highlight two possible explanations for the lack of structure in acoustic space in the Cabaceiras assemblage. First, the resource (space) is abundant and the species do not compete in acoustic space. Therefore, the lack of structure in acoustic space might be due to the small niche overlap between species. Considering the high overlap in calling microhabitat and the existence of a positive correlation between acoustic partitioning and species richness (Chek et al. 2003), the lack of acoustic structure can be related to the small number of species engaging in calling activity in the Cabaceiras assemblage. Alternatively, acoustic competition might occur, but is not manifested in call differences. Competition for acoustic spaces can guide males to adjust the timing of advertisement calls, or attract females with preferences for other sound attributes as a strategy to reduce overlap and allow coexistence (see Chek et al. 2003). The investigation of other aspects of the temporal and spatial niche, such as the distance to the edge of the pond, the position within the calling microhabitat and the perch height (Rossa-Feres and Jim 2001), and the period of reproductive activity (Bertoluci and Rodrigues 2002), might help to determine the niche relationships of the species of the Cabaceiras assemblage.

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Supplemental material

Supplemental material for this article can be accessed here.

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