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Acoustic space partition by four syntopic Hylidae (Anura) in open habitat in Central Brazil

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ABSTRACT: The use and partition of the acoustic space by anuran species are of special interest in evaluating inter-specific interactions in acoustic traits. Here we evaluate the acoustic space partitioning by four species of Hylidae at Estação Ecológica de Águas Emendadas, Distrito Federal, Central Brazil. The acoustic niche overlap among species was smaller than expected by chance, indicating low overlap in the use of the acoustic space by these species. The low overlap in call parameters found is related to their phylogenetic distances, suggesting that the acoustic space use in the Cerrado is determined mainly by historical factors than by ecological constraints in the acoustic overlap. On the other hand, the low overlap in call parameters suggests that the acoustic space in the Cerrado is shared by species of different hylid lineages.

Keywords: anurans, advertisement call, Brazilian Cerrado, null model, phylogenetic distance.

RESUMO (Partição do espaço acústico por quatro espécies simpátricas de Hylidae em área aberta no Brasil Central): O uso e partição do espaço acústico por espécies de anuros é de especial interesse para avaliar interações interespecíficas em traços acústicos. Aqui, avaliamos a partição do espaço acústico de quatro espécies de Hylidae na Estação Ecológica de Águas Emendadas, Distrito Federal, Brasil central. A sobreposição do nicho acústico entre as espécies foi menor do que o esperado ao acaso, indicando baixa competição no uso do espaço acústico por essas espécies. A baixa sobreposição nos parâmetros de canto encontrados está relacionada às suas distâncias filogenéticas, sugerindo que o uso do espaço acústico no Cerrado é determinado principalmente por fatores históricos que por pressões ecológicas pela partilha do recurso. Por outro lado, a pequena sobreposição nos parâmetros acústicos sugere que o espaço acústico no Cerrado pode ser compartilhado com eficiência por espécies de diferentes linhagens de hilídeos.

Palavras-chave: anuros, canto de anúncio, Cerrado brasileiro, modelo nulo, distância filogenética.

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INTRODUCTION

Ecological communities are comprised of a set of interacting species that co-occur in space and time (McPeek & Miller 1996, Begon *et al.* 2007). Since the use of resources by one species may affect the availability of this resource by another species, competition has been historically considered the most important ecological interaction structuring biological communities (Gotelli & McCabe 2002, Michalet *et al.* 2015, Gallien *et al*. 2017). Thus, studies focusing on resource partition in communities are of special interest in Ecology (Begon *et al.* 2007).

Acoustic communication plays a pivotal role in Anuran behavior and reproductive biology, and several studies have focused on the use of acoustic parameters and space in anuran communities from open areas (Rossa-Feres & Jim 2001, Vasconcelos & Rosa-Ferres 2008, Lima *et al.* 2019). The putative partitioning of the acoustic (signal) space has been suggested as one of the causes of mating calls diversification in frogs (Chek *et al.* 2003), especially due to interference competition between species, that may affect male fitness. Male calls are the main fitness signal for female selection and male-male competition, thus being extremely important in anuran sexual selection (Duellman & Trueb 1986, Kelley 2004, Bradbury & Vehrencamp 2011, Kohler *et al.* 2017).

When two species are using the same acoustic channel, the sound emitted by one species can mask the sound emitted by another one, creating a putative pressure for sound differentiation and diversification. Lower overlap in acoustic parameters between animal calls and background noise (including the noise produced by another species in the habitat) can be produced by long term selection or by behavioral adjustments on timing and calling characteristics, depending on the intensity, predictability, and duration of the background noise (Brumm 2006, Röhr *et al.* 2016).

Call structure is an important feature associated with species' signals, allowing inter-specific recognition, avoiding species hybridization (Taper & Case 1992, Littlejohn 1977), and allowing males' coexistence in the same acoustic space during reproductive periods (Cardoso *et al*. 1989, Cardoso & Velliard 1990). Because of this, spectral acoustic parameters are strongly shaped by sexual selection and are less variable than temporal parameters (such as calling rate) (Gerhardt 2012, Guarnizo *et al*. 2012, Röhr *et al*. 2020). On the other hand, temporal parameters are much more variable between males, having a much more relevant role on mate selection by females (e.g. Bernal *et al*. 2009, Röhr *et al*. 2020). Thus, temporal parameters are much more prone to respond to local environmental conditions (e.g. Littlejohn 2001, Wells 2007), while spectral parameters are strongly shaped by phylogeny (Garey *et al*. 2018).

In restricted acoustic spaces, the communication efficacy depends on limiting aspects associated with the environment, such as the background noise, the number of species or individuals using the same frequency range, or the overlap of frequency ranges. Considering the effects of competition for acoustic space, it is important to guarantee a successful signal transmission when mate attraction is essential for species permanence in the environment (Greenfield & Karandinos 1979, Greenfield 1983, Löfstedt & Pers 1985, Löfstedt *et al*. 1991). To guarantee the signal transmission, anurans use strategies to avoid the acoustic competition (Sinsch *et al*. 2012, Protázio *et al*. 2014, Toledo *et* *al*. 2015), including adaptations to avoid or reduce interspecific acoustic interferences (Boul *et al*. 2007). These strategies underlie the reproductive isolation between species (Duellman 1967, Wells 1977, Lamb & Avise 1986, Cardoso & Vielliard 1990) as well as the species recognition (Wells 2007, Pombal 2010), favoring the call diversification within communities (Bernal *et al*. 2009). Acoustic space represents an environmental resource that can be used by different species or lineages at the same time (Sinsch *et al*. 2012, Protázio *et al*. 2014, Toledo *et al*. 2015). Several studies used null models to evaluate and compare patterns observed in communities (Harvey *et al*. 1983, Colwell & Winkler 1984). However, very few studies have used this tool to evaluate acoustic signals overlaps within frog communities (Otte 1989, Lüddecke *et al*. 2000, Chek *et al*. 2003) and on a local scale (Garey *et al*. 2018).

In the Cerrado biome, anurans are active mainly during the reproductive periods (Santoro & Brandão 2014), forming large interspecific choruses around available water bodies. Since advertisement calls are emitted while several species can be found calling simultaneously at reproductive habitats in Brazilian Cerrado (e.g. Cardoso & Haddad 1992, Pombal 1997), we are interested in the patterns of co-occurrence on call parameters of four abundant Cerrado hylid species, that are commonly found simultaneously at breeding sites (Brandão *et al*. 2016), presenting extended reproductive period (sensu Wells 1977). More specifically, we tested whether the observed overlap of the acoustic spectral niche among species in the same family is different from what is found by chance, using a null model approach (Gotelli 2000). We also evaluated if the observed pattern is related to the phylogenetic distances between the studied frog species (Jetz & Pyron 2018), highlighting the role of historical processes on the partition of acoustic space by these species.

MATERIALS AND METHODS

We conducted the study in Estação Ecológica de Águas Emendadas (ESECAE), an important protected area located in the northeast portion of the Distrito Federal in Brasília, Brazil (Figure 1), that occupies 10,547.21 ha (De Carvalho 2008). The climate is tropical (Aw) and tropical altitude (Cw), according to Koppen's classification (Álvares *et al*. 2013). The rainfall is concentrated between November and January and the dry season runs from June to October. The annual average precipitation is 1,552.1 mm and the maximum evapotranspiration is concentrated between August and September (Maia & Baptista 2008). ESECAE contains several Cerrado physiognomies with open fields, wet grasslands, cerrado *stricto sensu*, gallery forests, mesophytic forests, and dense cerrado formations (Maury *et al*. 1994, Silva-Júnior & Felfili 1996). We collected data close to "Lagoa Bonita" (15°34'55.87''S/ 47°41'38.54''W; 960 m a.s.l.), a natural lake surrounded by buriti palms (*Mauritia flexuosa*), that grow over hydromorphic soil. At the lake surroundings, there are patches of mesophytic forest, cerrado *stricto sensu*, and open wet fields (Munhoz & Ribeiro 2008).

We sampled along a floodable area delimited by an artificial drainage trench close to the edge of two deactivated fishponds near the lake (15°35'21.10''S/ 47°41'55.98''W). In each area, we installed 18 quadrants of 25 m^2, totaling 36 quadrants (900m^2). The investigated species were the yellow-spotted treefrog *Boana albopunctata* (Spix 1824), the Lagoa Santa treefrog *Dendropsophus rubicundulus* (Reinhardt & Lütken

1862), the snouted treefrog *Scinax fuscovarius* (Lutz 1925,) and the brown-bordered snouted treefrog *Scinax fuscomarginatus* (Lutz 1925).

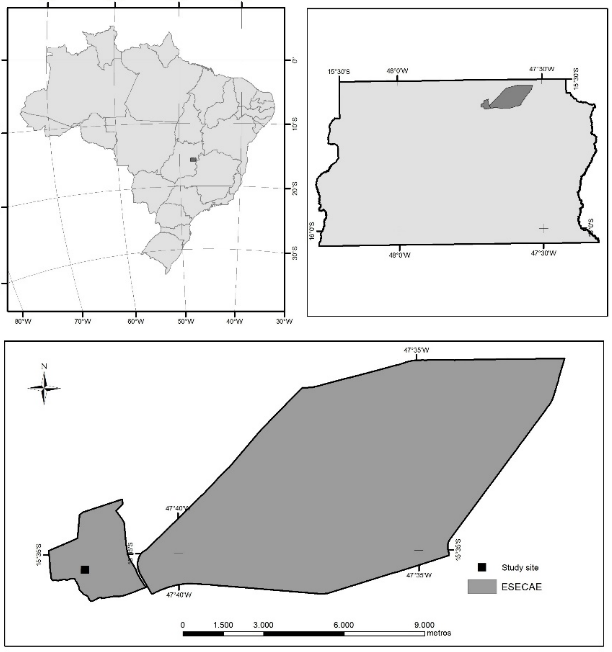

Figure 1. Location of the study area. Polygon (dark gray) representing the Estação Ecológica de Águas Emendadas (ESECAE), Brasília-DF, and the location of the highlighted sampling area (black square).

These species were recorded for eleven months, between March 2016 and February 2017, twice a week, from 0700 to 0900 PM. To perform recordings, we used a Marantz PMD 222 recorder or a Zoom H1 Handy Recorder 200M stereo recorder, and a Seinheiser ME 66 unidirectional microphone. All recordings were done using mono-channel, with a 44.1Hz sample rate and 16 bits. During recordings, we kept a standard distance of 50 cm from the calling individual, and after recording, we captured and marked each one by toe-clipping (Heyer *et al.* 1995), to avoid pseudoreplication.

We edited the sound in Audacity 2.0.5 software (Kohler *et al.* 2017), with a sampling rate of 44,100 Hz and Raven Pro 1.5 Beta (Bioacoustics Research Program 2012). The oscillogram, spectrogram, and amplitude spectrum were generated using R software in Seewave package v. 1.6 (Sueur *et al.* 2008). The settings used were: Hanning window, 80% overlap, and 256 point resolution (FFT). The values extracted for the spectral parameters were the minimum and maximum frequencies (Hz). The parameters nomenclature follows Duellman & Trueb (1994), Wells (2007), Preininger *et al.* (2016), and Kohler *et al.* (2017).

We obtained the spectral parameters used in the analysis (maximum and minimum frequencies: F_{max} and F_{min}). Although the dominant frequency is widely used in anuran bioacoustics studies, we decided to use minimum and maximum frequencies as more confident measurements of acoustic space use, since dominant or peak frequencies represent a unique point in the acoustic space, while the range between minimum and maximum frequencies represents a window of space used by each species. The same parameters were used for other animal groups, such as grasshoppers and birds (Schmidt *et al.* 2012; Dingle *et al.* 2008), and in studies evaluating the acoustic space use by dendrobatid frogs (Amézquita *et al.* 2011).

We used Czechanowski niche overlap index (Feinsinger *et al.* 1981) to evaluate the overlap in spectral calling traits. This index was calculated for pairs of species and ranges from 0 (no overlap) to 1 (complete overlap). We evaluated whether observed overlap in the use of acoustic space differed from that expected by chance, using null models (Gotelli 2000).

The studied species' use of frequency range varied from 843.8 to 4979.83 Hz. This frequency range was subdivided into 42 channels of 100 Hz for the analysis (Schmidt *et al.* 2012). These channels were considered the range of acoustic space that a species can use. Significance values were determined by comparing the observed overlap index with the values obtained by chance, considering α < 0.05. We used the Niche Overlap module of the EcosimR program (Gotelli & Ellisson 2013) on platform R version 2.15.1 (R Development Core Team 2011), with the randomization algorithms RA2 and RA3, applied to 10,000 randomizations. Randomization algorithms differ in the rearrangement of the original community data and are recommended for their effectiveness in niche overlapping studies with different resource states (Schmidt *et al*. 2013). RA2 algorithm replaces the chosen variable in the original matrix with a uniform number between zero and one but keeps the structure of zeros in the original matrix (Winemiller & Pianka 1990). If the vocal apparatus in anuran species has morphological limitations that constrain sound parameters, then RA2 may be the appropriate algorithm to define the species in the acoustic space, i.e. putative morphophysiological constraints on sound emissions for any species are expressed in the RA2 algorithm. The RA3 algorithm maintains the niche width of the species (frequency distribution), whereas each zero of the matrix is rearranged. Considering that the presence of one species limits the access of another species to a certain portion of the sound space, RA3 may be the appropriate measure to detect some patterns of co-occurrence in the assembly structure.

We also evaluated the phylogenetic distances of the species employing the function *cophenetic.phylo* in the ape package (Paradis *et al.* 2004), which considers differences in genetic changes along branch-lengths, based on Jetz & Pyron's (2018) phylogeny. To test the relationship between genetic distance (transformed for log) and call frequency overlap (values transformed for arcsene of square root), we used a linear model.

RESULTS AND DISCUSSION

We recorded calls of 46 individuals of *B. albopunctata*, 40 *D. rubicundulus*, 31 *S. fuscomarginatus*, and 27 *S. fuscovarius*. The frequency range observed in recordings is, with some differences, in accordance with the literature. For *B. albopunctata*, however, the obtained range was from 1808.8 to 3703.7 Hz, which is higher than the values described in the literature (930 to 2,500 Hz; Furtado *et al.* 2016). For *D. rubicundulus*, calls range from 3609.4 to 4306.6 Hz (3093 to 4171 Hz; Teixeira & Giareta 2015) and for *S. fuscomarginatus* we obtained values from 3656.2 to 5081.8 Hz (3512 to 4940 Hz; Bastos *et al*. 2003). For *S. fuscovarius*, we obtained a wider range, going from 990.5 to 4171.9 Hz, while the maximum frequency described in the literature is much lower (680 to 960 Hz; Kwet 2001). The differences observed in the ranges of some parameters should be the result of a larger sampled number in our study, to differences in individuals sizes between localities or taxonomic issues related to *S. fuscovarius* populations (see comments on species in De La Riva *et al.* 2000). In Figure 2, we present the oscillogram and the spectrogram representation of the studied species.

According to niche overlap analyses, the observed overlap index was lower than expected by chance (p = 0.03, mean of simulated index = 0.32, observed index = 0.28), when using the RA2 algorithm. The same result occurred using the RA3 algorithm, where the probability of random use of the parameters was higher than the observed index value (p = 0.001, mean of the simulated index = 0.34, observed index = 0.28). In both situations, the null model suggests that the use of acoustic space by these species is structured (Figure 3).

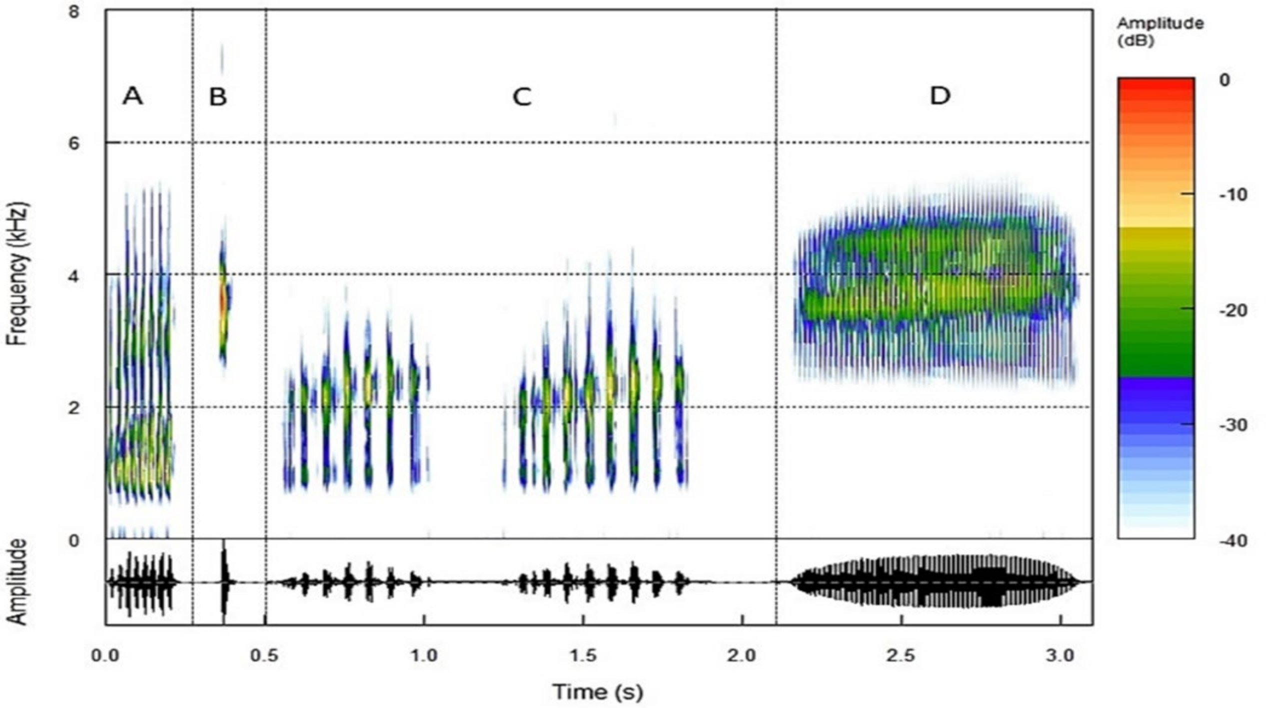

Figure 2. Comparison of wave oscillogram (amplitude in dB vs time in seconds, below) and spectrogram (frequency in kHz vs time, above) of the four studied species, being *Scinax fuscovarius* (A), *Dendropsophus rubicundulus* (B), *Boana albopunctata* (C), and *Scinax fuscomarginatus* (D).

When we evaluated the spectral overlap of calls from studied species, we found a higher overlap value for *B. albopunctata* vs. *S. fuscovarius*, then for *D. rubicundulus* vs. *S. fuscomarginatus*. The lowest overlap value was registered for *B. albopunctata* vs. *S. fuscomarginatus* (Table 1). We recovered that these species are well distributed along the proposed phylogeny for the Hylidae Family (Figure 4), except for the *Scinax* species (*S. fuscomarginatus* and *S. fuscovarius*), also recovering high values for branch-lengths (Table 1).

Table 1. Phylogenetic distance (above diagonal) and spectral overlap (below diagonal) between pairs of studied species. The acronyms are *D. rubi* (*Dendropsophus rubicundulus*), *B. albo* (*Boana albopunctata*), *S. fuscov* (*Scinax fuscovarius*), *S. fuscom* (*Scinax fuscomarginatus*).

	D. rubi	***B. albo***	***S. fuscov***	***S. fuscom***
D. rubi		155.328	137.038	137.038
B. albo	0.019		155.329	155.329
S. fuscov	0.246	0.680		66.598
S. fuscom	0.556	0.009	0.193	

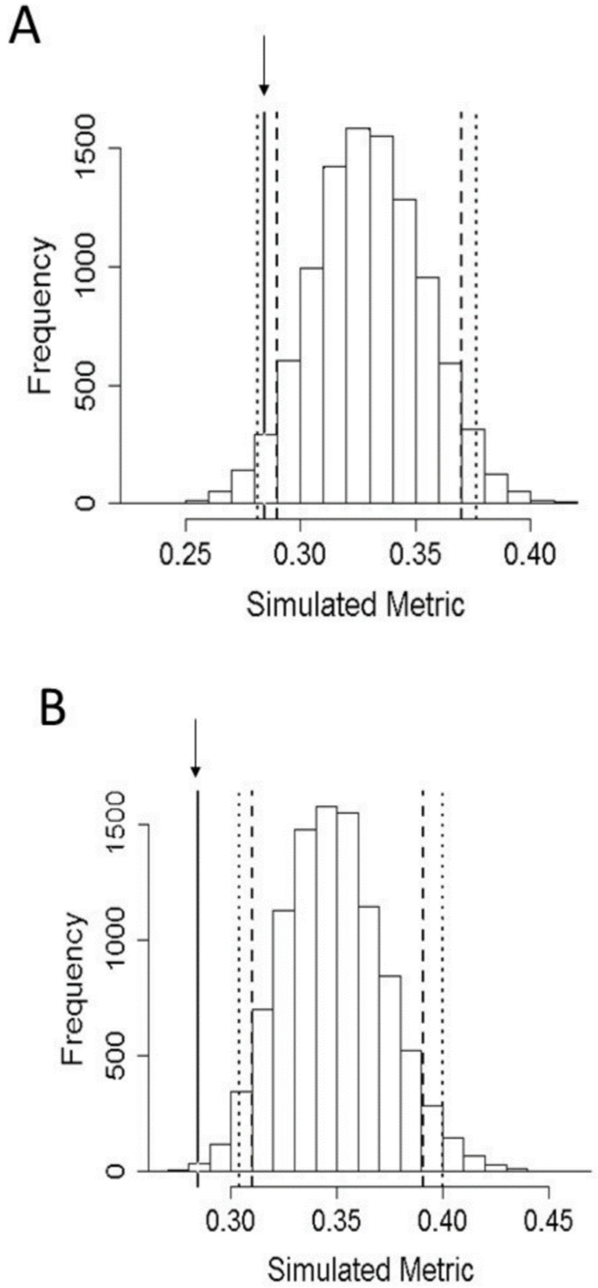

Figure 3. Frequency distribution of the observed (0.28, indicated by an arrow in A e B) and modeled values of niche overlap between the four species of Hylidae (*Dendropsophus rubicundulus, Scinax fuscovarius, Scinax fuscomarginatus,* and *Boana albopunctata*), at the Estação Ecológica de Águas Emendadas, using the RA2 (A; p = 0.032) and RA3 (B; p = 0.001) algorithms. The observed overlap was lower than that expected at random in both cases. Dotted and dashed lines: confidence interval.

We found that the studied Hylidae species overlapped less than expected by chance in the use of acoustic parameters analyzed. Although similar results are often considered related to pressures generated by competition (Gascon 1991), and to non-random patterns of community structure (Balance *et al*. 1997, Bourne & York 2001, Morris *et al.* 2004, Boschilia *et al.* 2008, Kunte 2008, Kruger *et al*. 2010, Razgour *et al.* 2011), spectral call parameters in frogs occurring in open or in forested areas in Southeast Brazil showed high phylogenetic signal (Garey *et al*. 2018), suggesting that low overlap in these parameters is often produced by historical than ecological factors. Despite our low number of evaluated species, we found a negative relationship between phylogenetic distance and call frequency overlap between species pairwise ($r^2 = 0.01$; $p = 0.73$; $Y = -0.08 + 4.32X$). Despite the low explanatory power of our model, it suggests that we cannot assume that competition has a relevant effect on the observed low overlap on species call parameters. It is interesting to note that, despite the higher observed overlap between *Boana albopunctata* vs *Scinax fuscovarius* calls, *Boana albopunctata* usually calls from higher perches in vegetation, whereas *Scinax fuscovarius* males often do it from the soil or other lower perches, suggesting that the use of other ecological dimensions can minimize the putative confounding effects of the recovered frequency overlap.

The selection of stereotyped call parameters in frogs is relevant to guarantee species isolation by allowing successful recognition among members of the same species during reproduction (Bosh & De La Riva 2004). Differentiation in resource utilization allows for species coexistence (Gilbert *et al*. 2008), and we found that these lineages are presenting low overlap on calling frequency. Since the acoustic space is circumstantially limiting for species, the overlap in one dimension tends to lead to differentiation in others, as can be expected when

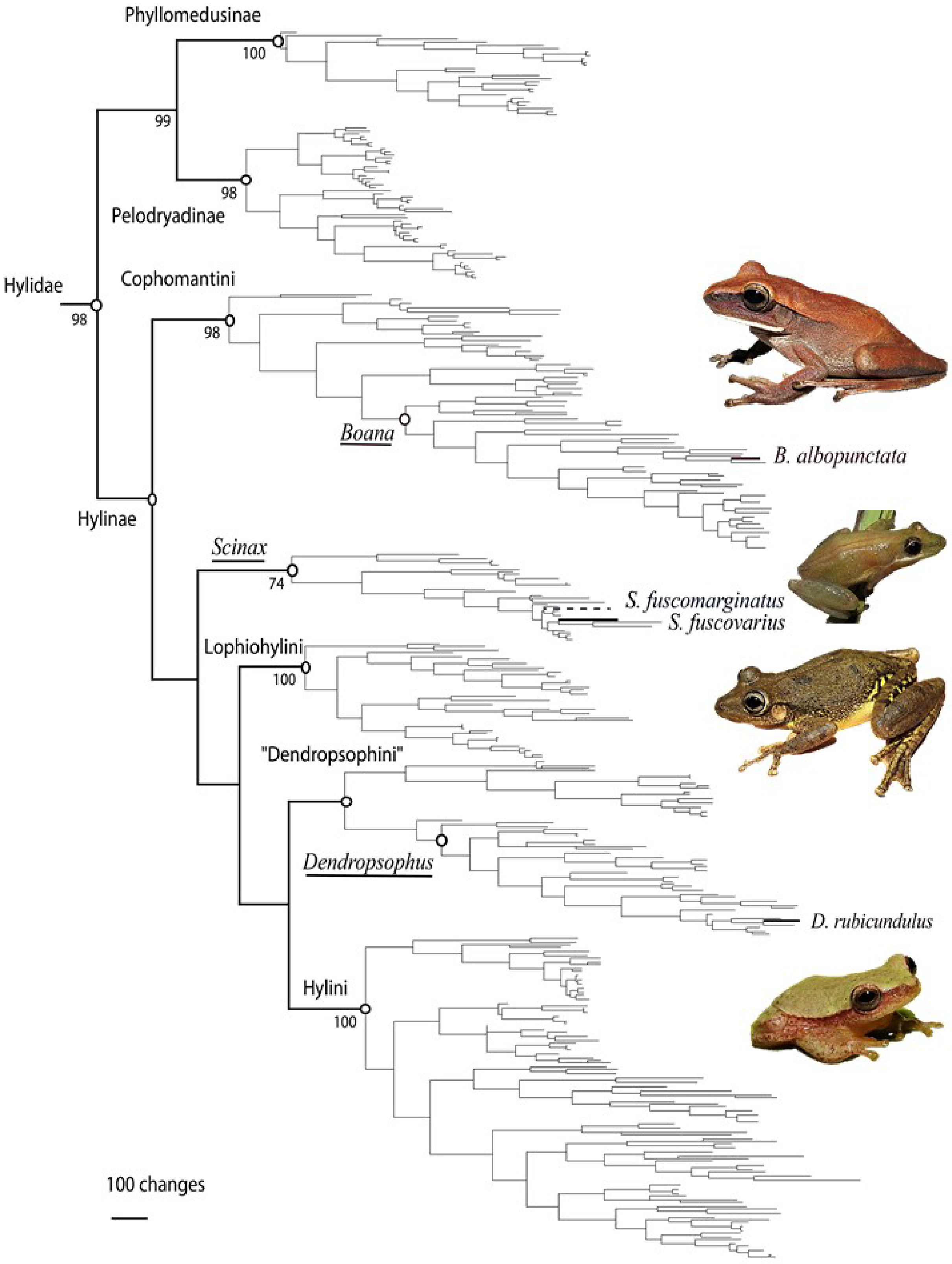

Figure 4. Phylogenetic tree of the Hylidae Family, showing subfamilies and genera of the four studied species (from top to below, *Boana albopunctata*, *Scinax fuscomarginatus*, *Scinax fuscovarius*, and *Dendropsophus rubicundulus*). Bootstrap support values are indicated at nodes. Adapted from Wiens et al. (2010) and Duellman et al. (2016).

there is niche complementarity (Santos & Rossa-Feres 2007, Silva *et al*. 2008), an interesting aspect of calling evolution that can be assessed in future research, especially in closely related species.

Differences in the spectral parameters by different lineages can allow for the co-existence of high phylogenetic diversity of frogs observed in the Cerrado biome (see Silvano *et al*. 2016), including the species studied herein. The multidimensional characteristic of advertisement calls (Gerhardt 2012), its structural complexity, and the typical species behavior, and habitat use suggests that phylogeny exerts a strong role in the structure of Cerrado amphibian communities, contributing for the observed co-occurrence of several species in the same frog family (Ryan *et al*. 1990, Bould 2007, Kaeffer & Lima 2012).

The selection of different environmental features that can increase reproductive fitness, such as microhabitats, perch height, and call characteristics, can allow for the co-existence of frogs that use a similar acoustic space (Vielliard & Cardoso 1996, Luddecke 2000). Since vegetation structure and microclimatic gradients (Römer 1998) are prone to cause deleterious effects to sounds, such as signal reverberation, reflection, and absorption (Forrest 1994), the choice of micro-habitats and the individual position in relation to habitat structure, may influence the quality of produced sounds and mating (Römer 1998, Mello *et al*. 2018). Although adjustments on temporal call parameters can be used by frogs to cope with environmental noise (Röhr *et al*. 2016), we expected that spectral parameters, such as call frequencies, had a stronger phylogenetic influence (Garey *et al*. 2018). Thus, ecological interactions and species' evolutive history shaped the current relationships observed in the environment.

CONCLUSION

The differences observed in the use of acoustic space by these sympatric species were likely driven by historical processes, and ecological interactions can be more related to microhabitat use. The recovered patterns of overlap in the analyzed calling traits of the species, i.e., smaller overlap than expected by chance, seems to be produced by historical processes, but further studies should be conducted to fill the current gaps identified in the present study. If competition exerted influence on species resources use, segregation on the use of acoustic space allows the co-occurrence of the investigated Hylidae. However, historical factors acting on resource partitioning, as evidenced by the phylogenetic distance between the observed species, suggests that the evaluated calling parameters (frequency) are phylogenetically constrained.

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