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ESTRUTURA TEMPORAL E ESPACIAL DE COMUNIDADES DE ANUROS EM RIACHOS DE MATA NA RPPN SERRA DO CARAÇA (CATAS ALTAS, MINAS GERAIS)

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Introdução geral

Comunidades são agrupamentos de espécies moldados por interações bióticas (Pianka 1973) que coexistem no espaço e no tempo (Begon *et al.* 1996). O principal objetivo de estudos de ecologia de comunidades é identificar como os fatores abióticos e bióticos determinam a distribuição e abundância das espécies (Norton 1991).

A coexistência de espécies em uma taxocenose é possibilitada, dentre outros fatores, pela partição de recursos disponíveis no ambiente (Blair 1961, Duellman e Pyles 1983, Aichinger 1987, Cardoso *et al.* 1989, Haddad e Sazima 1992, Pombal 1997, Eterovick e Sazima 2000, Eterovick e Barros 2003), que é determinada tanto pelos fatores ecológicos quanto históricos, uma vez que espécies relacionadas filogeneticamente costumam apresentar os mesmos nichos ecológicos (Cadle e Greene 1993). Duellman (1989) sugere ainda que para explicar o padrão observado na partilha de recursos deve-se levar em consideração, além desses fatores, a própria história do ambiente. A existência ou a aparente falta de padrões na estrutura das comunidades podem refletir condições climáticas, geológicas ou outras forças que atuaram no passado e que não agem mais nos dias atuais (Ricklefs 1987).

A partilha de recursos pode ser influenciada pelas preferências das espécies (Wisheu 1998) em relação a alimentação, uso do espaço e época de atividade (Pianka 1973), e resulta de necessidades fisiológicas dos organismos e interações bióticas dentro do ecossistema (Zweimüller 1995).

A segregação das espécies nas comunidades pode ocorrer em função da estrutura da vegetação, da durabilidade dos riachos (temporários ou permanentes) e da movimentação da água (lótico ou lêntico) (Bernarde e Anjos 1999), a escolha destes locais de reprodução pelas espécies de anuros está relacionada com adaptações morfológicas, fisiológicas e comportamentais (Crump 1971, Pough *et al.* 1977, Cardoso *et al.* 1989). Além dessas diferenças no ambiente para reprodução (Rossa-Feres e Jim 1994), há diferenças nos sítios (Duellman 1967, Cardoso *et al.* 1989), na temporada e no turno de vocalização (Cardoso e Haddad 1992, Rossa-Feres e Jim 1994, Pombal 1997) que também podem determinar a partilha de recursos. A variedade de modos reprodutivos tem implicações diretas na diversidade de espécies ocupando uma determinada área e na utilização dos recursos ambientais (Crump 1982). Diferenças na utilização desses recursos podem reduzir a competição e permitir que uma maior variedade de espécies consiga coexistir (MacArthur 1972).

A coexistência entre as espécies é possível não só por elas apresentarem padrões distintos quanto à ocupação ambiental, mas também porque demonstram distribuição estacional diferenciada (Duellman 1978). Heatwole (1982) indica que, para anfíbios, o padrão sazonal parece ser mais importante que o espacial no processo de isolamento reprodutivo.

As variáveis ambientais precipitação, temperatura (Toft e Duellman 1979) e nível dos corpos d'água influenciam o comportamento dos anuros (Heyer *et al.* 1994). A época do ano e a duração do período de atividade das espécies são determinadas principalmente pela temperatura nas regiões temperadas e pela precipitação nas regiões tropicais e sub-tropicais (Duellman e Trueb 1994), mas deve-se considerar a partilha temporal como um mecanismo secundário de isolamento reprodutivo porque, em geral, as espécies neotropicais apresentam grande sobreposição na estação chuvosa e não hibridizam (Blair 1961), desta forma o espaço acústico poderia ser o fator de maior importância como determinante deste isolamento (Pombal 1997, Bernarde e Anjos 1999).

Diversos registros de declínios levaram à hipótese de que os anfíbios sofrem com maior intensidade do que outros grupos de vertebrados os efeitos das mudanças ambientais impostas pelos homens (Beebee 1996). Há possibilidade de que o desaparecimento de populações de anuros reflita degradação do ambiente, e este fenômeno parece estar ocorrendo em escala mundial (Vitt *et al.* 1990, Lips 1998, Houlanhan *et al.* 2000). Entretanto faltam evidências sobre a verdadeira causa de muitos declínios, principalmente pela falta de conhecimento sobre a ecologia das espécies, sobretudo na região tropical (Beebee 1996).

A grande diversidade de ambientes existentes no estado de Minas Gerais, aliada a um panorama neotropical, possibilitam a ocorrência de uma alta diversidade de anfíbios, ultrapassando 200 espécies, o que representa cerca de 1/3 do total registrado para o país (Costa *et al.* 1998, SBH 2005).

Estudos abordando partilha de recursos em comunidades de anuros na região sudeste do Brasil incluem os trabalhos de Cardoso *et al.* (1989), Cardoso e Haddad (1992), Nascimento *et al.* (1994), Rossa-Feres e Jim (1994), Pombal (1997), Feio *et al.* (1998), Eterovick e Sazima (2000), Bertoluci e Rodrigues (2002a, 2002b), Eterovick e Barros (2003). Heyer *et al.* (1988) indicam a necessidade de estudos sobre a anurofauna nesta região não só pela diversidade de ecossistemas encontrados, mas também devido à descaracterização ambiental que a região vem sofrendo, decorrente de eventos naturais ou provocados pela ação humana. A elaboração de estratégias de conservação depende de uma boa base teórica, ou as medidas tomadas podem ser ineficazes (Beebee 1996).

Este estudo foi realizado com o objetivo de verificar aspectos da estrutura espacial e temporal em comunidades de anuros na RPPN Serra do Caraça (Catas Altas, MG). No capítulo 1, a distribuição das espécies pelos riachos foi relacionada com o volume de cada riacho e a distribuição temporal relacionada com fatores climáticos (temperatura e pluviosidade). O capítulo 2 aborda o uso espacial com base na diversidade de microambientes e seu uso pelos anuros.

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CAPÍTULO 1

Spatial and temporal distribution of anuran amphibians in streams at the RPPN Serra do Caraça, southeastern Brazil

Resumo

A comunidade de anuros da RPPN Serra do Caraça, localizada no município de Catas Altas (MG), foi estudada no período de agosto de 2003 a outubro de 2004 em oito riachos permanentes de mata. Foram registradas 19 espécies de anuros pertencentes a quatro famílias: Bufonidae (10.53%), Centrolenidae (5.26%), Hylidae (63.16%) e Leptodactylidae (21.05%). Houve uma relação negativa significativa entre o número de espécies presentes e o volume dos riachos. Não houve uma relação entre os fatores abióticos (precipitação e temperatura) e a diversidade de espécies por mês e a diversidade de espécies vocalizando, mas os anuros apresentaram diferenças quanto à distribuição temporal. Das 19 espécies encontradas, 12 apresentaram atividade de vocalização e para 10 espécies foram encontrados indícios de atividade reprodutiva como fêmeas ovadas, pares em amplexos, desovas, girinos e jovens recém metamorfoseados. O tamanho dos riachos parece ser um importante fator determinando a riqueza de espécies de anuros local, a relativa estabilidade climática dos riachos de mata favorecem as espécies de anuros com período reprodutivo longo bem como o aumento do período reprodutivo de espécies mais flexíveis.

Palavras chaves: Anfíbios anuros, distribuição temporal, fatores abióticos.

Abstract

Anuran communities were studied at eight permanent forest streams located in the Reserva Particular do Patrimônio Natural (RPPN) Serra do Caraça, municipality of Catas Altas, Minas Gerais state, southeastern Brazil, from August 2003 to October 2004. A total of 19 anuran species was recorded in four families: Bufonidae (10.53%), Centrolenidae (5.26%), Hylidae (63.16%), and Leptodactylidae (21.05%). Number of species present in the streams was negatively related to stream volume. Rainfall and mean monthly temperatures were not related to anuran species diversity or diversity of species with calling males per month, though species differed in their temporal distributions. From the 19 species recorded, 12 exhibited calling activities during the study period and 10 were assumed to have reproduced based on records of gravid females, amplexed pairs, egg clutches, tadpoles, or post metamorphic froglets, considered as indicatives of reproduction. Stream size seems to be an important factor determining local anuran species richness, while the relatively stable climatic conditions of forested sites seems to favor anuran species with long breeding periods as well as the increase of breeding periods of more flexible species.

Key Words: Anura, temporal distribution, abiotic factors

Introduction

The co-existence among populations of different species at a given site is possible due to specific behavior and interspecific interactions that influence social organization, spatial and temporal distribution (MacNally, 1979), contributing to a higher local species diversity. Competition, predation, and factors independent of biotic interactions, such as specific requirements, were considered as the main forces shaping anuran communities by Toft (1985).

The Theory of Island Biogeography predicts the number of species to increase with area and decrease with isolation level of an island (MacArthur and Wilson, 1967), what may happen, for instance, because larger areas may include a larger variety of habitat types and resources (Williams, 1964). Zimmerman and Bierregaard (1986) found species-area relationships to be of little importance in anuran communities at Central Amazon, the availability of suitable reproductive sites being the most important factor determining most species distribution. Considering size variation within a given type of reproductive site, Heyer et al. (1975) hypothesized tadpole species richness to be higher at ponds of intermediate size, due to a trade-off between pond permanency and predation pressures.

Environmental heterogeneity is important to determine the number of species that can use a given habitat (Cardoso et al., 1989), so that higher species richness can be expected in an area with more microhabitats and ecological niches (MacArthur, 1968). In anurans, different reproductive modes may occur among sympatric species (Duellman, 1989) and aid to resource partitioning. Shared resources may include calling sites, oviposition sites, acoustic space, annual and daily calling periods (Crump, 1971; Hödl, 1977; Cardoso and Haddad, 1992; Pombal, 1997). During the larval stage, anurans may differ in habitats and microhabitats used food type and size, daily and annual activity periods (Wild, 1996). The diversity of reproductive modes directly influences species diversity and patterns of resource use (Crump, 1982). When partition of resources related to reproduction fail or do not exist, species hybridization may take place (Haddad et al., 1990; Haddad et al., 1994; Pombal, 1997).

In temperate regions, temperature is the main abiotic factor controlling anuran reproductive activities, while rainfall assumes a greater importance in tropical regions (Duellman and Trueb, 1994). Anuran communities occurring at sites with low annual humidity variations include several species that reproduce continuously or sporadically throughout the year (Crump, 1974; Duellman, 1978; Wiest, 1982). At seasonal neotropical sites, the occurrence of two well defined seasons, a dry and a wet one, is expected to promote some variation regarding anuran species temporal distribution.

Studies on anuran communities are scarce in Brazil once we consider the great amphibian richness in the country (775 species; SBH, 2005) and are badly needed for conservation purposes (Eterovick et al., 2005). Knowledge on abiotic factors that influence the structure of anuran communities may be important to understand how species can keep co-existing and how human influence may disturb their assemblages. Such knowledge is badly needed once several amphibian populations are suspected to be declining in Brazil (Eterovick et al., 2005), as well as many other countries (Lips, 1998; Lips et al., 2003; 2004; Young et al., 2001; 2004).

Attempting to improve the knowledge on neotropical amphibian community organization, we aimed to (1) determine the species composition of anuran communities occurring at eight streams at the RPPN Serra do Caraça, (2) test whether local species richness is influenced by stream volume, (3) test whether abiotic factors such as rainfall and temperature influence the temporal distribution of species activities, and (4) look for patterns of seasonal variations in community composition.

Study site

The Reserva Particular do Patrimônio Natural (RPPN) Serra do Caraça is located in the municipality of Catas Altas (20º 05'S, 43º 29'W), Minas Gerais state, southeastern Brazil. The reserve includes 10187.89 ha in the southern portion of the Espinhaço mountain range, between 850 and 2070 m above sea level (Fig. 1). The region is formed by the orographic systems of Minas Gerais and Bahia states (Derby 1966), representing a contact zone between the Cerrado and Atlantic Forest biomes in its southern portion and a transition zone between both biomes in its northern portion (Giulietti and Pirani 1988, Giulietti *et al*. 1997).

The region has two seasons, a dry from April to September and a wet, from October to March (Fig. 2).

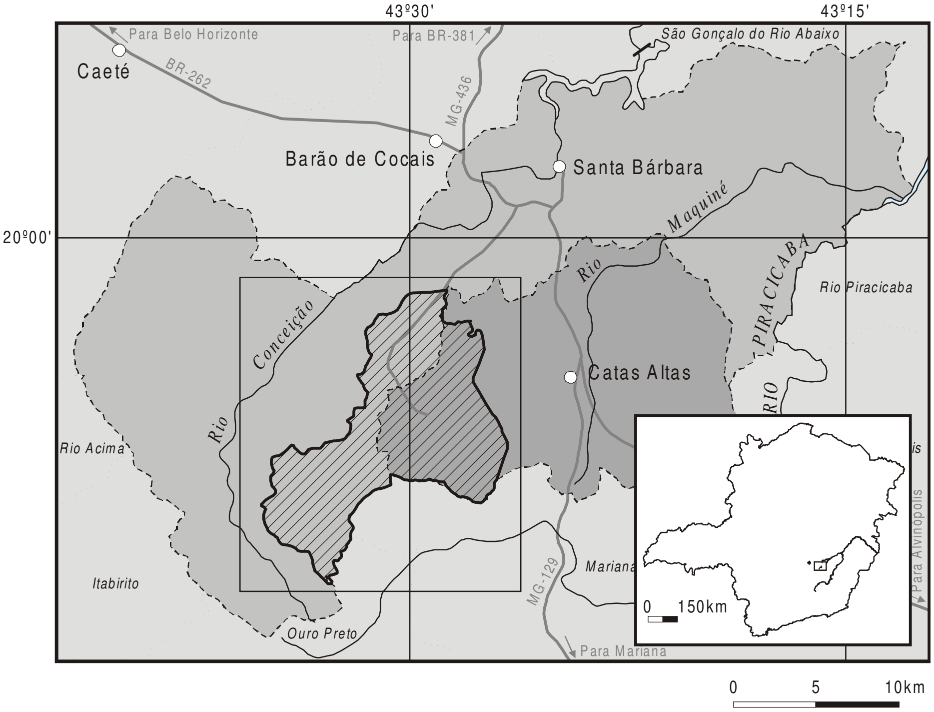

Figure 1. Location of the RPPN Serra do Caraça in Minas Gerais state, southeastern Brazil.

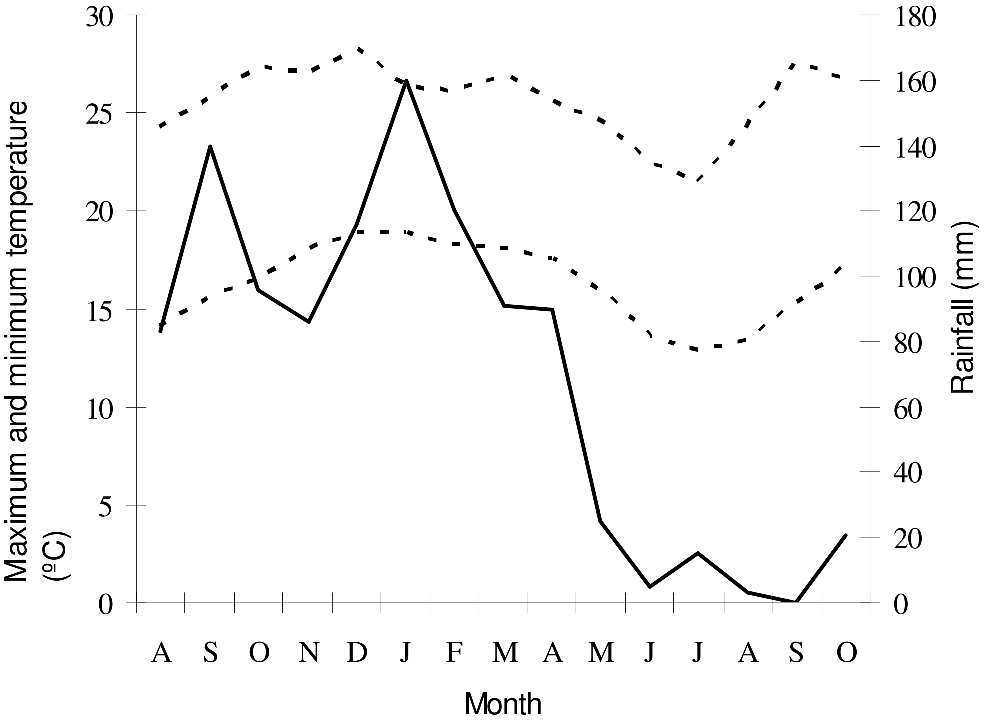

Figure 2. Mean monthly rainfall (solid line), maximum and minimum temperatures (dotted lines) at the RPPN Serra do Caraça, southeastern Brazil, from August 2003 to October 2004.

Methods

The inventory of anuran species in the studied streams was conducted through monthly three-day samplings from August 2003 to October 2004. Anuran species were searched for during the day (diurnal frogs and tadpoles) and at night (nocturnal species; from sunset to about 11:00 pm). Eight permanent forest streams with varied widths and water volumes were sampled (Fig. 3) throughout 150 m sections marked along their courses.

Data on maximum and minimum temperatures were obtained from the Meteorological Station of João Monlevade municipality (Minas Gerais state) located 47.5 km from the study site. Air and water temperatures and rainfall were measured in the field with a thermometer (to the nearest 0.5° C) and a rain gauge, respectively.

Adult anurans were located through visual search or auditory inspection for their calls. Gravid females, amplexed pairs, egg clutches, tadpoles, and post metamorphic froglets were considered as indicatives of the occurrence of reproduction at the site.

Species that could not be identified in the field had some individuals collected and fixed following Heyer *et al.* (1994), for posterior identification. Specimens were deposited in the herpetological collection of the Museu de Ciências Naturais of the Pontifícia Universidade Católica de Minas Gerais.

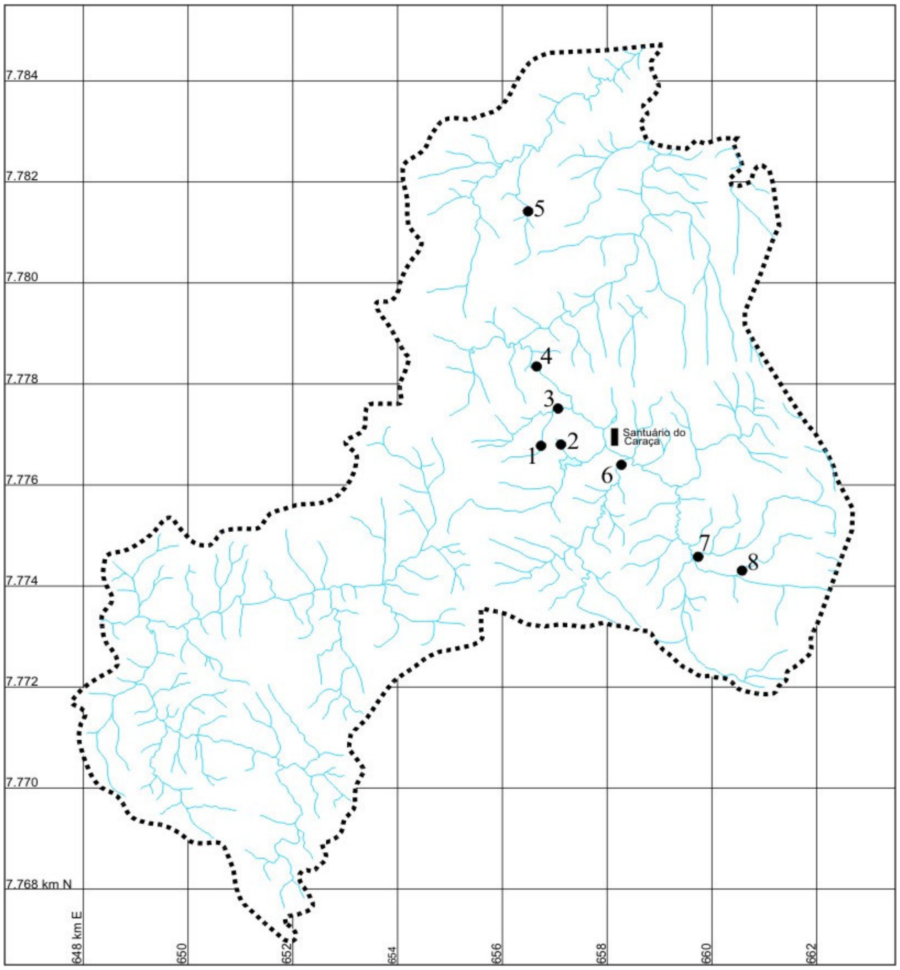

Figure 3. Location of the eight sampled streams at the RPPN Serra do Caraça (Catas Altas municipality, Minas Gerais state, southeastern Brazil).

To estimate monthly species diversity (H) we used Shannon' s diversity index (Pielou 1975):

$$H = - \sum pi \log_n pi$$

where *pi* represents the proportion of individuals of species "i" recorded per month, in relation to total number of individuals recorded in the month considered.

Stream volume was estimated multiplying the length of the sampled section (150 m) by mean stream width and depth. Mean stream width was calculated based on ten measurements (taken every 15 m in the sampled section) and mean stream depth was calculated based on 75 measurements (taken every 2 m in the sampled section, at varied distances from the right margin: 1/6, 1/3, 1/2, 2/3, and 5/6 stream width at the measured point). The number of anuran species present and the number of species calling in each stream were related to stream volume using adjustment curves (Zar 1999). Data normality was tested for through residual analyses.

To evaluate the relationships among mean air and water temperatures, monthly rainfall and species diversity per month, as well as diversity of species with calling males per month, we used multiple linear regressions (Zar 1999). All the statistical tests were conducted using the software BioEstat (BioEstat 2003).

Results

During the study period, we recorded 19 anuran species in the families Bufonidae (10.53%), Centrolenidae (5.26%), Hylidae (63.16%), and Leptodactylidae (21.05%) at the RPPN Serra do Caraça (Table 1). Species distribution was not uniform among streams, Stream 5 (see Fig. 3) being the one with the greatest species richness (n = 9) and Stream 6 sheltering only *Hylodes uai* (Table 1).

Anuran species richness was negatively related to stream volume ($R^2 = 0.760$, $F = 23.166$, $p < 0.004$, Fig. 3A). Residuals of the relationship between species richness and stream volume showed that data had normal distribution ($p = 0.668$). By the other side, the residuals of the relationship between species with calling males and stream volume indicated that data did not have normal distribution ($p = 0.010$), maybe due to the lower sample size, so it was not possible to analyse these data. Therefore, a tendency of increase in the number of species with calling males with the decrease of stream volume could be noticed (Fig. 5), as it happened with total number of species.

Table 1. Distribution of 19 anuran species in eight forest streams (S1 - S8) and estimated volume of sampled stream sections at the RPPN Serra do Caraça, southeastern Brazil.

Species	S1	S2	S3	S4	S5	S6	S7	S8
Bufonidae								
Bufo pombali Baldissera, Caramaschi & Haddad, 2004		X			X			
Bufo rubescens Lutz,1925			X					
Centrolenidae								
Hyalinobatrachium cf. *eurygnathum*	X							
Hylidae								
Hyla albopunctata Spix, 1824	X							
Hyla sp. (gr. *circumdata*)		X		X	X			
Hyla faber Wied-Neuwied, 1821		X			X			
Hyla martinsi Bokerman, 1964	X		X	X	X		X	X
Hyla minuta Peters,1872					X			
Hyla nanuzae Bokermann & Sazima, 1973	X	X		X	X			
Hyla polytaenia Cope, 1868					X			
Phyllomedusa burmeisteri Boulenger, 1882					X			
Scinax luizotavioi (Caramaschi & Kisteumacher, 1989)		X	X	X	X		X	
Scinax machadoi (Bokermann & Sazima, 1973)	X		X				X	X
Scinax aff. *Perereca*	X	X						
Scinax sp. (gr. *ruber*)		X						
Leptodactylidae								
Crossodactylus sp.	X		X	X			X	
Hylodes uai Nascimento, Pombal & Haddad, 2001	X	X		X		X	X	X
Physalaemus aff. *olfersii*				X				
Proceratophrys boiei (Wied-Neuwied, 1824)				X				
Species richness	8	8	5	8	9	1	5	3
Estimated volume of sampled section (m^3)	47.08	17.27	118.44	19.37	72.18	235.63	104.02	283.66

Species diversity was not related to monthly rainfall or mean air and water temperatures ($R^2 = 0.077$, $F_{3,11} = 1.3887$, $p = 0.298$). Diversity of species with calling males was not related to these climatic parameters either ($R^2 = 0.1862$, $F_{3,11} = 2.0679$, $p = 0.162$).

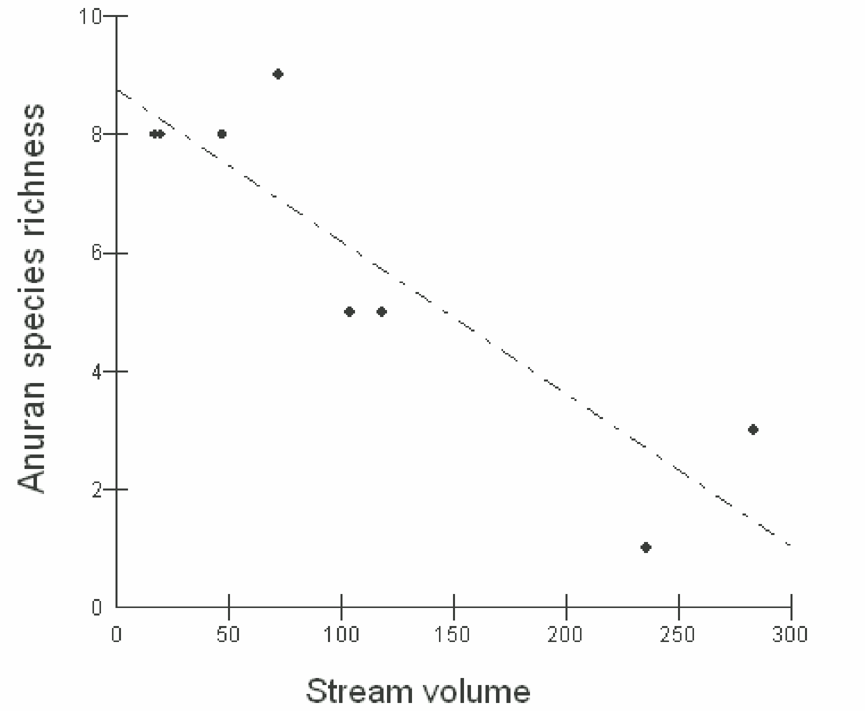

Figure 4. Relationship between estimated volume of stream sampled sections (m^3) and anuran species richness at the RPPN Serra do Caraça, southeastern Brazil.

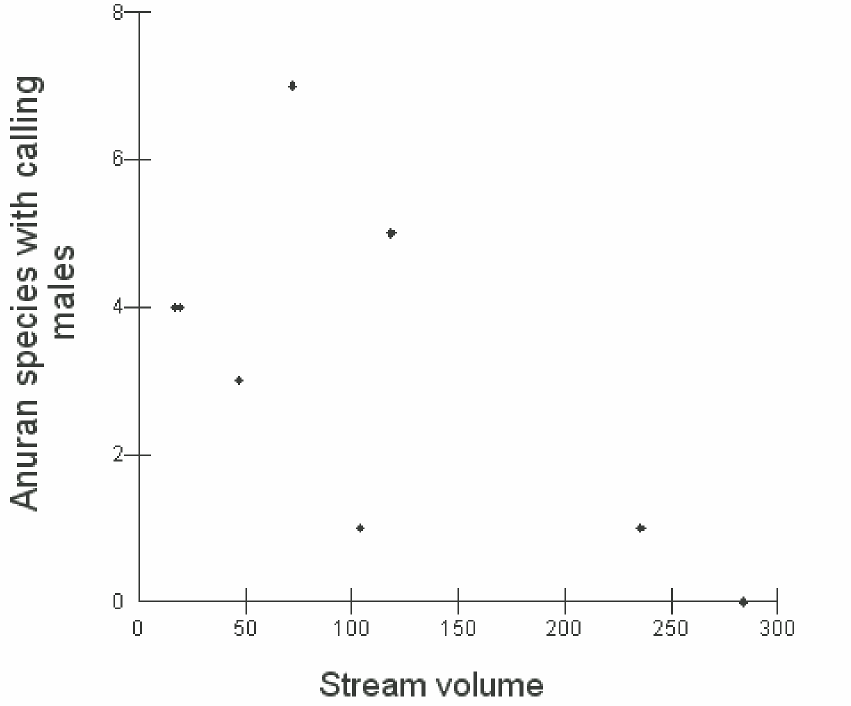

Figure 5. Relationship between estimated volume of stream sampled sections (m^3) and number of anuran species with calling males at the RPPN Serra do Caraça, southeastern Brazil.

From the 19 anuran species recorded at the studied streams, 12 were observed in calling activities (Table 2). Some species showed prolonged calling periods, such as *Hyla minuta*, *H. nanuzae*, *Scinax luizotavioi* and *Crossodactylus* sp.. For these species, calling males were recorded year-round. Other species were opportunistic, being active in periods with suitable climatic conditions throughout the year, such as *Bufo pombali*, *Hyla faber, H. martinsi,* and *H. polytaenia,* which chose the hottest and wettest period; *Hylodes uai*, which was active by the end of the rainy season and the onset of the dry season, and *Proceratophrys boiei*, which called with the first rains of the year (Table 2). Data obtained for *Phyllomedusa burmeisteri* and *Hyalinobatrachium* cf. *eurygnathum* were not enough to determine specific activity periods due to small sample size.

Although emission of mating calls may be considered as an indicative of reproduction by some authors, the occurrence of calling activities does not necessarily mean that the species reproduced or will actually reproduce (Cardoso and Haddad, 1992). Thus, we preferred to be conservative and not to consider calling males as an indicative of a species reproduction. We then detected reproductive activities for 10 species: *Bufo pombali*, *Hyla* sp. (gr. *circumdata*), *H. faber*, *H. martinsi*, *H. nanuzae*, *Scinax machadoi*, *Scinax* sp. (gr. *ruber*), *S. luizotavioi*, *Crossodactylus* sp. and *Hylodes uai* (Table 2).

Inferences could not be made on the temporal distribution of reproductive activities of *Bufo pombali, Hyla* sp. (gr. c*ircumdata*), *H. faber*, *Scinax* sp. (gr. *ruber*) and *Hylodes uai* due to the small number of individuals recorded for these species.

Table 2. Activities and life stages recorded for the anuran species at the RPPN Serra do Caraça, southeastern Brazil, from August 2003 to October 2004: (•) silent individuals; (M) calling males; (F) gravid females; (a) amplexed pairs; (*) egg clutch; (T) tadpoles, and (fr) post metamorphic froglet.

Species	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Bufo pombali	**T**	•	**MT**	**M**	**M**					•					
B. rubescens			•					•							
Hyalinobatrachium cf. *eurygnathum*					**M**			**M**							**M**
Hyla albopunctata														•	
Hyla sp. (gr. *circumdata*)	•	•			**F**		**F**						•		
Hyla faber			**M**	**M**	**M**	**M**	**M**								**M a**
H. martinsi	**T**	•**T**	**MFT**	**MT**	**MT**	**MT**	**FT**	**T**	•**T**	**T**	•**T**	•**T**	**T**	•**T**	**T**
H. minuta	**M**	**M**	**M**	**M**	**M**	**M**	**M**	**M**	**M**	**M**	**M**	**M**	**M**	**M**	**M**
H. nanuzae	•	**M**	**M**	**Mfr**	**MF**	**fr**	**M**	**MF**	**MF**	**M**	**M**		**MF**	**MF**	**Mfr**
H. polytaenia	•		**M**	**M**	•	•	**M**	•							•
Phyllomedusa burmeisteri				**M**											**M**
Scinax aff. *perereca*	•														
S. machadoi	**T**	**T**	**T**	**T**	•**T**	**T**	**T**	•**T**	**T**	**T**	**T**	**F**	**T**	**T**	•**T**
Scinax sp. (gr. *ruber*)			**F**												
S. luizotavioi	**M**	**MF**	**M**			**M**	**M***	**M**	**MF***	**MFfr**	**M**	**M**	**MF**	**MF**	**M**
Crossodactylus sp.	**MT**	**MT**	**MFT**	**MFT** **fr**	**MFT**	•**T**		**MFT**	**MFT**	**MFT**	**MFT**	**MFT**	**MFT**	**MFT**	**MFT**
Hylodes uai	**T**			**T**	**T**		**T**	**MT**	**M**	**M**	**T**				
Physallaemus aff. *olfersii*								•							
Proceratophrys boiei	**M**	**M**	**M**												**M**

Discussion

Density of vegetation cover along stream margins constitute an important factor influencing choice of reproductive sites by anurans (Werner and Glennemeier, 1999). The greatest proportion of hylids recorded in the streams may be related to the highest diversity of calling sites available for this group, since the presence of all vegetation strata provides several microhabitats to be explored by these climbing treefrogs. The presence of adhesive discs at hylid fingertips adapts species of this family to explore the vegetation vertically (Cardoso et al., 1989), besides being able to explore also other microhabitats such as rocks and leaf litter, as other frogs do.

The differential use of sampled streams by anuran species reflects selection of breeding habitats, known to occur in this group (Collins and Wilbur, 1979; Gascon, 1991). Stream 5 has a large backwater that function as a permanent pond and sheltered both species typical of forest streams and species that reproduce in open habitats such as *Hyla minuta*, *Hyla polytaenia* and *Phyllomedusa burmeisteri* (see Cardoso et al., 1989). The remaining streams were relatively uniform throughout the sampled sections and bordered by all vegetation strata, varying in size among them, though.

Variation of habitat types, interspecific interactions, disturbances, colonization processes, local, regional and continental selection and evolution processes may all inspire models proposed to understand stream communities (Ricklefs and Schluter, 1993). Larger fragments are supposed to shelther greater habitat diversity and are, thus, expected to shelther greater species diversity (Lack, 1976). Alternatively, larger fragments may suffer less species extinctions and more colonization events, resulting in a higher species richness (MacArthur and Wilson, 1967). In the studied streams, the negative relationship between stream sampled section estimated volume and anuran species richness stresses the influence of habitat variability on species distribution, since species seem to choose the most suitable breeding habitats along a stream size gradient, most species preferring smaller streams. The same pattern was recorded by Eterovick (2003) in streams at the Serra do Cipó, a site close to the RPPN Serra do Caraça, in the southern portion of the Espinhaço mountain range. Both works, though, point to the hypothesis that Island Biogeography Theory does not apply to anuran species in streams.

Zimmerman and Simberloff (1996) stressed that the evolution of neotropical anurans favored species that breed in lenthic water bodies, contrary to the pattern observed at southeastern Asia, because ancestral lineages that evolved in these two continents had adaptations to lenthic and lotic aquatic habitats, respectively. Parris and McCarthy (1999) found anuran assemblages to be richer in larger streams in Australia. By the other side, anuran species in the RPPN Serra do Caraça may prefer to breed in small sections of streams, which are washed by strong currents just during the rainfall peaks, since these species have few adaptations to live in strong currents during their larval stage, as it also happens at the Serra do Cipó (Eterovick, 2003). We suppose that living downstream, in larger sections with larger water volume, would imply in a greater demand on tadpoles for adaptations to swim against the current, attach themselves to substrates and search for shelters in shallow microhabitats. Alternatively, tadpoles lacking adaptations to life in strong currents might have more opportunities to escape the occasional relatively strong water flows that wash small streams, that is, stream sections closer to the source.

Anuran annual breeding period and duration of breeding activities are related to seasonal climatic variations in temperature and rainfall (Toft and Duellman, 1979). Species that occur in permanent shaded water bodies, with high humidity during most of the year, usually show a long reproductive period (Rossa-Feres and Jim, 1994). The lack of association between climatic variables (rainfall and temperature) and monthly anuran species diversity and between climatic variables and diversity of species with calling males may be due to local habitat conditions at the RPPN Serra do Caraça. The preserved forest vegetation at stream margins and stream permanence may contribute to maintain air humidity and temperature relatively stable and predictable for anuran species. Colwell (1974) had already noticed forest habitats to be more stable and predictable than open habitats.

Tadpoles of *Scinax machadoi* were recorded in all sampling months, indicating continuous reproduction and/or long development. Nevertheless, the number of adult individuals located was relatively low, maybe due to the species small size, cryptic coloration, and low, irregular mating call (Bokermann and Sazima, 1973), making it difficult to locate. In Stream 8, a single gravid female was recorded within the sampling section, on July 2004. Besides *Scinax machadoi*, only tadpoles of *Hyla martinsi* and *Hylodes uai* were recorded in this stream. There is a waterfall upstream next to the sampled section, and it is possible that adults of these species reproduce upstream to this waterfall, at smaller sections of the stream, and egg clutches and/or tadpoles are carried downstream to the sampled section.

Crossodactylus sp. showed reproductive activities year-round, as reported for *Crossodactylus* sp. at the Parque Estadual Mata dos Godoy (Paraná state, south Brazil; Bernarde and Anjos, 1999) and *Crossodactylus bokermanni* at the Serra do Cipó (Minas Gerais state, southeastern Brazil) (Eterovick and Sazima, 2004). As other species in the subfamily Hylodinae (Leptodactylidae), the species of *Crossodactylus* occurring at the RPPN Serra do Caraça is diurnal; males call close to or on the soil, at moist microhabitats where they may reduce water loss (Cardoso and Martins, 1987; Cardoso and Haddad, 1992).

For the species that did not show strong indicatives of reproduction but mating calls, it was not possible to describe a temporal distribution pattern for breeding activities, because males' calling period may be longer than the actual specific breeding period (Wiest, 1982; Donnelly and Guyer, 1994).

The species showing the greatest plasticity in stream occupancy were those presenting the most indicatives of reproduction (gravid females, egg clutches, tadpoles, and post metamorphic froglets), such as *Hyla martinsi*, *H. nanuzae, Scinax luizotavioi, S. machadoi*, *Crossodactylus* sp., and *Hylodes uai,* which were observed almost year-round. *Hyla martinsi* had abundance peaks at the hottest and most humid months, but its tadpoles were recorded in all months, what may be due to continuous reproduction and/or long tadpole development. *Hyla nanuzae* had a long breeding period with an activity peak during the rainy season, its breeding period being longer than the one recorded at the Serra do Cipó (Eterovick and Sazima, 2004), a more markedly seasonal and open habitat. *Scinax luizotavioi* was recorded in almost all sampling months, with an activity peak during the dry season. Differences in reproductive periods had already been interpreted as a potential mechanism to avoid interspecific competition (Bertoluci and Rodrigues, 2002). Nevertheless, climatic factors and physiological adaptations acquired during species evolution may play a more important role in determining breeding periods of anurans, since even populations of the same species may show variations in breeding pattern at different sites, subject to different climatic conditions, as noticed here for *Hyla nanuzae*. Besides, 31.6% of the anuran species recorded in forest streams at the RPPN Serra do Caraça showed indicatives of reproduction or reproductive activities year-round, contrasting with only 11.6% (18.5% considering only species that reproduce in streams or associated to them) of the anuran species of the Serra do Cipó, a less stable, open habitat (Eterovick, 2003; Eterovick and Sazima, 2004).

Species typical of forest habitats are probably more specialized and have reproductive modes with more restrictive needs (see Duellman and Trueb, 1994) being potentially more sensitive to habitat changes. The RPPN Serra do Caraça is located in the domains of the Espinhaço mountain range, where many Brazilian endemic genera and local endemic species occur (Costa et al., 1998). The Espinhaço is an important area for amphibian conservation in the state of Minas Gerais and its surroundings are suffering strong human impacts caused by mining activities and tourism. Once species spatial and temporal distribution patterns are known, departures from these patterns may be considered as indicatives of environmental disturbances, aiding to species conservation and management.

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CAPÍTULO 2

Microhabitat choice and partitioning by anurans in forest streams in southeastern Brazil

Resumo

A utilização do nicho espacial pelos anuros adultos foi estudada em oito riachos de mata na RPPN Serra do Caraça localizada no município de Catas Altas (Minas Gerais). Os microambientes avaliados foram classificados em 18 tipos baseados nos substratos, na distância e na altura da água. Um total de 440 anuros de 19 espécies apresentaram grande seletividade na utilização desses microambientes. Espécies com nichos mais amplos (mais generalistas) não ocuparam um maior número de riachos do que as espécies mais especialistas, nem os riachos com uma maior riqueza de espécies apresentaram espécies com valores mais estreitos de nicho. As espécies apresentaram variados níveis de sobreposição na utilização dos microambientes. O padrão de distribuição observado neste estudo sugere que a competição não é um importante fator influenciando a estrutura espacial das comunidades de anuros de riachos permanentes de mata.

Palavras-chaves: Anfíbios anuros, distribuição espacial, utilização de microambientes, largura de nicho, plasticidade comportamental.

Abstract

The use of niche spatial dimension by anuran amphibians was studied in eight forest streams in the RPPN Serra do Caraça, Catas Altas municipality, Minas Gerais state, southeastern Brazil. Microhabitats were sampled and classified in 18 types based on substrate and height above ground/water. A total of 440 individual anurans of 19 species was recorded using these types of microhabitats. Anurans showed selectivity in microhabitat use. Species with broader niches (generalists) did not occur in more streams than species with narrower niches (specialists), and streams with higher species richness did not shelter more specialists. Species showed variable levels of superposition in microhabitat use. The distribution patterns observed in the studied anuran assemblages suggest that competition is not an important factor influencing the spatial structure of these assemblages in permanent forest streams.

Key words: Anuran amphibians, spatial distribution, microhabitat use, niche breadth, behavioral plasticity

Introduction

Species co-existence in an assemblage is possible due to partition of available resources (Blair 1961, Duellman and Pyles 1983, Aichinger 1987, Cardoso *et al.* 1989, Haddad and Sazima 1992, Rossa-Feres and Jim 1994, Pombal 1997, Eterovick and Sazima 2000, Eterovick and Barros 2003), which are distributed in three main niche dimensions: time, space, and food (Pianka 1973). The use of such resources is a compromise between physiological needs of organisms and biotic interactions among them within the ecosystem (Zweimüller 1995).

Differences in resource use may reduce competition and make the co-existence of a higher number of species possible (MacArthur 1972). Competition intensity between species may be related to the level of overlap in use of a critical resource (MacArthur and Levins 1967). When use of a resource result in competition, species may diverge in order to avoid it, reducing overlap in resource use (Schoener 1982). According to Pianka (1973), a species niche is the set of resources it uses, and species under competition pressure are expected to narrow their niches or tolerate greater niche overlap in richer assemblages.

In general, resource partitioning by amphibians is related to several specific needs (Crump 1971) and differences in reproductive modes (Duellman 1989). The highest the diversity of reproductive modes in an assemblage, the highest the number of species expected to be able to co-exist, maybe due to a more efficient pattern of resource partitioning (Crump 1982).

Habitat partitioning represents the occupancy of the spatial dimension of species niches (Pianka 1973) and it may be the most important niche dimension to be partitioned by adult anurans (Toft 1985). Variable and heterogeneous habitats favor an increase in species richness, since a higher combination of microhabitat types and ecological niches is available (MacArthur 1968). The choice of specific microhabitats within this habitat mosaic is related to morphological, physiological and behavioral adaptations of species (Crump 1971, Pough et al. 1977, Cardoso *et al*. 1989). Species with broader niches are expected to be more widespread may tolerate a larger variety of habitat conditions (Gaston *et al.* 1997, Pyron 1999). Besides, species closely related phylogenetically tend to be associated to the same or similar ecological niches, and in such instances historical factors are more important than recent ecological ones in determining species distribution (Inger 1969).

Studies on microhabitat use by anurans are scarce (Eterovick and Fernandes 2001, Eterovick and Barros 2003), nevertheless anuran reproductive sites may be studied as well limited ecosystems where spatial niche can be characterized and quantified (Eterovick and Barros 2003) making studies on spatial organization of anuran assemblages feasible. Considering the diversity of microhabitats used by adult anurans as a measurement of their niche breadth (Pianka 1973), we aimed to test whether (1) anurans select actively their microhabitats, (2) species with broader niches (generalists) occur in a higher number of streams, (3) species occurring in richer assemblages have narrower niches, and (4) species partition microhabitats.

Study site

The Reserva Particular do Patrimônio Natural Serra do Caraça is located at Catas Altas municipality (20° 05'S; 43° 29'W), Minas Gerais state, southeastern Brazil. The reserve encompasses 10 187.89 ha in the southern portion of the Espinhaço mountain range, from 850 to 2070 m above sea level (Fig. 1). The region is formed by the orographic systems of Minas Gerais and Bahia states (Derby 1966), representing a contact zone between the Cerrado and Atlantic Forest biomes in its southern portion and a transition zone between both biomes in its northern portion (Giulietti and Pirani 1988, Giulietti *et al.* 1997).

The region has two seasons, a dry from April to September and a wet, from October to March.

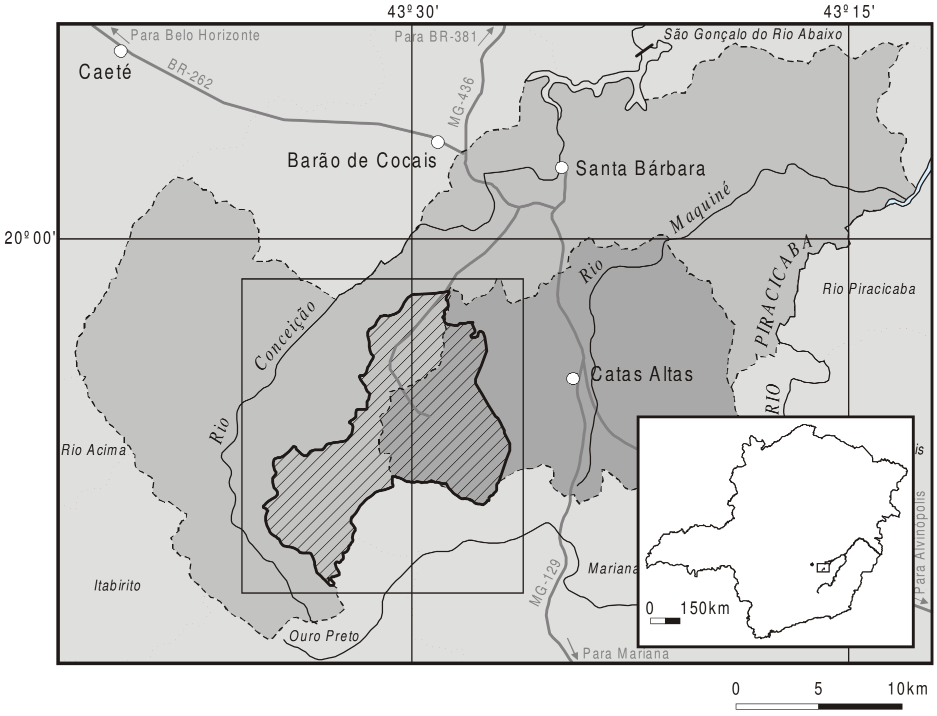

Figure 1. Location of the RPPN Serra do Caraça, Minas Gerais state, southeastern Brazil.

Methods

The work was conducted during three-day monthly field trips from August 2003 to October 2004, when eight permanent forest streams were regularly sampled (Fig. 2). Each month, 150 m sections marked, one at each stream, were inspected in search for anurans through visual and auditory searching procedures. For each individual located, we recorded substrate used and height from the ground.

Specimens not identified in the field were preserved according to Heyer *et al.* (1994) for posterior identification and then deposited in the herpetological collection of the Museu de Ciências Naturais of the Pontifícia Universidade Católica de Minas Gerais.

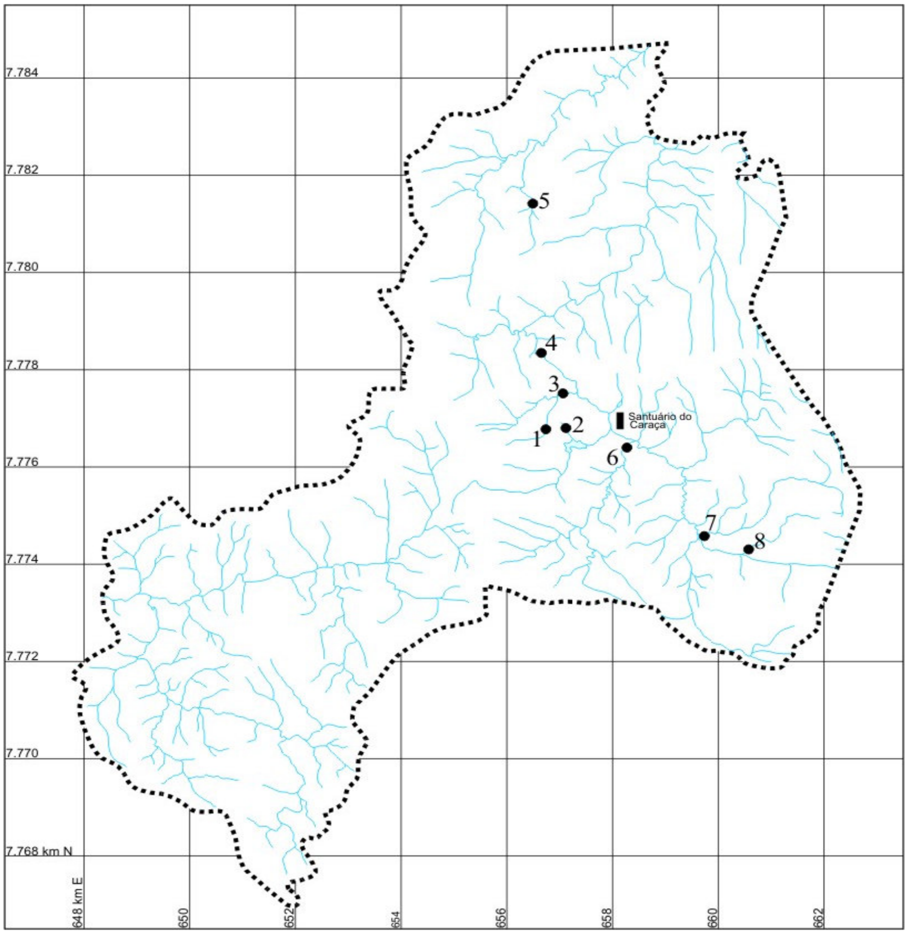

Figure 2. Location of the eight sampled streams at the RPPN Serra do Caraça, southeastern Brazil.

Microhabitat selection

Microhabitat availability was quantified using a new method proposed herein. Five pictures of the marginal habitat were taken for each stream, within the marked 150 m sampling section. The pictures were taken at 15, 45, 75, 105, and 135 m from the beginning of the section. The margin (right or left) to be photographed was randomly assigned at the first point, and then the margins were alternated at each following point. To standardize picture size, a metric tape was extended at the photographed point and the width of each picture corresponded to 3 m. The bottom of each picture was positioned where stream water contacted stream margin at the middle point. All the pictures were taken with the same camera and by the same person, without flash.

An uniform 15 x 21 line grid was superposed to each picture (Fig. 3) and microhabitats occurring at line intersections were recorded at three height classes (0-70 cm, >70-140 cm, and >140 cm). As the pictures were taken in a perpendicular position in relation to the photographed area, height from the ground (measured to characterize microhabitats used by recorded frogs) could be then assigned to the height classes used in the pictures (Fig. 3). Microhabitats were classified into 18 types resulting from the combination of the three height classes and seven substrate types: green leaves (including ferns, bromeliads, grasses), brown leaves, branches (including roots, fallen branches, lianas), rocks, leaf litter, bare soil (including sand, mud and river banks), and water (Table 1). Microhabitats of leaf litter above 140 cm and of water above 70 cm were not recorded and were so eliminated from the analyses.

Absolute numbers recorded for availability and use of microhabitat types were compared through Chi-square tests (Zar 1999), assuming that a random distribution of anurans throughout the streams (no microhabitat selection) would result in proportional values of use and availability. A significant difference between observed and expected values would so indicate microhabitat selection by anurans at the studied streams.

Figure 3. Picture taken at the first point (15 m) of Stream 3, with the 15 x 21 line grid superposed to quantify available microhabitats in three height classes at the RPPN Serra do Caraça, southeastern Brazil. Each height class encompasses five horizontal grid lines.

Niche breadth

Niche breadth was estimated for each anuran species using Simpson' s diversity formula (Pianka 1973):

$$D = 1 / \sum Pi^2$$

where *Pi* represents the proportion microhabitat "i" was used by the species considered in relation to the total number of microhabitat use records for this species.

First, the diversity of microhabitats used by each species was estimated using data from all streams where it occurred (A) and the diversity of available microhabitats was also estimated for the same set of streams used by the species considered (S). Then, the diversity of microhabitats used by each species was estimated separately for each stream where it occurred (A'), and the diversity of available microhabitats was estimated for each stream (S'). The A index was estimated for species with more than nine records (n = 7 species) and the A' index was estimated for species with more than seven records (n = 6 species) in a given stream.

A conservative estimate of niche breadth was given by A/S, since species occurring in streams with greater microhabitat diversity could appear to have greater microhabitat use diversity if they were randomly distributed in the habitat. So we tried to minimize the effect of habitat heterogeneity on species niche breadths in order to compare them. We assumed that higher A/S values would indicate species with greater plasticity in microhabitat use, suggesting a generalist behavior, and we tested whether such species would occur in a greater number of streams using linear regressions (Zar 1999). We considered the number of streams where a species was recorded as the dependent variable and the species niche breadth as the independent variable.

We also hypothesized that the number of species occupying a stream did would influence on niche breadth of the species present, as assumed by Pianka (1973). We then related niche breadth of species occurring in each stream (as the dependent variable) to stream species richness (as the independent variable) using linear regressions (Zar 1999). Statistical analyses were conducted in the software BioEstat (BioEstat 2003).

Niche overlap

To estimate niche overlap between anuran species regarding microhabitat use, we used the formula proposed by Pianka (1973):

$$O_{jk} = \frac{\sum P_{ij} P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}}$$

where P_{ij} and P_{ik} are the proportional uses of microhabitat "i" by species "j" and "k" respectively. We used this index only for species occurring in the same stream.

Results

A total of 440 individual anurans from 19 species (Appendix 1) was observed using 16 out of the 18 recorded microhabitats. They used branches, bare soil and green leaves in heights of 0-70 cm in proportions greater than expected ($X^2 = 928.56$, $p < 0.001$, Table 1). None of the species used leaf litter or bare soil at heights of >70-140 cm (Table 1).

The high number of records obtained for *Scinax luizotavioi*, *Hyla nanuzae* and *Crossodactylus* sp. made the conduction of specific analyses of microhabitat use possible, and all these species showed microhabitat preferences. *Scinax luizotavioi* used preferentially branches at heights of 0-70 cm ($X^2 = 274.38$, $p < 0.001$). *Hyla nanuzae* used preferentially rocks at heights of 0-70cm ($X^2 = 215.18$, $p < 0.001$) and *Crossodactylus* sp. used preferentially bare soil at heights of 0-70 cm ($X^2 = 3418.7$, $p < 0.001$).

Table 1. Microhabitats available in the eight studied streams and used by 19 anuran species at the RPPN Serra do Caraça, southeastern Brazil.

Microhabitats	Available	Used	Expected
Green leaves, 0-70 cm	1675	80	61.10
Green leaves, >70-140 cm	2102	14	76.7
Green leaves, > 140 cm	1985	12	72.43
Brown leaves, 0-70 cm	332	7	12.10
Brown leaves, >70-140 cm	459	3	16.75
Brown leaves, > 140 cm	332	1	12.10
Branch, 0-70 cm	1081	109	39.43
Branch, >70-140 cm	1325	26	48.35
Branch, > 140 cm	1710	28	62.4
Rock, 0-70 cm	274	36	10
Rock, >70-140 cm	48	4	1.75
Rock, > 140 cm	4	2	0.15
Leaf litter, 0-70 cm	82	28	3
Leaf litter, >70-140 cm	23	0	0.84
Bare soil, 0-70 cm	383	81	14
Bare soil, >70-140 cm	151	0	5.50
Bare soil, > 140 cm	35	1	1.3
Water, 0-70 cm	57	8	2.1
Total	12058	440	440

Niche breadth

Species with broader niches (generalists), that is, those with higher A/S values, did not occupy more streams than species with narrow niches (R^2 = -18.33%, p = 0.795, Table 2).

Table 2. Number of streams occupied and diversity of microhabitats used by seven anuran species and diversity of available microhabitats in the set of streams used by them in the RPPN Serra do Caraça, southeastern Brazil.

Species (n)	Number of streams occupied	Diversity in microhabitat use (A)	Diversity of available microhabitats (S)	A/S
Hyla sp. (gr. c*ircumdata*) (9)	3	3.24	8.45	0.38
Hyla martinsi (19)	4	4.69	7.54	0.62
Hyla minuta (13)	1	2.60	6.30	0.41
Hyla nanuzae (104)	4	6.72	7.77	0.87
Hyla polytaenia (12)	1	4.00	6.30	0.63
Scinax luizotavioi (123)	5	2.99	7.62	0.40
Crossodactylus sp. (104)	3	2.62	7.89	0.33

The number of species occupying a stream did not influence on niche breadth of the species present (A'/S', Table 3) ($R^2 = 4.95\%$, $p = 0.237$).

Table 3. Diversity of microhabitats used by six anuran species, diversity of microhabitat availability in local streams and estimated niche breadth for species in particular streams (A' /S') at the RPPN Serra do Caraça, southeastern Brazil. Streams are numbered like in Figure 2.

Species (number of streams used)	Streams used (number of records)	Diversity in microhabitat use (A')	Diversity of available microhabitats (S')	A'/S'
Hyla martinsi (4)	3 (8)	2.13	8.46	0.25
	4 (7)	3.77	6.54	0.58
Hyla minuta (1)	5 (13)	2.60	6.30	0.41
Hyla nanuzae (4)	2 (12)	6.55	7.66	0.85
	4 (32)	5.51	6.54	0.84
	5 (55)	4.84	6.30	0.77
Hyla polytaenia (1)	5 (12)	4.00	6.30	0.63
Scinax luizotavioi (5)	2 (33)	3.96	7.66	0.52
	4 (76)	2.63	6.54	0.36
	5 (9)	2.45	6.30	0.39
Crossodactylus sp. (3)	3 (78)	2.29	8.46	0.27
	7 (43)	2.92	6.43	0.45

Niche overlap

Species had variable values of spatial niche overlap, and even species with great superposition in microhabitat use could also superposition in their temporal distribution (Afonso and Eterovick, unpubl. data).

Hyla nanuzae and *S. luizotavioi* ($O_{jk} = 0.668$) co-occurred on August 2003, March, April, September, and October 2004 in Stream 2.

Hyla nanuzae and *S. luizotavioi* ($O_{jk} = 0.635$) co-occurred on August and September 2003, from March to June and from August to September 2004 in Stream 4.

Hyla nanuzae and *S. luizotavioi* ($O_{jk} = 0.529$) co-occurred on March, May, August and September 2004 in Stream 5.

Hyla nanuzae and *H. polytaenia* ($O_{jk} = 0.373$) co-occurred on August and October 2003 and December and March 2004 in Stream 5.

Hyla nanuzae and *H. minuta* ($O_{jk} = 0.511$) co-occurred on August and September 2003 and on March, May, August and September 2004 in Stream 5.

Scinax luizotavioi and *H. polytaenia* ($O_{jk} = 0.754$) co-occurred on March and September 2004 in Stream 5.

Scinax luizotavioi and *H. minuta* ($O_{jk} = 0.950$) co-occurred on March, May, August and September 2004 in Stream 5.

Hyla minuta and *H. polytaenia* ($O_{jk} = 0.682$) co-occurred on August and October 2003 and March and September 2004 in Stream 5.

Discussion

Environmental complexity, species niche breadth, niche overlap and behavioral plasticity are all factors that may influence community structure (Inger and Colwell, 1977; Cardoso et al., 1989). Environmental complexity is important to determine the number of species that can exploit a given habitat (Cardoso et al., 1989). In forests, the complexity is represented, in part, by the presence of all vegetation strata, creating a tridimensional space with many microhabitat types. The use of all such space may favor the reduction of competition among congeneric species (Meserve, 1977).

Spatial distribution is related to morphological (Cardoso et al., 1989), physiological (Pough et al., 1977) and behavioral adaptations associated to anuran reproductive modes (Crump, 1971). The anuran species occurring at the RPPN Serra do Caraça showed selectivity in microhabitat use, branches at heights between 0 and 70 cm being the preferred microhabitats. The high number of hylids present in the study site can help explain the preference for microhabitats on the vegetation, as the presence of adhesive discs at hylid fingertips turn species of this family able to explore the vegetation vertically (Cardoso et al., 1989). Besides, these treefrogs can also use rocks and leaf litter as substrates as other frogs do. This may contribute to a large niche breadth in species of this family. In fact, the Leptodactylid *Crossodactylus* sp. had niches narrower than most Hylids studied (see Tables 2 and 3). Physiological differences in tolerance to water loss may also influence on microhabitat choice (Pough et al., 1977). Species preference for microhabitats at heights from 0 to 70 cm may be due to a higher humidity expected to occur close to the ground (Cardoso and Martins, 1987; Cardoso and Haddad, 1992).

Scinax luizotavioi and *Hyla nanuzae* followed the pattern of spatial distribution recorded for hylids at other sites (see Pombal, 1997; Eterovick and Sazima, 2004). These species preferred to use branches and rocks respectively, both at heights from 0 to 70 cm. *Crossodactylus* sp. preferred to use bare soil at heights of 0-70 cm. Since this species is diurnal, the frogs call from the ground or close to it, at microhabitats that provide more protection against water loss due to high humidity (Cardoso and Martins, 1987; Cardoso and Haddad, 1992). As the remaining species recorded are nocturnal, *Crossodactylus* sp. is not supposed to compete for space with them, so that the narrow niche recorded for this species may be due to specific behavior and physiologic tolerances other than competitive interactions with other anuran species.

According to Pianka (1973), species occurring in streams with higher species richness would be expected to have narrower niches or greater niche overlap if subjected to competition for the spatial niche dimension. Though, values of species niche breadths were not related to species richness in streams at the RPPN Serra do Caraça. This may indicate that the available niche space is not completely occupied, and competition is not strong enough to influence community structure making species narrow their niches (Pianka, 1973). A similar pattern was recorded for tadpoles at montane meadow streams at Serra do Cipó, southeastern Brazil (Eterovick and Barros, 2003).

The streams studied at Serra do Caraça are permanent and do not undergo abrupt changes, being relatively stable if compared to temporary streams, as the ones studied by Eterovick and Barros (2003) at Serra do Cipó. Habitat stability could provide suitable conditions for species with narrow niches, and allow species to specialize in microhabitat use (Donohue et al., 2001). Besides, forest habitats are considered more stable and predictable than open habitats (*sensu* Colwell, 1974). Future studies addressing niche breadth of anuran species in less stable and open habitats will be useful to assess the role of environmental stability in shaping anuran assemblage structure.

Species pairs with higher values of niche overlap regarding microhabitat use may show less overlap in other niche dimensions, such as food and time, in order to avoid interspecific competition (Pianka, 1973). According to Toft (1985), the spatial niche dimension is more important than food and time to be partitioned by anurans, since the trophic niche is closely related to microhabitats used by the species (Inger and Colwell, 1977). At the study site, many species with spatial niche superposition also showed overlap in period of occurrence, reinforcing the little importance of competition in structuring local anuran assemblages.

Scinax luizotavioi and *H. minuta* were the species with the highest value of niche overlap ($O_{jk} = 0.950$). Although these species used the same microhabitats, they were distributed throughout the stream in a way that *S. luizotavioi* was more frequent at stream sections with more closed canopy and *H. minuta* was more frequent at open sections around large backwaters. *Scinax luizotavioi* was also observed calling in a lake surrounded by herbaceous and shrubby vegetation at Serra do Caraça by Caramaschi and Kisteumacher (1989). *Hyla minuta* can also use puddles and swamps besides stream backwaters (Eterovick and Sazima, 2004), occurring also in ponds at the RPPN Serra do Caraça (K. Kopp and P. C. Eterovick, unpubl. data). In spite of being able to occupy different types of water bodies, both *Scinax luizotavioi* and *Hyla minuta* had low values of niche breadth if compared with other co-occurring hylids (see Tables 2 and 3). These species may occupy habitats opportunistically but have an expected spatial distribution within them, regarding microhabitats used. Microhabitat use may be more likely related to specific behavior than to any kind of niche separation caused by competition, since there is a great availability of the preferred microhabitats in the set of habitats used by the species. By the other side, habitat occupancy may be related to differential migrating and colonization abilities of species, so that species niches were not related to number of streams occupied.

The observed variable levels of niche overlap between species pairs indicate that they differ in resource use although selective pressures may not be strong enough to lead to a complete species differentiation in microhabitat use, as also noticed by Eterovick and Barros (2003) for tadpole assemblages at Serra do Cipó, southeastern Brazil. Zimmerman and Simberloff (1996) showed that anuran community structure, regarding habitat type used for reproduction and development, is determined mainly by phylogenetic constraints of species colonizing each site instead of environmental or competitive pressures. These authors suggest that competition might assume a greater importance in a finer spatial scale, but here we show that competition does not seem to have a great interference in microhabitat use by adult anurans, at least in permanent streams.

The patterns of spatial distribution and microhabitat use of anuran assemblages in the RPPN Serra do Caraça indicate that competition may not have an important influence on their structure. Species may show temporal and spatial overlap within a given habitat (stream), or use the same microhabitats in a set of habitats (streams and ponds), even side by side or scattered throughout the water body. Although species show patterns of microhabitat preferences, microhabitats seem to be abundant enough to allow coexistence without restrictions in specific preferences caused by competition. The role of habitat stability in shaping species spatial niche is still little explored. Studies on anuran assemblages from intermittent streams and sites with open vegetation, employing the new method proposed here, will aid to the knowledge on how habitat stability and predictability influence species niche breadth.

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Appendix 1

Anuran amphibians recorded at eight permanent streams in the RPPN Serra do Caraça, southeastern Brazil, from August 2003 to October 2004.

BUFONIDAE
Bufo pombali Balsissera, Caramaschi & Haddad, 2004
Bufo rubescens Lutz, 1925

CENTROLENIDAE
Hyalinobatrachium cf. *eurygnathum*

HYLIDAE
Hyla sp. (gr. *circumdata*)
Hyla faber Wied-Neuwied, 1821
Hyla martinsi Bokermann, 1964
Hyla minuta Peters, 1872
Hyla nanuzae Bokermann & Sazima 1973
Hyla polytaenia Cope, 1868
Phyllomedusa burmeisteri Boulenger, 1882
Scinax aff. *perereca*
Scinax machadoi (Bokermann & Sazima, 1973)
Hyla albopunctata Spix, 1824
Scinax sp. (gr. *ruber*)
Scinax luizotavioi (Caramaschi & Kisteumacher, 1989)

LEPTODACTYLIDADE
Crossodactylus sp.
Hylodes uai Nascimento, Pombal & Haddad, 2001
Procerathophrys boiei (Wied-Neuwied, 1824)
Physallaemus aff. *olfersii*

Conclusões gerais

- Foram registradas 19 espécies de anuros pertencentes a três famílias: Bufonidae (10,53%), Hylidae (68,42%) e Leptodactylidae (21,05%) na RPPN Serra do Caraça (Catas Altas, MG) no período de agosto de 2003 a outubro de 2004.
- Houve uma relação significativa entre o número de espécies presentes e o volume dos riachos, mostrando que os riachos com maior volume de água apresentam menor número de espécies.
- A diversidade de espécies e a diversidade de espécies vocalizando não foram relacionadas com os fatores climáticos (precipitação e temperatura), mas as espécies de anuros demonstraram preferência quanto à época de atividade.
- Entre as 19 espécies registradas, 12 apresentaram atividade de vocalização e oito apresentaram indícios de atividade reprodutiva. As espécies com maior plasticidade na ocupação ambiental foram as que apresentaram mais indícios de reprodução.
- Um total de 440 anuros apresentou grande seletividade na utilização de 18 tipos de microambientes.
- As espécies consideradas como sendo mais generalistas não ocuparam um maior número de riachos, não sendo sua distribuição no ambiente relacionada à plasticidade comportamental.
- O número de espécies ocupando um riacho não influenciou a largura de nicho das espécies presentes, o que poderia indicar que o nicho espacial não está sendo totalmente ocupado e a competição provavelmente não está estruturando as comunidades estudadas.

- As espécies de anuros apresentaram valores intermediários de sobreposição de nichos, mostrando a utilização diferencial dos recursos.
- As espécies de anuros da RPPN Serra do Caraça apresentam baixa plasticidade comportamental no uso de microambientes, provavelmente porque riachos permanentes são mais estáveis e previsíveis se comparados a riachos temporários.