Neotropical Biology and Conservation
13(4):303-312, october-december 2018
Unisinos - doi: 10.4013/nbc.2018.134.04

Seasonal variation in the composition of ground-dwelling anuran (Amphibia) assemblages in southern Brazil

Variação sazonal na composição de taxocenoses de anuros (Amphibia) terrestres no sul do Brasil

André Luís Luza[1]
luza.andre@gmail.com

Fernanda Anziliero Gonçalves[2]
fanzilierog@gmail.com

Noeli Zanella[2]
zanella@upf.br

Abstract

Climate seasonality may differently influence habitat quality and heterogeneity depending on habitat type. We examined whether the taxonomic, functional and phylogenetic composition of ground-dwelling anuran assemblages from grassland and forest habitats vary seasonally. We tested the hypothesis that the forest anuran assemblage varies less seasonally than the grassland assemblage. We monitored anurans using pitfall trap arrays in two areas, sampled across four seasons over a two-year period. For the functional composition, we acquired information on species morphology, reproduction, and habitat use to represent the anuran niche. For the phylogenetic composition, we used the most comprehensive anuran phylogeny. We used Principal Coordinate Analysis and Analysis of Variance to evaluate seasonal variations in assemblage composition along the study period. Our data revealed significant seasonal variation in the taxonomic and phylogenetic composition of anuran assemblages. Variation in taxonomic composition was higher in the grassland than in the forest assemblage, while variation in phylogenetic composition was higher in the spring-summer than in the autumn-winter seasons. We did not identify seasonal variation in functional composition. Seasonal variations in taxonomic and phylogenetic composition, but not in functional composition, indicate that the species with a fluctuating seasonal abundance have similar life-history traits, but belong to different lineages.

Keywords: anuran traits, Brazilian highland grasslands, habitat variability, temporal beta diversity, temporal turnover.

Resumo

A sazonalidade no clima pode alterar a qualidade e a disponibilidade de habitats dependendo do tipo de habitat. Neste trabalho, testamos a hipótese de que a estrutura taxonômica, funcional e filogenética da taxocenose de anuros florestais varia menos temporalmente do que a campestre. Monitoramos anuros utilizando armadilhas de interceptação e queda em duas áreas, amostradas ao longo de quatro estações de dois diferentes anos. Para a análise da composição funcional das taxocenoses de anuros, obtivemos informações de atributos morfológicos, reprodutivos e de uso de hábitat para representar o nicho das espécies de anuros. Para a análise da composição filogenética das taxocenoses, utilizamos a filogenia mais abrangente em número de espécies de anuros. Os resultados mostraram uma variação sazonal significativa na composição taxonômica e filogenética das taxocenoses. A variação na composição taxonômica foi maior no campo do que na floresta. A variação na composição filogenética foi maior na primavera-verão do que no outono-inverno. Não identificamos variação na composição funcional. As variações sazonais na composição taxonômica e filogenética, mas não na

[1] Universidade Federal do Rio Grande do Sul. Programa de Pós-Graduação em Ecologia. Av. Bento Gonçalves, 9500, Caixa postal 15007, 91501-970, Porto Alegre, RS, Brazil.
[2] Universidade de Passo Fundo. Instituto de Ciências Biológicas. BR 285, Bairro São José, 99052-900, Passo Fundo, RS, Brazil.

---

composição funcional, indicam que as espécies de anuros que variam em abundância ao longo das estações do ano possuem atributos de história de vida similares, mas pertencem a linhagens diferentes.

Palavras-chave: atributos de anuros, beta diversidade temporal, Campos do Planalto Sul-Brasileiro, variabilidade do habitat, substituição temporal de espécies.

Introduction

The study of anurans is particularly intriguing because their sensitivity to water loss through their skin entails a physiological challenge for living under variant and extreme conditions. Their evolution has resulted in a diversity of strategies for acquiring resources, reproducing, avoiding predation and competing in variant and extreme environments (Duellman and Trueb, 1994; Haddad and Prado, 2005; Silva *et al.*, 2012). Although biotic processes (*e.g.*, competition and predation) were previously considered to be the main factors influencing the diversity of anuran assemblages, climate seasonality has recently been recognized as a strong contributing factor (Both *et al.,* 2008; Rievers *et al.,* 2014). It has been suggested that seasonality in temperature, photoperiod and rainfall might control the peaks of anuran reproduction and richness in subtropical and temperate regions, whereas abundant rainfall might sustain continuous anuran reproduction in tropical regions (Prado *et al.,* 2005; Both *et al.,* 2008; Canavero *et al.,* 2008). Further, climate seasonality can differentially influence the vegetation heterogeneity and resource quality of an area, as the effects of climate seasonality depend on the habitat type (Maragno *et al.,* 2013; Gonçalves *et al.,* 2015). Here, we evaluated the seasonal variations in the composition of anuran assemblages from forest and grassland habitats, which are two habitats differently influenced by climate seasonality.

Plant architecture, phenology and tolerance to climate seasonality influences the vertical and horizontal stratification of habitats, which in turn alters the niche availability within forest and grassland habitats, offering differential opportunities for anuran reproduction, habitat selection, predator avoidance and food intake (Urbina-Cardona *et al.,* 2006; Both *et al.,* 2008; Oliveira *et al.,* 2013; Gonçalves *et al.,* 2015). The main seasonal changes in the forest structure are due to increases in tree flowering, fruiting and litter production, but not in canopy cover (Liebsch and Mikich, 2009; Longhi *et al.,* 2011). In grasslands, the peak of plant reproduction, biomass production by both grasses and forbs and the consumption of dry biomass by soil microorganisms occur during the warm seasons (spring and summer) (Soares *et al.,* 2005; Overbeck *et al.,* 2006). In contrast, a low production of biomass and the accumulation of unconsumed biomass occur during cold seasons (autumn and winter), which results in large seasonal differences in the vertical and horizontal structure of grasslands (Soares *et al.,* 2005; Overbeck *et al.,* 2006). Since different ecological factors drive the heterogeneity and intrinsic dynamics of grassland and forest habitats, the structure of anuran assemblages should also differ, with more pronounced dynamics in more seasonal habitats (Inger and Colwell, 1977).

Structural particularities of habitats, as well as their intrinsic dynamics, should strongly influence not only species but also the functional and phylogenetic composition of anuran assemblages (Inger and Colwell, 1977; Urbina-Cardona *et al.,* 2006; Maragno *et al.,* 2013). Differences in richness have been observed when comparing anuran assemblages in stable and heterogeneous habitats to assemblages in unstable and homogeneous habitats (Inger and Colwell, 1977; Xavier and Napoli, 2011; Oliveira *et al.,* 2013; Jimenez-Robles *et al.,* 2017). Furthermore, habitats that are less altered by climate might have more stable anuran assemblages than habitats experiencing large seasonal changes in structure (Inger and Colwell, 1977). However, how the taxonomic, functional and phylogenetic dimensions of anuran diversity varies over time and space is virtually unexplored (*e.g.*, Silva *et al*., 2012; Trimble and van Aarde, 2014; Jimenez-Robles *et al.,* 2017). The lack of life-history traits that facilitate the persistence during climatic extremes (*e.g.*, cold temperatures and drought) can promote the disappearance of a species from a given habitat (Silva *et al.,* 2012). If the anuran species fluctuating in abundance over time have lineage-specific life-history traits, we could expect large seasonal variation in the taxonomic, functional and phylogenetic composition of the anuran assemblages. On the other hand, if the species fluctuating in abundance over time have similar life-history traits but are from different lineages (*i.e.*, evolutionarily convergent), we could expect large seasonal variations in both the taxonomic and phylogenetic composition, but not in the functional composition of the anuran assemblages. Finally, if the anuran species are highly persistent in the habitat over time (*i.e.*, low fluctuations in abundance), we could expect a lack of seasonal variations in the taxonomic, functional and phylogenetic composition of anuran assemblages. Thus, seasonal changes in habitat structure due to climate seasonality may result in anuran assemblages composed of distinct species with different physiological tolerances, reproductive modes and habitat preferences.

We aimed to examine whether the taxonomic, functional and phylogenetic composition of ground-dwelling anuran assemblages from grassland and forest habitats varied over seasons. We tested the hypothesis that the forest anuran assemblage would exhibit less seasonal variation in taxonomic, functional and phylogenetic composition than the grassland assemblage. Such result is expected since forests experience fewer seasonal changes in vegetation height, vertical stratification and productivity than grasslands do (Inger and Colwell, 1977). In contrast, we expected large seasonal variations in the species, functional and phylogenetic composition of the grassland anuran assemblage because the reproduction and biomass production of grassland plants strongly differs between warm and cold seasons (Soares *et al*., 2005; Overbeck *et al*., 2006). Thus, the grassland anuran assemblage of warm seasons should differ in its composition of species, lineages and life-history traits when compared to the grassland assemblage of cold seasons.

Material and methods

Study site

We conducted the study at two areas in the municipality of Passo Fundo, Rio Grande do Sul State, in southern Brazil. The elevation of the areas varies between 630 and 740 m. The climate is predominantly subtropical (Cfb climate according to Köppen, 1948), which is characterized by a mean annual temperature of 14-16 °C, an annual rainfall between 1,900 and 2,200 mm with a lack of hydric deficits, and the occurrence of frost and eventually snow during the winter (IBGE, 2002; Alvares *et al*., 2013). The grassland area (*Fazenda da Brigada*; 28°14'56" S, 52°19'52" W) comprises one of the last large remnants (≈ 600 hectares) of *Aristida jubata* grasslands in the region. *Aristida jubata* (Arechav.) Herter, a tussock grass, dominates the herbaceous strata of the grassland site (Figure 1), whereas patches of Araucaria forest are found along streams. Marshes and water reservoirs are the main types of hydric resources found in the grassland habitat. Araucaria forest covers nearly the entire extent of the forest area (≈ 200 hectares of forest; 28°13'56" S, 52°20'15" W), with *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae) dominating the forest canopy. Small streams with rocks are the main types of hydric resource occurring in the forest habitat. The distance between the two sites is 2 km.

Sampling of ground-dwelling anurans

We monitored the occurrence of anurans in each area during different seasons of the year (autumn, winter, spring and summer) for two years (from May 2001 to

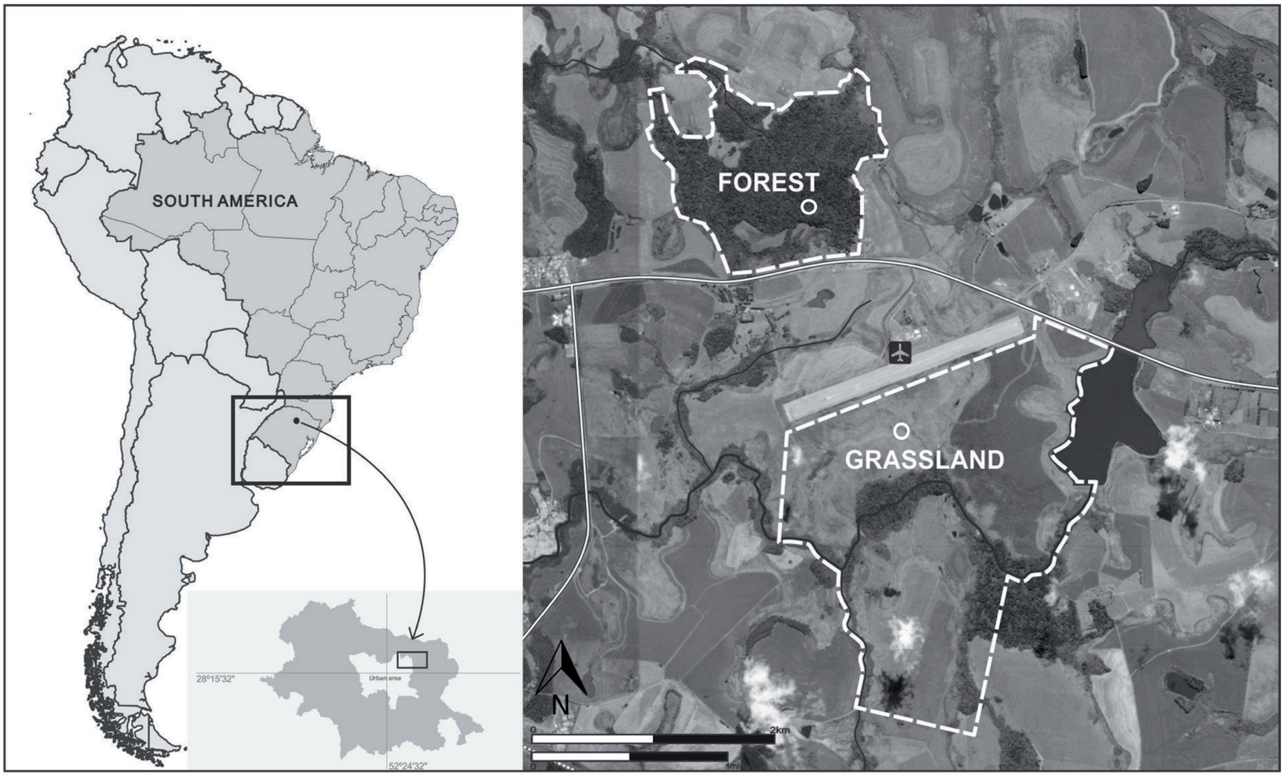

Figure 1. Study areas located in the municipality of Passo Fundo, Rio Grande do Sul, southern Brazil. Dashed lines represent the extent of the grassland and forest habitats, and the empty white circles represent the position of the T-shaped pitfall-trap arrays.

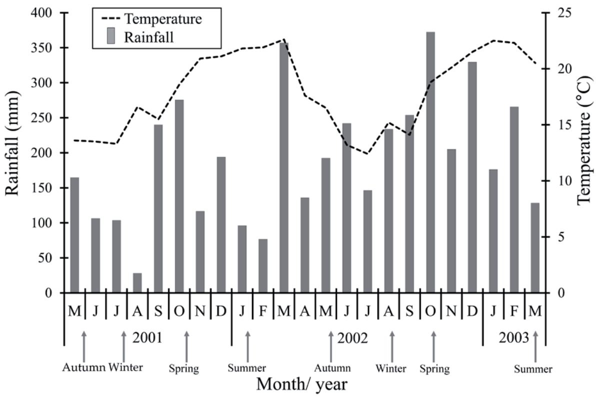

Figure 2. Mean monthly temperature and rainfall in the municipality of Passo Fundo, Rio Grande do Sul State, Brazil, during the sampling period. Arrows represent the sampled months. Data were obtained from EMBRAPA (2016).

March 2003; see arrows in Figure 2), with a total sampling effort of 240 days and 5,760 trapping hours. Each habitat contained a sampling unit comprising a T-shaped pitfall-trap array with fourteen 150-L plastic buckets separated by 20 m. We kept the pitfall traps open for three days of each week of the sampling month, totaling twelve days of pitfall trapping per season, and checked the traps daily. Only adult individuals were considered in the analysis. We collected all trapped individuals and deposited them in the anuran scientific collection of the Museu Zoobotânico Augusto Ruschi (Universidade de Passo Fundo, Passo Fundo, RS, Brazil). The Brazilian Environmental Institute (IBAMA) approved the fieldwork procedures (process # 02/2002). We standardized the number, disposition and period of pitfall opening between habitats and among seasons to facilitate comparisons. The forest array was located more than 100 m from the forest edge, while the grassland array was at least 700 m from the nearest forest edge. Repeated sampling of the same habitat over time circumvented the lack of a spatial replication of habitats (*i.e.* several forest and grassland habitats), allowing the temporal variations in anuran assemblage composition over time to be tested. The average temperature during the sampling periods was below 15 °C in winter and autumn, and mostly warm (average near 20 °C) during spring and summer (Figure 2). These data were sampled by the Brazilian Agricultural Research Corporation (EMBRAPA, 2016), approximately 6 km from the sampling sites.

Functional and phylogenetic composition

To evaluate whether functional composition changed with seasonality, we acquired information on species life-history traits from the literature (Table 1). We used information on morphological (snout-vent length), reproductive (reproductive modes) and habitat-use (cryptozoic behavior) traits for each species, since they seemed to best represent the nuances of anuran niches (Silva *et al.,* 2012; Tsianou and Kallimanis, 2016). Snout-vent length (SVL, averaged measures for males and females) relates to the species sensitivity to habitat changes, with larger species being less sensitive to humidity deficits and more vagile, facilitating their ability to find resources and favorable conditions (Trimble and van Aarde, 2014; Tsianou and Kallimanis, 2016). Reproductive modes describe the species choice for specific oviposition sites, which indicates the dependency of the species on water sources (Duellman and Trueb, 1994; Haddad and Prado, 2005; Prado *et al.*, 2005; Hartmann *et al.*, 2010). Finally, cryptozoic behavior describes the habit of living hidden in shelters (holes and leaf litter). Such behavior may be favored over non-cryptozoic behavior in open habitats, since staying protected from solar desiccation and predation may be advantageous, particularly during unfavorable periods.

We used a dated phylogeny to obtain the phylogenetic distance between the anuran species registered over the two years of the study. We pruned the phylogenetic tree of Pyron and Wiens (2011) to obtain the phylogenetic distance between all species found in the forest and grassland habitats. Although the phylogeny from Pyron and Wiens is the most comprehensive phylogeny for the group, we added three species that were not included in the phylogeny (*Leptodactylus latrans* (Steffen, 1815), *Elachistocleis bicolor* (Guérin-Meneville, 1838) and *Physalaemus henselii* (Peters, 1872)). These species were randomly inserted in their respective genera using functions from the 'phytools' package (Revell, 2012) in R (R Core Team, 2017). Scientific nomenclature of *Physalaemus* aff. *gracilis* follows Frost (2018). We built a functional dendrogram and a phylogeny to visualize the functional and phylogenetic relationships between species. The functional-dendrogram scale is in Gower distance and the scale of the phylogenetic-tree is given in millions of years (according to Pyron and Wiens, 2011). We built the functional dendrogram using Gower distance (because of the categorical, binary and quantitative trait values) and the UPGMA clustering algorithm.

Data analysis

In order to determine whether the composition of ground-dwelling anuran assemblages from the forest and grassland habitats varied over time, we analyzed matrices of taxonomic, functional and phylogenetic composition where each sampling unit comprised of a month of sampling in a particular habitat. Before the analysis, we used Hellinger's transformation on the matrix of taxonomic composition to decrease the discrepancies in abundance among the sampled species (Legendre and Legendre, 2012) (see Table 1).

We then used the Hellinger-transformed matrix to calculate the functional and phylogenetic compositions. Functional and phylogenetic composition matrices were obtained by fuzzy-weighting species incidences by their functional and phylogenetic relationships (Pillar *et al.,* 2009). Fuzzy-weighted functional and phylogenetic composition matrices contain the trait - and phylogeny - weighted abundances of anuran species, defined according to the functional and phylogenetic relationships among species occurring in a given month (Pillar *et al.,* 2009).

We explored seasonal variation in the taxonomic, functional and phylogenetic composition of anuran assemblages using Principal Coordinate Analysis (PCoA) based on the square-rooted dissimilarity between pairs of sampled months; we used the Lingoes correction to avoid the negative eigenvalues (Legendre and Legendre, 2012; Legendre, 2014). We used the Bray-Curtis dissimilarity to express the variation in taxonomic composition, and the Euclidean distance to express the variation in functional and phylogenetic composition (Legendre and Legendre, 2012). We excluded the grassland sampling from the winter of 2002, because the lack of captures biased the variance explained by the first ordination axis. Ordination axes are the best way of interpreting how much a site varies over time in relation to other sites, because averaged pairwise dissimilarities only account for the compositional variation between two time periods (Legendre, 2014; Anderson *et al.*, 2006).

We tested the hypothesis that the forest anuran assemblage would exhibit less seasonal variation than the grassland assemblage by applying the one-way Analysis of Variance test to the eigenvectors of the first and second PCoA axes, which captured most of the seasonal variation in the composition of anuran assemblages. In the Analysis of Variance, we related the seasonal variation in taxonomic, functional and phylogenetic composition (represented by PCoA axes) with the interaction between season and habitat, in order to determine in which season a given habitat would show the largest variation in composition. We summarized the pitfall-trap data to compare composition between the most contrasting climatic conditions found in the region (autumn and winter were considered as 'cold' seasons; spring and summer were considered as 'warm' seasons) because we did not have a sufficient sample size to compare each season. We identified differences in the taxonomic, trait and phylogenetic composition of habitats and seasons using contrast analysis (TukeyHSD Test). We conducted the functional and phylogenetic fuzzy-weighting analyzes in the 'SYNCSA' package (Debastiani and Pillar, 2012), dissimilarity-index analysis in the 'vegan' package (Oksanen *et al.*, 2018), ordination analysis in the 'ape' package (Paradis *et al.*, 2004), and both the Analysis of Variance and TukeyHSD (honestly significant difference) Test in the 'stats' package (R Core Team, 2017).

Results

We recorded nine species of ground-dwelling anurans belonging to four families (Table 1). The most abundant species were *Physalaemus* aff. *gracilis*, *P. cuvieri* Fitzinger, 1826, and *P. henselii* (1,095, 197, and 111 individu-

Table 1. Life-history traits and the number of individuals of species of ground-dwelling anurans, presented according to habitat type and season in southern Brazil. SVL= snout-vent length. See reference list in the table notes.

Family/Species	Reproductive mode	Habit	SVL (mm)	Grassland		Forest		Total number of individuals
				Autumn Winter	Spring Summer	Autumn Winter	Spring Summer	
Bufonidae								
Rhinella icterica	2[1]	Terrestrial [1,2]	125.8[8]	0	2	0	50	52
Leptodactylidae								
Leptodactylus gracilis	30[1]	Cryptozoic [1,2]	44.5[9]	0	3	0	0	3
Leptodactylus latrans	11[1]	Terrestrial [1,2]	92.81[10]	0	16	0	0	16
Leptodactylus plaumanni	30[1]	Terrestrial [1,2]	40.5[8]	0	12	0	0	12
Physalaemus cuvieri	11[1]	Terrestrial [1,2]	28.8[8]	20	161	6	10	197
Physalaemus aff. gracilis	11[1]	Terrestrial [3,5,6]	29[5]	35	17	683	360	1095
Physalaemus henselii	11[1]	Terrestrial [3,6,7]	23.1[11]	68	43	0	0	111
Microhylidae								
Elachistocleis bicolor	1[1]	Cryptozoic [1,2]	29[12]	0	5	0	3	8
Odontophrynidae								
Odontophrynus americanus	1[1]	Cryptozoic [4]	43.8[13]	7	13	19	36	75
Total	-	-	-	**130**	**272**	**714**	**460**	**1,576**

Notes: (1) Haddad *et al*. (2008); (2) Haddad *et al*. (2013); (3) Maneyro and Carreira (2012); (4) Achaval and Olmos (2007); (5) Camargo *et al*. (2005); (6) Dixo and Verdade (2006); (7) Pupin *et al*. (2010); (8) Kwet *et al.* (2010); (9) Borges-Martins *et al*. (2007); (10) Hartmann *et al.* (2010); (11) Maneyro *et al.* (2008); (12) Rodrigues *et al.* (2003); (13) Valdez and Maneyro (2016).

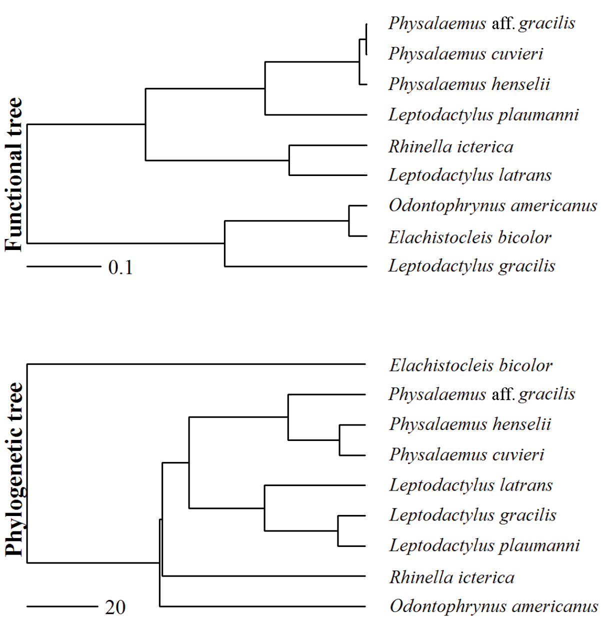

Figure 3. Functional and phylogenetic relationships among the ground-dwelling anuran species registered in forest and grassland habitats in southern Brazil. The functional-dendrogram scale is in Gower distance and the scale of the phylogenetic-tree is given in millions of years.

als, respectively). We did not record *Elachistocleis bicolor*, *Leptodactylus gracilis* (Duméril and Bibron, 1840), *Leptodactylus latrans*, *Leptodactylus plaumanni* Ahl, 1936 or *Rhinella icterica* (Spix, 1984) in the cold months (autumn and winter). Overall, we recorded more species in the grassland than in the forest habitat (Table 1). We observed that *P.* aff. *gracilis* and *R. icterica* were more abundant in the forest habitat*,* while *P. cuvieri* and *P. henselii* were more abundant in the grassland habitat. Species that occurred exclusively in the grassland habitat were *L. gracilis, L. latrans*, *L. plaumanni*, and *P. henselii*. The species *Odontophrynus americanus* (Duméril and Bibron, 1841) maintained a stable abundance throughout the seasons in both habitats.

Exploratory analyses of the functional and phylogenetic relationships between the species showed that *P. cuvieri*, *P.* aff. *gracilis*, *P. henselii* and *L. plaumanni* formed a group of small-sized species (Figure 3). *Elachistocleis bicolor*, *Leptodactylus gracilis* and *O. americanus* formed a functional group of cryptozoic species. *Rhinella icterica* and *Leptodactylus latrans* formed a group of large-sized species (Figure 3). Different reproductive modes were scattered among these three groups.

The results showed significant seasonal variation in the taxonomic and phylogenetic composition; but we did not find seasonal variation in the functional composition (Table 2). The analysis of the first ordination axis showed that the forest anuran assemblage exhibited less seasonal variation in taxonomic composition than the grassland assemblage did (Figures 4 and 5). The analysis of the second ordination axis showed seasonal variations in taxonomic composition within the grassland assemblage (Figures 4 and 5). In contrast, grassland assemblages of the warm seasons varied more in phylogenetic composition than grassland and forest assemblages of the cold seasons (Figures 4 and 5).

Discussion

Results showed that the seasonal variation in the taxonomic composition was more pronounced in the grass-

Table 2. Results of the one-way Analysis of Variance, testing for seasonal variations in the taxonomic, functional and phylogenetic compositions of anuran assemblages from forest and grassland habitats in the municipality of Passo Fundo, Rio Grande do Sul, southern Brazil, according to the interaction between season and habitat type (Factor).

		Df	Sum Sq	Mean Sq	F	P(>F)
Taxonomic composition						
Axis I (41.24%)	Factor	3	1.468	0.489	86.643	0.000
	Residuals	11	0.062	0.006		
Axis II (19%)	Factor	3	0.524	0.175	10.652	0.001
	Residuals	11	0.180	0.016		
Functional composition						
Axis I (36.67%)	Factor	3	0.028	0.009	1.796	0.206
	Residuals	11	0.056	0.005		
Axis II (23.93%)	Factor	3	0.015	0.005	1.377	0.301
	Residuals	11	0.040	0.004		
Phylogenetic composition						
Axis I (39.13%)	Factor	3	0.135	0.045	6.243	0.010
	Residuals	11	0.079	0.007		
Axis II (14.06%)	Factor	3	0.042	0.014	4.474	0.028
	Residuals	11	0.035	0.003		

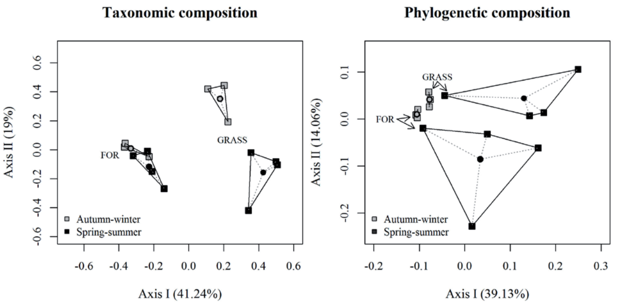

Figure 4. Principal Coordinate Analysis plot, showing seasonal variation in the taxonomic (left) and phylogenetic (right) composition of anuran assemblages in forest and grassland habitats from southern Brazil.

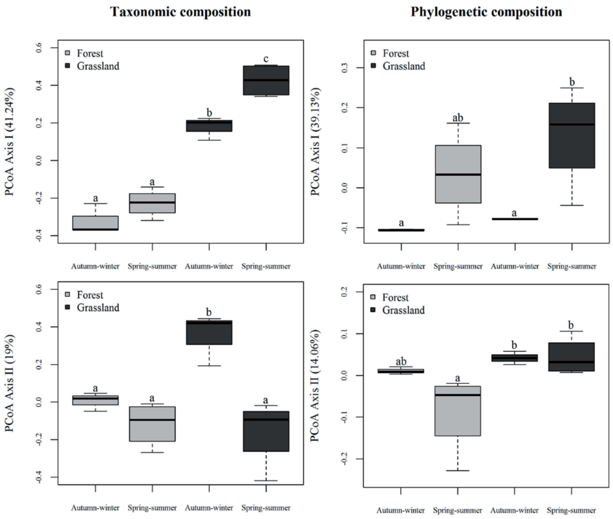

Figure 5. Box-plot of Analysis of Variance and contrast analysis showing significant seasonal variation in the taxonomic and phylogenetic composition of anuran assemblages from southern Brazil over two years. Seasonal variation in taxonomic and phylogenetic composition was represented by ordination axes (axis I- above, axis II- below). Boxes represent the mean, 1st and 3rd quartiles of ordination eigenvectors. Boxes followed by different letters indicate significant differences (P ≤ 0.05) in the contrast analysis.

land assemblage than in the forest assemblage, while seasonal variation in the phylogenetic composition was more pronounced in warm (spring-summer) than in cold seasons (autumn-winter). Many studies show evidence for within-habitat variation in anuran assemblage composition across seasons due to the varying environment (*e.g.,* Both *et al*., 2008; Canavero *et al.,* 2008; Santos *et al.*, 2008; Santos-Pereira *et al.*, 2011; Rievers *et al.*, 2014). However, a few studies attempt to understand whether assemblages from different habitats show distinct degrees of variation in composition across seasons (*e.g.,* Inger and Colwell, 1977; Maragno *et al.,* 2013). Here, we further support previous findings (Inger and Colwell, 1977; Maragno *et al.,* 2013) that assemblages from structurally less stable habitats suffer high variation in composition across seasons.

Seasonality in temperature, rainfall and photoperiod influence the phenology and productivity of plant communities (Soares *et al.,* 2005; Overbeck *et al.,* 2006; Liebsch and Mikich 2009; Longhi *et al.,* 2011), causing changes to habitat heterogeneity and resource availability, which consequently influence the peaks of anuran species reproduction and their patterns of habitat use (Inger and Colwell, 1977; Both *et al.,* 2008; Canavero *et al.,* 2008; Santos *et al.,* 2008; Maragno *et al.,* 2013). As forest habitats are seasonally more stable than grassland habitats in regard to habitat structure, we initially suspected that anuran taxonomic, functional and phylogenetic composition would be more stable throughout the changing seasons in the forest habitat. This pattern was confirmed, indicating that the intrinsic dynamics of habitats might cause seasonal variation in their species and lineage composition. These results do not imply that the forest assemblage remains unchanged over time (*e.g.,* Santos-Pereira *et al.,* 2011), but rather that the forest assemblage changes less than the grassland assemblage. The low seasonal variability in the forest assemblage, which we found to mainly consist of a subset of open-habitat and generalist species (*e.g., Physalaemus* aff. *gracilis* and *P. cuvieri*), could be due to the ability of these species to exploit the less-variant conditions and resources found in forest habitats, allowing them to maintain stable population sizes over time (Haddad *et al*., 2013, Bolzan *et al*., 2016).

Seasonal changes in grassland vegetation structure are characterized by the flowering of tussock grasses (*e.g. Andropogon lateralis* and *Aristida jubata*), the increase in biomass production and the recruitment/regrowth of woody plants during warm months (Soares *et al.,* 2005; Overbeck *et al.,* 2006). The grassland vegetation structure offers a great diversity of food items, calling sites, and shelters (for protection from predation and high solar exposure) for grassland-specialist anurans (Xavier and Napoli, 2011; Gonçalves *et al.,* 2015). Grasslands are of major importance for Leptodactylidae anurans which include grassland-specialist species (*e.g. Physalaemus henselii*, *Leptodactylus plaumanni*) with seasonal reproduction and adaptations to temporary ponds and unstable hydroperiods (*e.g.,* spawning in foam nests) (Duellman and Trueb, 1994; Santos *et al.,* 2008; Kwet *et al.,* 2010; Maneyro and Carreira, 2012). The difference in anuran species dominance in grasslands throughout the seasons matches the reproductive period of the species (Both *et al.,* 2008; Santos *et al.,* 2008), showing that anuran species occupying grasslands are sensitive to seasonal changes in primary productivity and grassland phenology (Soares *et al.,* 2005; Overbeck *et* *al.,* 2006). Individuals of *Physalaemus henselii* are more reproductively active than other species during the cold seasons (Maneyro *et al.,* 2008). In turn, individuals of *P. cuvieri*, *L. latrans* and *Physalaemus* aff. *gracilis* are more reproductively active during warm seasons (Camargo *et al.*, 2005; Kwet *et al.,* 2010; Maneyro and Carreira, 2012), although *Physalaemus* aff. *gracilis* tend to be reproductively active throughout the year (Bortolini *et al.,* 2018). Such reproductive patterns of different species explain the seasonal change in composition observed in the grassland anuran assemblage.

Although our study was limited to two sites, our data of anuran abundances collected over two years revealed seasonal variations in the structure of the anuran assemblages. Our main result was the identification of seasonal variation in the taxonomic and phylogenetic composition of ground-dwelling anuran assemblages, but this variation was not found for their functional composition. Such results can be explained by the ability of functionally similar and generalist species, which are less dependent on water availability, to transit between habitats. For example, *Physalaemus* aff. *gracilis* and *P. cuvieri*, occurring in both the forest and grassland habitats, are habitat-generalist species which reproduce in one habitat (where the species are more abundant) and acquire food in the other (Maragno *et al*., 2013). The movement of generalist species decreases the differences in functional composition over time due to the species' high similarity in size, reproductive mode and habitat use (Maragno *et al*., 2013). Finally, we observed that the seasonal variation in the phylogenetic composition was more pronounced in warm (spring-summer) than in cold seasons (autumn-winter). The seasonal variation in the phylogenetic structure was caused by the occurrence of *Elachistocleis bicolor*, the most phylogenetically distinct species (Figure 3). *Elachistocleis bicolor* occurs mainly in open areas and shows explosive reproduction during the rainy periods of warm seasons (Kwet *et al*., 2010).

We observed seasonal variations in the taxonomic and phylogenetic composition, but not in the functional composition, of the anuran assemblages. Changes in habitat structure due to climate seasonality influenced the taxonomic and phylogenetic structure of anuran assemblages by promoting the replacement of species with similar functional traits. We perceived that the abundance of species that are adapted to and reproductively active during the cold seasons decreases with the increase of the abundance of species that are adapted to and reproductively active during the warm seasons. Overall, the results indicate that the species of anurans that fluctuate in abundance over the seasons belong to different lineages but have similar life-history traits. The patterns registered in our study provide a benchmark on how communities from native forests and grasslands vary in composition through time.

Acknowledgements

We thank the Universidade de Passo Fundo (UPF) for their logistical support, and IBAMA (Brazilian Environmental Institute) for authorizing the researcher license (process # 02/2002). We also thank the Rio Grande do Sul state police and private landowners for granting permission to access study areas. We thank the *Núcleo de Arquitetura e Desenvolvimento Urbano e Comunitário* (NADUC-UPF) for providing the map, and the undergraduate students from UPF for their assistance with fieldwork.

References

ACHAVAL, F.; OLMOS, A. 2007. *Anfibios y reptiles del uruguay*. Montevideo, 160 p.

ALVARES, C.A.; STAPE, J.L.; SENTELHAS, P.C.; GONÇALVES, J.L.M.; SPAROVEK, G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, **22**(6):711-728. https://doi.org/10.1127/0941-2948/2013/0507

ANDERSON, M.J.; ELLINGSEN, K.E.; MCARDLE, B.H. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, **9**(6):683-693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

BOLZAN, A.M.R.; SACCOL, S.A.; SANTOS, T.G. 2016. Composição e diversidade de anuros da maior unidade de conservação no bioma Pampa, Brasil. *Biota Neotropica*, **16**(2):e20150113.

BORGES-MARTINS, M.; COLOMBO, P.; ZANK, C.; BECKER, F.G.; MELO, M.T.Q. 2007. Anfíbios. *In*: F.G. BECKER; R.A. RAMOS; L.A. MOURA (eds.), *Biodiversidade: Regiões da Lagoa do Casamento e dos butiazais de Tapes, Planície Costeira do Rio Grande Do Sul*. Brasília, Ministério Do Meio Ambiente, p. 276-291.

BORTOLINI, S.V.; GONÇALVES, F.A.; ZANELLA, N. 2018. Reproductive aspects of a population of *Physalaemus gracilis* (BOULENGER 1883) (Anura: Leptodactylidae) from south Brazil. *Neotropical Biology and Conservation*, **13**(1):37-44. https://doi.org/10.4013/nbc.2018.131.05

BOTH, C.; KAEFER, I.L.; SANTOS, T.G.; CECHIN, S.Z. 2008. An austral anuran assemblage in the Neotropics: seasonal occurrence correlated with photoperiod. *Journal of Natural History*, **42**(3-4):205-222. https://doi.org/10.1080/00222930701847923

CAMARGO, A.; NAYA, D.E.; CANAVERO, A.; ROSA, I. DA; MANEYRO, R. 2005. Seasonal activity and the body size–fecundity relationship in a population of Physalaemus gracilis (Boulenger, 1883) (Anura, Leptodactylidae) from Uruguay. *Annales Zoological Fennici,* **42**(5):513-521.

CANAVERO, A.; ARIM, M.; NAYA, C.A.; ROSA, I.; MANEYRO, R. 2008. Activity patterns in an anuran assemblage: the role of seasonal trends and weather determinants. *North-Western Journal of Zoology,* **4**(1):29-41.

DEBASTIANI, V.J.; PILLAR, V.D. 2012. SYNCSA — R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. *Bioinformatics*, **28**(15):2067-2068. https://doi.org/10.1093/bioinformatics/bts325

DIXO, M.; VERDADE, V.K. 2006. Herpetofauna de serrapilheira da Reserva Florestal de Morro Grande, Cotia (SP). *Biota Neotropica*, **6**(2):1-20. https://doi.org/10.1590/S1676-06032006000200009

DUELLMAN, W.E.; TRUEB, L. 1994. *Biology of amphibians.* Baltimore, The Johns Hopkins University Press, 696 p.

EMBRAPA. 2016. Informações meteorológicas/Meteorological reports. Laboratório de Agrometeorologia, EMBRAPA Trigo, Passo Fundo, RS/BR. Available at: http://www.cnpt.embrapa.br/pesquisa/agromet/app/principal/. Accessed on: 10/10/2016.

FROST, D.R. 2018. Amphibian Species of the World: an Online Reference. Version 6.0. Available at: http://research.amnh.org/herpetology/amphibia/index.html. Accessed on: 29/08/2018.

GONÇALVES, D.S.; CRIVELLARI, L.B.; CONTE, C.E. 2015. Linking environmental drivers with amphibian species diversity in ponds from subtropical grasslands. *Anais da Academia Brasileira de Ciências,* **87**(3):1751-1762. https://doi.org/10.1590/0001-3765201520140471

HADDAD, C.F.B.; PRADO, C.P.A. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. *Bioscience,* **55**(3):207-217. https://doi.org/10.1641/0006-3568(2005)055[0207:RMIFAT]2.0.CO;2

HADDAD, C.F.B.; TOLEDO, L.F.; PRADO, C.P.A. 2008. *Anfíbios da Mata Atlântica.* São Paulo, Editora Neotropica LTDA, 243 p.

HADDAD, C.F.B.; TOLEDO, L.F.; PRADO, C.P.A.; LOEBMANN, D.; GASPARINI, J.L.; SAZIMA, I. 2013. *Guia dos anfíbios da Mata Atlântica – diversidade e biologia.* São Paulo, Anolis Books, 542 p.

HARTMANN, M.T.; HARTMANN, P.A.; HADDAD, C.F.B. 2010. Reproductive modes and fecundity of an assemblage of anuran amphibians in the Atlantic rainforest, Brazil. *Iheringia,* **100**(3):207-215. https://doi.org/10.1590/S0073-47212010000300004

IBGE. 2002. Mapas do clima do Brasil/Brazil climate maps. Ministério do Planejamento, Orçamento e Gestão, Brasília/DF. Instituto Brasileiro de Geografia e Estatística. Available at: ftp://geoftp.ibge.gov.br/mapas_tematicos/mapas_murais/clima.pdf. Accessed on: 10/10/2015.

INGER, R.F.; COLWELL, R.K. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. *Ecological Monographs,* **47**(3):229-253. https://doi.org/10.2307/1942516

JIMÉNEZ-ROBLES, O.; GUAYASAMIN, J.M.; RON, S.R.; DE LA RIVA, I. 2017. Reproductive traits associated with species turnover of amphibians in Amazonia and its Andean slopes. *Ecology and Evolution,* **7**(8):2489-2500. https://doi.org/10.1002/ece3.2862

KÖPPEN, W. 1948. *Climatología: Con un estudio de los climas de la Tierra.* México, Fondo de Cultura Econômica, 479 p.

KWET, A.; LINGNAU, R.; DI-BERNARDO, M. 2010. *Pró-Mata: Amphibians of the Serra Gaúcha, South of Brazil.* 2nd ed., Porto Alegre, EDIPUCRS, 148 p.

LEGENDRE, P.; LEGENDRE, L. 2012. *Numerical ecology.* 3rd ed., Oxford, Elsevier, 1006 p.

LEGENDRE, P. 2014. Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography,* **23**(11):1324-1334. https://doi.org/10.1111/geb.12207

LIEBSCH, D.; MIKICH, S.B. 2009. Fenologia reprodutiva de espécies vegetais da Floresta Ombrófila Mista do Paraná, Brasil. *Brazilian Journal of Botany,* **32**(2):375-391. https://doi.org/10.1590/S0100-84042009000200016

LONGHI, R.L.; LONGHI, S.J.; CHAMI, L.B.; WATZLAWICK, L.F.; EBLING, A.A. 2011. Produção de serapilheira e retorno de macronutrientes em três grupos florísticos de uma Floresta Ombrófila Mista, RS. *Ciência Florestal,* **21**(4):699-710. https://doi.org/10.5902/198050984514

MANEYRO, R.; CARREIRA, S. 2012. *Guía de anfibios del Uruguay.* Montevideo, Ediciones de la Fuga, 207 p.

MANEYRO, R.; NÚÑEZ, D.; BORTEIRO, C.; TEDROS, M.; KOLENC, F. 2008. Advertisement call and female sexual cycle in Uruguayan populations of Physalaemus henselii (Anura, Leiuperidae). *Iheringia,* **98**(2):210-214. https://doi.org/10.1590/S0073-47212008000200007

MARAGNO, F.P.; SANTOS, T.G.; CECHIN, S.Z. 2013. The role of phytophysiognomies and seasonality on the structure of ground-dwelling anuran (Amphibia) in the Pampa Biome, southern Brazil. *Anais da Academia Brasileira de Ciências,* **85**(3):1105-1115. https://doi.org/10.1590/S0001-37652013005000042

OLIVEIRA, M.C.L.M.; SANTOS, M.B.; LOEBMANN, D.; HARTMAN, A.; TOZETTI, A.M. 2013. Diversity and associations between coastal habitats and anurans in southernmost Brazil. *Anais da Academia Brasileira de Ciências,* **85**(2):575-583. https://doi.org/10.1590/S0001-37652013005000036

OVERBECK, G.E.; MÜLLER, S.C.; PILLAR, V.D.; PFADENHAUER, J. 2006. Floristic composition, environmental variation and species distribution patterns in burned grassland in southern Brazil. *Brazilian Journal of Biology,* **66**(4):1073-1090. https://doi.org/10.1590/S1519-69842006000600015

OKSANEN, J.; BLANCHET, F.G.; FRIENDLY, M.; KINDT, R.; LEGENDRE, P.; MCGLINN, D.; MINCHIN, P.R.; O'HARA, R.B.; SIMPSON, G.L.; SOLYMOS, P.; STEVENS, M.H.H.; SZOECS, E.; WAGNER, H. 2018. Vegan: Community Ecology Package. R package version 2.4-6.

PARADIS, E.; CLAUDE, J.; STRIMMER, K. 2004. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics,* **20**(2):289-290. https://doi.org/10.1093/bioinformatics/btg412

PILLAR, V.D.; DUARTE, L.D.S.; SOSINSKI, E.E.; JONER, F. 2009. Discriminating trait-convergence and trait-divergence assembly patterns in ecological community gradients. *Journal of Vegetation Science,* **20**(2):334-348. https://doi.org/10.1111/j.1654-1103.2009.05666.x

PRADO, C.P.A.; UETANABARO, M.; HADDAD, C.F.B. 2005. Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. *Amphibia-Reptilia,* **26**(1):211-221. https://doi.org/10.1163/1568538054253375

PUPIN, N.C.; GASPARINI, J.L.; BASTOS, R.P.; HADDAD, C.F.B.; PRADO, C.P.A. 2010. Reproductive biology of an endemic Physalaemus of the Brazilian Atlantic forest, and the trade-of between clutch and egg size in terrestrial breeders of the P. signifer group. *Herpetological Journal,* **20**(1):147-156.

PYRON, R.A.; WIENS, J.J. 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution,* **61**(2):543-583. https://doi.org/10.1016/j.ympev.2011.06.012

R CORE TEAM. 2017. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

REVELL, L.J. 2012. Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution,* **3**(2):217-223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

RIEVERS R.C.; PIRES, R.M.S.; ETEROVICK, P.C. 2014. Habitat, food, and climate affecting leaf litter anuran assemblages in an Atlantic forest remnant. *Acta Oecologica,* **58**(1):12-21. https://doi.org/10.1016/j.actao.2014.04.003

RODRIGUES, D.J.; LOPES, F.S.; UETANABARO, M. 2003. Padrão reprodutivo de Elachistocleis bicolor (Anura, Microhylidae) na Serra da Bodoquena, Mato Grosso do Sul, Brasil. *Iheringia,* **93**(4):365-371. https://doi.org/10.1590/S0073-47212003000400003

SANTOS, T.G.; KOPP, K.; SPIES, M.R.; TREVISAN, R; CECHIN, S.Z. 2008. Distribuição temporal e espacial de anuros em área de Pampa, Santa Maria, RS. *Iheringia,* **98**(2):244-253. https://doi.org/10.1590/S0073-47212008000200013

SANTOS-PEREIRA, M.; CANDATEN, A.; MILANI, D.; OLIVEIRA, F.B.; GARDELIN, J.; ROCHA, C.F.D. 2011. Seasonal variation in the leaf-litter frog community (Amphibia: Anura) from an Atlantic Forest Area in the Salto Morato Natural Reserve, southern Brazil. *Zoologia,* **28**(6):755-761. https://doi.org/10.1590/S1984-46702011000600008

SILVA, F.R.; ALMEIDA-NETO, M.; PRADO, V.H.M.; HADDAD, C.F.B.; ROSSA-FERES, D.C. 2012. Humidity levels drive reproductive modes and phylogenetic diversity of amphibians in the Brazilian Atlantic Forest. *Journal of Biogeography,* **39**(9):1720-1732. https://doi.org/10.1111/j.1365-2699.2012.02726.x

SOARES, A.B.; CARVALHO, P.C.F.; NABINGER, C.; SEMMELMANN, C.; TRINDADE, J.K.; GUERRA, E.; FREITAS, T.S.; PINTO, C.E.; FONTOURA JR, J.A.; FRIZZO, A. 2005. Produção animal e de forragem em pastagem nativa submetida a distintas ofertas de forragem. *Ciência Rural,* **35**(5):1148-1154. https://doi.org/10.1590/S0103-84782005000500025

TRIMBLE, M.J.; VAN AARDE, R.J. 2014. Amphibian and reptile communities and functional groups over a land-use gradient in a coastal tropical forest landscape of high richness and endemicity. *Animal Conservation,* **17**(5):441-453. https://doi.org/10.1111/acv.12111

TSIANOU, M.A.; KALLIMANIS, A.S. 2016. Different species traits produce diverse spatial functional diversity patterns of amphibians. *Biodiversity and Conservation,* **25**(1):117-132.
https://doi.org/10.1007/s10531-015-1038-x

URBINA-CARDONA, J.N.; OLIVARES-PÉREZ, M.; REYNOSO, V.H. 2006. Herpetofauna diversity and microenvironment correlates across a pasture–edge–interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. *Biological Conservation*, **132**(1):61-75. https://doi.org/10.1016/j.biocon.2006.03.014

VALDEZ, V.; MANEYRO, R. 2016. Reproductive biology of *Odontophrynus americanus* females (Duméril e Bribon, 1841) (Anura, Cycloramphidae) from Uruguay. *Pan-American Journal of Aquatic Sciences*, **11**(3):188-196.

XAVIER, A.L.; NAPOLI, M.F. 2011. Contribution of environmental variables to anuran community structure in the Caatinga Domain of Brazil. *Phyllomedusa*, **10**(1):45-64.
https://doi.org/10.11606/issn.2316-9079.v10i1p45-64

Submitted on May 14, 2018
Accepted on September 30, 2018