

# Revisiting the drivers of acoustic similarities in tropical anuran assemblages

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**Abstract.** Acoustic signaling is key in mediating mate choice, which directly impacts individual fitness. Because background noise and habitat structure can impair signal transmission, the acoustic space of mixed-species assemblages has long been hypothesized to reflect selective pressures against signal interference and degradation. However, other potential drivers that received far less attention can drive similar outputs on the acoustic space. Phylogenetic niche conservatism and allometric constraints may also modulate species acoustic features, and the acoustic space of communities could be a side-effect of ecological assembly processes involving other traits (e.g., environmental filtering). Additionally, the acoustic space can also reflect the sorting of species relying on public information through extended communication networks. Using an integrative approach, we revisit the potential drivers of the acoustic space by addressing the distribution of acoustic traits, body size, and phylogenetic relatedness in tropical anuran assemblages across gradients of environmental heterogeneity in the Pantanal wetlands. We found the overall acoustic space to be aggregated compared with null expectations, even when accounting for confounding effects of body size. Across assemblages, acoustic and phylogenetic differences were positively related, while acoustic and body size similarities were negatively related, although to a minor extent. We suggest that acoustic partitioning, acoustic adaptation, and allometric constraints play a minor role in shaping the acoustic output of tropical anuran assemblages and that phylogenetic niche conservatism and public information use would influence between-assemblage variation. Our findings highlight an overlooked multivariate nature of the acoustic dimension and underscore the importance of including the ecological context of communities to understand drivers of the acoustic space.

**Key words:** bioacoustics; communication; community phylogenetics; sensory drive; sensory ecology.

## INTRODUCTION

Animals use information available in the environment to make decisions that directly influence individual fitness (Danchin et al. 2004). In a variety of taxa, acoustic communication mediates mate choice and territoriality (Bradbury and Vehrencamp 2011), often favoring the intriguing cacophonous phenomena of mixed-species aggregations (Hödl 1977, Brumm 2013). Because conditions during signal transmission may impair communication, temporal and spectral components of vocalizations (acoustic traits) are traditionally considered to be under selection for optimized intraspecific

communication and reduced interspecific competition (sensory-drive framework; Endler 1992). Within this framework, two main hypotheses have been largely evoked to explain present-day distributions of acoustic traits in communities: (1) selection against masking interference or mismatches in mate recognition drives signal divergence (acoustic partitioning hypothesis, APH; Hödl 1977, Drewry and Rand 1983) and (2) selection for optimized transmission through the environment drives signal convergence (acoustic adaptation hypothesis, AAH; Morton 1975, Ey and Fischer 2009). Under these hypotheses, selection would favor predictable distributions of acoustic traits in communities (“acoustic space” hereafter), so that the acoustic space would be more different (dispersed) or similar (aggregated) than expected at random, respectively. However, previous conflicting results have prevented reaching general insights on these hypotheses (Kime et al. 2000, Chek

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et al. 2003, Boncoraglio and Saino 2007, Tobias et al. 2014, Toledo et al. 2014). Moreover, although a lot of effort has been put into understanding the acoustic space of ecological communities in the light of the sensory-drive framework (Chek et al. 2003, Boncoraglio and Saino 2007, Luther 2009, Schmidt et al. 2012, Roca and Proulx 2016), the role of ubiquitous behavioral and ecological interactions have received far less attention.

Species sorting through environmental filtering is one of the major mechanisms involved in the assembly of communities (Vellend 2016). If environmental heterogeneity determines the sorting of species with specific ecological traits, the acoustic space might emerge as a by-product of the combined effect of environmental filtering and phylogenetic niche conservatism. First, because closely related species usually share similar characteristics, such as acoustic properties of their vocalizations (Kraft et al. 2007, Gingras et al. 2013, Garey et al. 2018), similar distributional patterns of phylogenetic relatedness and acoustic traits in communities could arise due to phylogenetic niche conservatism (niche conservatism hypothesis, NCH). Second, variation in particular acoustic features is strongly influenced by the organisms' body size (Rodríguez et al. 2014, Tonini et al. 2020), which is a key physiological and life-history trait often involved in community assembly (Kingsolver and Pfennig 2007, Farjalla et al. 2012). Variability in body size of coexisting species could thus influence how the acoustic space is distributed across communities (allometric constraint hypothesis, ACH). Finally, the sorting of species mediated by body size or other ecological traits could indirectly shape the distribution of acoustic traits in communities. For instance, communities composed of species with similar body sizes would have more similar acoustic features when compared to a random distribution.

Recent theory also argues that public information use has a fundamental role in population and community dynamics, which would imply a correlation between information (e.g., through acoustic signaling) and the spatial distribution of information sources (e.g., emitters; Gil et al. 2018, Goodale et al. 2020). In this sense, acoustic signaling not only mediates conspecific communication but also functions as a venue for information transfer between species. Once social information becomes publicly available to other individuals, it would underly decisions on foraging strategies, habitat selection, competitive, and trophic interactions (Seppänen et al. 2007, Schmidt et al. 2010, Parejo and Avilés 2016). In this sense, social information use would drive the sorting of ecologically similar species, often sharing similar acoustic traits (Goodale et al. 2010, Tobias et al. 2014), which would translate into aggregated distributions of acoustic traits (public information hypothesis, PIH).

Most approaches so far have evaluated distributional patterns of acoustic traits from local communities only, irrespective of between-communities variation and its

potential ecological correlates. Because distinct drivers might produce similar patterns on the acoustic space, this approach is of limited value and has led to mixed support for the proposed hypotheses in the literature (Kime et al. 2000, Chek et al. 2003, Boncoraglio and Saino 2007, Toledo et al. 2014). A broader view about the drivers shaping the acoustic space of animal communities needs to go further and address the interrelationships between acoustic, phylogenetic, and ecological characteristics of communities.

Most anurans rely on acoustic communication for breeding and resource defense (Wells and Schwartz 2007) and form mixed-species choruses with abundant individuals, generating high levels of background noise, especially on the tropics (Gerhardt and Huber 2002, Berg et al. 2006). Importantly, anuran assemblages are largely structured by habitat conditions given their high dependence on water for reproduction and moisture for preventing dehydration (Wells 2007). Altogether, these characteristics provide an ideal model to test for the hypotheses determining the acoustic space of communities.

Here we investigate the potential of specific drivers to explain the acoustic space of anuran assemblages in a tropical wetland. Distinct hypotheses predict specific patterns of similarity of acoustic traits between species at the assemblage level, whereby the acoustic space would tend toward dispersion (acoustic partitioning hypothesis) or aggregation (acoustic adaptation and public information hypotheses). Nonetheless, phylogenetic niche conservatism, allometric constraints on acoustic traits, and the fact that assemblages are shaped by distinct ecological processes can indirectly influence the acoustic output of assemblages. In this sense, we use an integrative approach addressing the acoustic, phylogenetic, and ecological characteristics of assemblages while considering between-site environmental complexity. Our approach is twofold and complementary, where we first assess the concordance on the distributions of acoustic traits, body size, and phylogenetic relatedness in local assemblages (Fig. 1a–c) and then address between-assemblage variation (Fig. 1d). We represent the distributional patterns of acoustic traits, body size, and phylogenetic relatedness in each assemblage with the average spacing between co-signaling species (mean pairwise distance; Fig. 1b) and test for nonrandom patterns toward aggregation or dispersion according to null distributions (Fig. 1c). To address the implications of phylogenetic niche conservatism and allometric constraints, we also test for the presence of phylogenetic signal in acoustic traits and body size and model the effect of body size on acoustic traits. Next, with causal direct and indirect relationships between the context of environmental heterogeneity (both local and landscape) and the distributions of acoustic traits, body size, and phylogenetic relatedness of assemblages, we analyze (i) the potential influence of environmental heterogeneity in selecting for species according to their ecological attributes (here represented

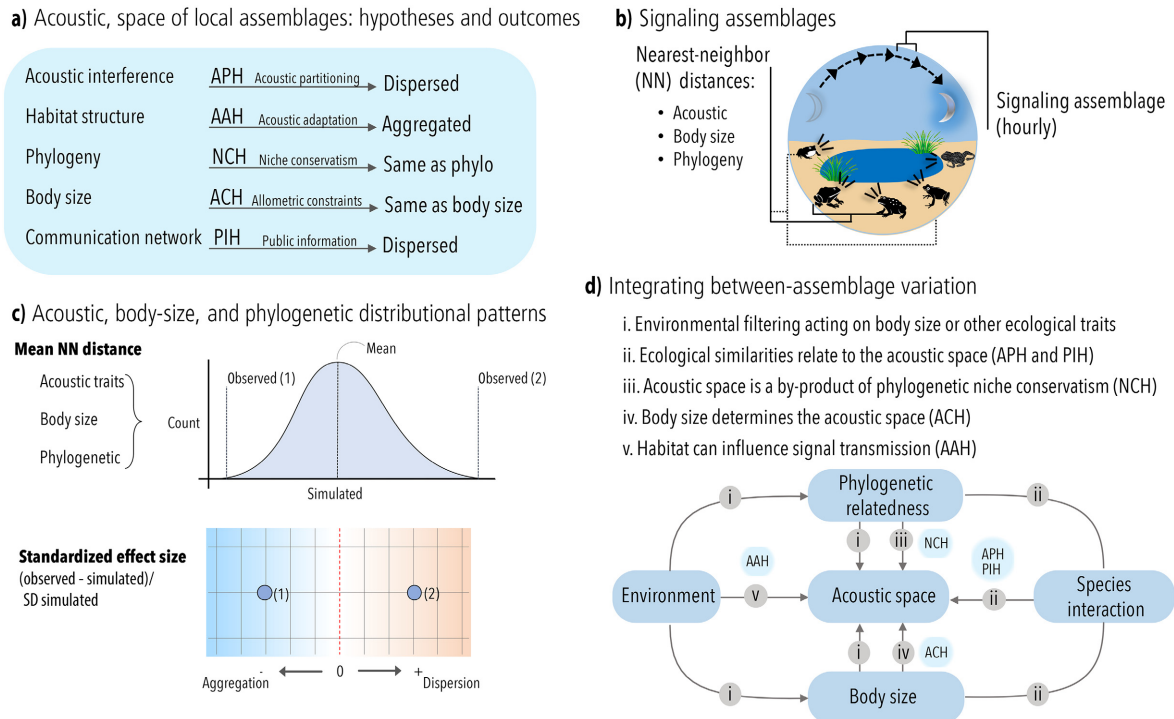


FIG. 1. (a) Main hypotheses regarding the potential drivers of the acoustic space of animal signaling assemblages. (b) Here, we evaluated the acoustic, phylogenetic, and body size similarities of signaling assemblages using the distributions of nearest-neighbor distances between co-signaling species. (c) We calculated mean values of nearest-neighbor distances between species (mean pairwise distance) and employed null models to check for trends toward aggregated or dispersed distributional patterns for acoustic traits, body size, and phylogenetic relatedness. (d.i–v) We tested if the overall patterns in the acoustic space differed from random and build a network of relationships to address between-assemblage variation of acoustic traits, body size, phylogenetic differences, and environmental heterogeneity. Findings from both analyses were combined to address the potential role of the distinct drivers in influencing the acoustic space across assemblages.

as phylogenetic relatedness and body size), which in turn, could influence the observed acoustic space (Fig. 1 d.i). We also expect (ii) upon a positive relationship of acoustic and ecological similarities across assemblages, the overall acoustic space of local assemblages would presumably be aggregated according to the public information hypothesis (Fig. 1d.ii), or dispersed according to the acoustic partitioning hypothesis (Fig. 1d.ii); (iii) a strong relationship between acoustic and phylogenetic similarities would arise with phylogenetic niche conservatism (Fig. 1d.iii), while (iv) a strong relationship between acoustic and body size similarities would arise due to allometric constraint (Fig. 1d.iv), and (v) a relationship of acoustic similarity with increasing environmental heterogeneity would emerge according to the acoustic adaptation hypothesis (Fig. 1d.v).

## METHODS

### Sampling site selection and characterization

We sampled anuran assemblages in an area of approximately 100 km<sup>2</sup> located in the Nhecolândia region (Fig. 2a) of South Pantanal wetlands in Brazil (Silva

and Abdon 1998). This tropical savanna region has a wet season from October to April and a dry season from May to September. Landscapes are characterized by permanent and seasonal ponds of fresh and brackish water embedded in a natural mosaic of grassland savannas, woody savannas, and forested areas (Evans and Costa 2013).

To capture a gradient of vegetation heterogeneity, we selected 39 permanent ponds located in landscapes ranging from forested to grassland savanna, spaced at a minimum of 1 km from each other (Appendix S1: Section S1, Fig. S1). We used the Normalized Difference Vegetation Index (NDVI; Rouse et al. 1974), a consolidated proxy of environmental structure (Pettorelli et al. 2011) to represent vegetation heterogeneity. NDVI was calculated from high-resolution images (RapidEye 3A, Planet Labs, San Francisco, California, USA, 5 m pixel size; Appendix S1: Section S1, Fig. S1) and averaged within a 200 m radius buffer (i.e., landscape) around each sample site.

We also characterized the terrestrial and aquatic habitats in more detail, since environmental differences at distinct scales can affect the propagation of acoustic signals (Bosch and De la Riva 2004, Erdtmann and Lima

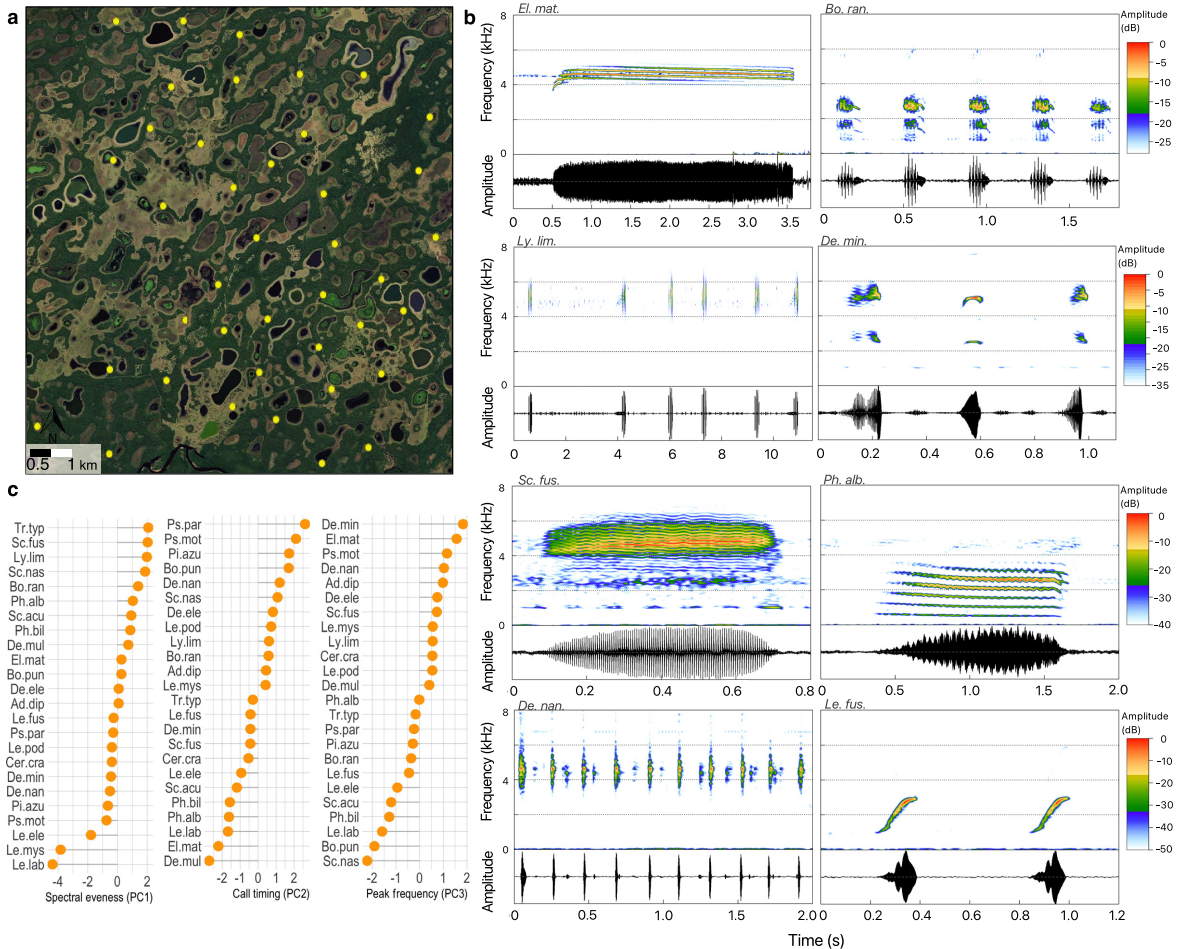


FIG. 2. Study area, advertisement calls, and acoustic traits of anuran species in south Pantanal wetlands. (a) Sample sites (yellow dots) in Aquidauana, state of Mato Grosso do Sul, Brazil (latitude 19.558234° S, longitude 56.123522° W, WGS84. Google Earth, [earth.google.com/web/](http://earth.google.com/web/)). (b) Spectrograms and oscillograms of the advertisement call of some of the recorded anuran species (species codes in Appendix S1: Table S1). Spectral and temporal parameters were quantified and synthesized with a principal component analysis, where (c) the three first axes represented, respectively, spectral evenness, call timing, and peak frequency.

2013), in addition to influence the structuring of anuran assemblages (Silva et al. 2011, Sugai et al. 2019b). Aquatic habitat was represented by the two first axes (summarizing 59% of the information; Appendix S1: Fig. S2) of a principal component analysis (PCA) on six variables: free water surface, aquatic vegetation, grass < 20 cm, grass > 20 cm, shrub vegetation, and pond depth (Appendix S1: Section S1). Terrestrial habitat was represented by the Leaf Area Index (LAI), a proxy of canopy openness (Bréda 2003) estimated with measurements from wide-angle optical sensors and a model of radiative transfer.

Acoustic monitoring

To determine species composition, we monitored the calling activity of anurans over the 39 sites using passive acoustic monitoring (Sugai et al. 2019a). During 10

consecutive days in the peak of the rainy season (January 2017), each site was recorded for up to five consecutive days using a rotation of 22 automated acoustic recorders (Wildlife Acoustics, Maynard, Massachusetts, USA) among sites. We deployed the automated recorders at 1.5 m height on trees or wood stakes up to 10 m from the ponds. Recorders were set to record in stereo mode with 6 and 12 dB gain on each channel, at a 44.1 kHz sample rate and 16-bit WAV format. We set a recording schedule to register 2 minutes every 20 minutes, starting 1 h before sunset and ending 1 h after sunrise (from approximately 16:30 to 07:30, UTC-4).

Each recording was examined by the main author to detect and identify advertisement calls of anuran species using aural recognition and visual inspection of spectrogram (Fast Fourier Transform [FFT] = 512, Hamming window) using the software Audacity (Audacity Team 2018) and Raven (Bioacoustics Research Program 2014).

Recordings preceding sunrise and sunset were characterized by low anuran activity and high overlap with bird and invertebrate activity (cicadas and katydids). Therefore, for subsequent analyses, we used only recordings from 19:00 h to 04:00 h. Signaling assemblages were represented by the sum of species incidence on each hour.

### *Acoustic traits*

Call structure is often species specific, with temporal and spectral call parameters underlying conspecific recognition (Schwartz and Bee 2013). To characterize advertisement calls, we obtained high-quality audio recordings using “shotgun” directional microphones (Sennheiser ME66, Wedemark, Germany) and manual digital sound recorders (Tascam [Los Angeles, California, USA] DR-40 and ZOOM [Tokyo, Japan] H4n Pro). During the breeding season (3–7 October 2016, 10–16 December 2016, 22–29 January 2017, 20–26 February 2017), we searched for calling males from sunset to approximately 02:00 at the sampling sites and recorded a minimum of 2 minutes from each individual at a distance of about 1.5 m. Recordings were registered at a 44.1 kHz sampling rate, WAV format, 16-bit, using manual controls for gain levels to avoid clipping. When possible, we captured the same recorded individuals and measured their snout-to-vent length (a proxy of body size) with a digital caliper. As we were unable to obtain directional recordings of all species registered in our study area, we complemented our acoustic data set with recordings from acoustic libraries and personal researcher’s databases, totalizing 115 individuals (Appendix S1: Section S1, Table S1).

From each advertisement call, we extracted six acoustic parameters over the temporal and frequency domains: call rate (number of calls per second), note duration (ms), interquartile range bandwidth (Hz), peak frequency (Hz), aggregate entropy, and average entropy (Appendix S1: Table S2; Charif et al. 2010, Köhler et al. 2017). Using the mean value of each parameter for each species, we performed a principal component analysis (PCA) on the log-transformed values using vegan package (Oksanen et al. 2010) in R software (R Core Team 2018). The three first PCA axes captured 92% of all variation in call parameters (Fig. 2b, c, Appendix S1: Fig. S3, Table S3). The first axis was positively correlated with measures of spectral evenness (aggregate entropy, average entropy, and interquartile range bandwidth), ranging from pure-tone-like calls to calls containing wide frequency ranges and harmonics. The second axis was associated with temporal parameters, being positively related to call rate and negatively related to note duration. The third axis was positively correlated with peak frequency and represented characteristics associated with the dominant pitch. Hereafter, we will refer to these three axes as the following acoustic traits: spectral evenness, call timing, and peak frequency.

For each acoustic trait, we tested for phylogenetic signal using Blomberg’s  $K$  and Mantel test (Appendix S1: Section S1). We also tested the relationship between acoustic traits and body size with a phylogenetic generalized least squares (PGLS) regression using the ape R package (Paradis and Schliep 2018), whereby residual errors are considered to be distributed according to the variance and covariance of phylogenetic distances (Grafen and Hamilton 1989). Here, we used a time-calibrated tree (Jetz and Pyron 2018) pruned to the species observed in our study area.

### *Distributional patterns of acoustic, body size, and phylogenetic relatedness in signaling assemblages*

To represent the distributional patterns of species’ attributes in signaling assemblages, we calculated mean pairwise distances for each of the acoustic traits (spectral evenness, call timing, and peak frequency), body size (snout-vent length; Appendix S1: Section S1), and phylogenetic relatedness, since species sharing more recent ancestry tend to retain more similar ecological requirements. Given potential confounding effects of allometric constraints on acoustic traits, we also assessed the distributional patterns of the model residuals from PGLS on each acoustic trait.

Then, we generated null distributions of mean pairwise distances for each signaling assemblages to be further compared with the observed ones. For each acoustic trait, body size, and phylogenetic relatedness, this procedure involved (1) computing pairwise distances between species and randomizing them within the family level, (2) selecting the pairs of most similar species (nearest-neighbor distances; Fig. 1b) in each signaling assemblages and averaging the random pairwise distances, (3) repeating the previous steps 5,000 times and obtaining a null distribution per signaling assemblage, and (4) computing the mean and standard deviation of null mean pairwise distances. We used the nearest-neighbor distances between species in assemblages instead of using all pairs combinations because stronger effects of biotic interactions are more likely to be detected between more similar species (Webb et al. 2002, Tucker et al. 2017).

Next, to summarize the differences between the observed mean pairwise distances and their null distributions, we calculated standard effect sizes (SES) by determining the difference between the observed and the mean of null distribution divided by its standard deviation. Positive SES on mean pairwise distances (SES<sub>dist</sub> hereafter) indicates that observed distances are greater than those from null models and thus, represent a tendency toward dispersion, while negative values indicate a tendency toward aggregation (Fig. 1c). Our approach is akin to the Nearest Relative Index (NRI) often used in trait-based and community phylogenetic approaches (Clarke and Warwick 1998, Webb et al. 2002). We further tested whether SES<sub>dist</sub> were different from null expectations (i.e., from 0) with a Wilcoxon test (Ingram



and Shurin 2009). For these procedures, we used *picante* (Kembel et al. 2010), *vegan* (Oksanen et al. 2010), and *ade4* (Jombart et al. 2010) R packages.

#### *Distributional patterns of body size and phylogenetic relatedness in local assemblages*

Because our analytical unit considers co-signaling species (signaling assemblages), and the potential influence of environmental filtering is expected to act on the total number of species registered at each site (i.e., local assemblages,  $n = 39$ ), we also addressed the effect of environmental heterogeneity on the assembly of local assemblages. For such purpose, we calculated SESdist considering the ecological attributes of species (body size and phylogenetic relatedness, a proxy of ecological similarities), calculated for the nearest-neighbor distances of all species at each site. Then, we fitted separate general linear models using aquatic habitat (first two PCA axes), terrestrial habitat (LAI), and vegetation heterogeneity (NDVI) as predictors, and SESdist on body size and phylogenetic relatedness from local assemblages as response variables. Model residuals were inspected to confirm normal distribution and homoscedasticity, and confidence intervals for coefficients were estimated using profile likelihood ratios. SESdist on body size and phylogenetic relatedness for each local assemblage were further used to account for the potential effects of environmental filtering on the observed acoustic structures of signaling assemblages.

#### *Structural equation modeling*

To consider multiple potential drivers of the acoustic space of assemblages, we used structural equation models (SEMs). We first built a single network of variables that worked both as predictors and responses under a hierarchical structure (see predictions Fig. 1d, Appendix S1: Fig. S4), which indicates direct and indirect relationships of multiple variables while reducing the probability of finding spurious correlations under a mechanistic approach (Shipley 2009). To build SEMs, SESdist on acoustic traits, body size, and phylogenetic relatedness of signaling assemblages were averaged per day for the following analysis. Then, we (1) fitted general linear mixed models (glmm) on SESdist of each acoustic trait from signaling assemblages as a function of body size and phylogenetic SESdist, and variables representing environmental heterogeneity (NDVI, terrestrial and aquatic habitats), and (2) fitted a glmm with body size and phylogenetic SESdist as a function of environmental heterogeneity variables. Site was included as random intercept effect in all models. To consider the potential effect of environmental filtering acting on local assemblages, we (3) included paths connecting phylogenetic and body size SESdist from local assemblages (calculated in the previous section) to their corresponding SESdist of signaling assemblages. Because we were

unable to link environmental heterogeneity variables and SESdist from local assemblages given the uneven grouping factors (single values per site), we informed the presence of correlated error structures between them. Goodness of fit was evaluated with a test of directed separation, where significance was assessed with Fisher's  $C$  statistic. We report  $R^2$  from fixed effect only (marginal) and fixed and random effects together (conditional). Path coefficients were standardized by their standard deviations, allowing them to be compared within the model and to compute indirect effects. SEMs were fit with *lme4* (Bates et al. 2015) and *piecewiseSEM* (Lefcheck 2016) in R.

## RESULTS

From a total of 5,916 2-minute audio recordings (197.2 h), we registered 24 species from four families, with Hylidae (12 species) and Leptodactylidae (nine species) being the most representative ones. The number of species per signaling assemblage (i.e., at the hourly scale) varied from 1 to 12 ( $5.5 \pm 2.07$  [mean  $\pm$  SD]), and per local assemblage (i.e., considering all species registered at each site) from 6 to 19 ( $10.5 \pm 3.07$ ).

We found no evidence of strong niche conservatism on acoustic traits and body size (Appendix S1: Table S4, Fig. S5), with only call timing approaching a Brownian model of trait evolution ( $K = 0.99$ ,  $r = 0.39$ ,  $P = 0.003$ ). As such, the observed acoustic space of these assemblages is not necessarily a by-product of phylogenetic niche conservatism. For frequency-based acoustic traits (spectral evenness and peak frequency), we found a negative relationship with body size while controlling for phylogenetic relatedness ( $R^2 = 0.14$  and  $0.24$ ,  $P = 0.03$  and  $0.01$ , respectively; Appendix S1: Table S5).

SES on mean distances (SESdist) for all acoustic traits, body size, and phylogenetic relatedness tended toward aggregated patterns (Fig. 3, Appendix S1: Table S6), with prevailing negative values different from null expectations (mean values different from 0; Appendix S1: Table S6). SESdist of the residuals from PGLS between acoustic traits and body size also tended toward an aggregated pattern, likewise the original values (Fig. 3). The exception was call timing, with mean original values approaching zero, whereas residual-based SESdist were primarily positive.

When we looked at the phylogenetic and body size SESdist of local assemblages, we found only body size to be related with the second habitat PCA axis ( $\beta = -0.57$ ,  $LCI = -0.96$ ,  $UCI = -0.17$ ; Appendix S1: Table S7). Therefore, increasing similarity of body size in local assemblages was associated with breeding sites containing shallower ponds and denser aquatic vegetation.

Using SEM, we found SESdist on spectral evenness to be positively related with vegetation heterogeneity ( $\beta = 0.31$ ,  $R_m^2 = 0.15$ ,  $R_c^2 = 0.55$ ; Fig. 4a), whereas SESdist on peak frequency showed a positive relationship with phylogenetic SESdist and a negative relationship

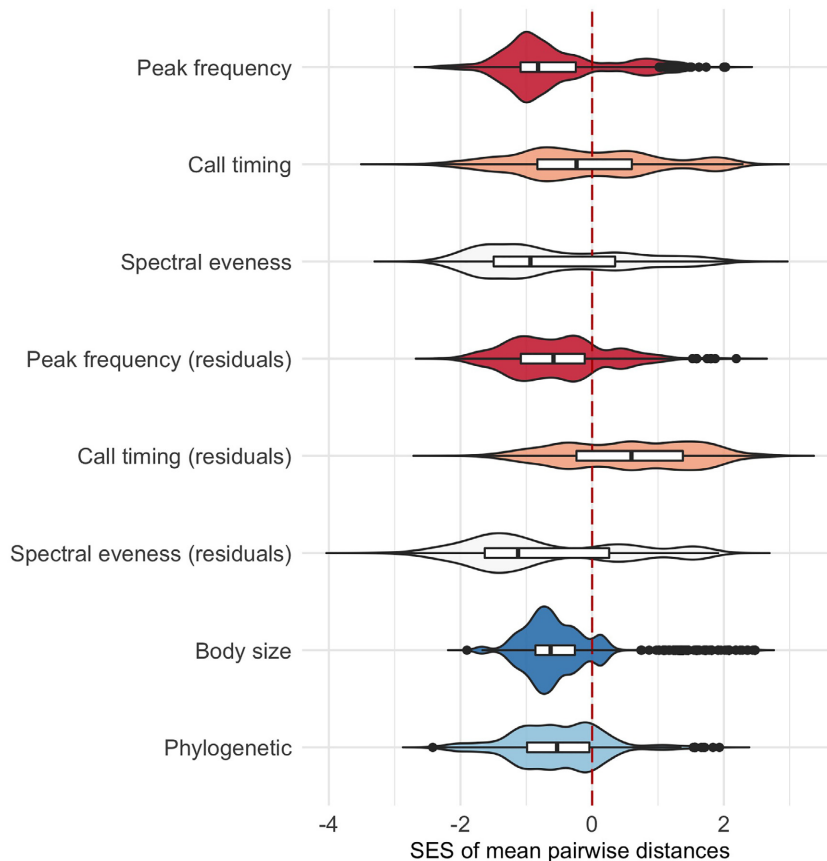


FIG. 3. Standardized effect sizes (SES) of mean pairwise distances of acoustic traits, acoustic traits without the effect of body size (residuals from a PGLS), body size, and phylogenetic distances of anuran assemblage from south Pantanal wetlands of Brazil. Box plots (white) showing mean, first and third quartiles (notches), and whiskers, surrounded by violin plots (kernel probability distribution). Boxplots represent median, first and third quartiles. Whiskers represent maximum and minimum of distributions, and dots represent outliers.

with and body size SESdist of signaling assemblages ( $\beta = 0.4$  and  $-0.14$ , respectively,  $R_m^2 = 0.16$ ,  $R_c^2 = 0.69$ ). Still within the SEM, SESdist on phylogenetic relatedness of signaling assemblages was positively related to the corresponding SESdist from local assemblages ( $\beta = 0.49$ ,  $R_m^2 = 0.28$ ,  $R_c^2 = 0.58a$ ), whereas SESdist on body size ( $R_m^2 = 0.13$ ,  $R_c^2 = 0.24$ ) was positively related to aquatic habitat (PC2,  $\beta = 0.27$ ) and vegetation heterogeneity (NDVI,  $\beta = 0.22$ ). The strongest indirect effect was through the moderation of phylogenetic structure on peak frequency structure ( $\beta$  ind. =  $0.39$ , Fig. 4 c).

#### DISCUSSION

Our findings of higher acoustic similarity in signaling anuran assemblages and the correlates of between-assemblage variation contribute to elucidate the drivers of the acoustic space. First, the absence of a dispersed acoustic space invalidates acoustic partitioning. Assemblages were more similar than expected at random both

in acoustic and phylogenetic relatedness, but the absence of strong phylogenetic signal in the spectral acoustic traits prevents endorsing niche conservatism alone to be the main driver. We found no remarkable differences in the acoustic space after controlling for the effects of body size, undermining a predominant influence of allometric constraints. Considering between-assemblage variation, we expected niche conservatism and allometric constraints to promote strong associations among acoustic space and phylogenetic and body size similarities, and we also raised that the acoustic space could be indirectly shaped by the sorting species according to their ecological attributes. Results differed according to each spectral acoustic trait, but indirect effects due to a potential effect of environmental heterogeneity were negligible. While aggregation in peak frequency similarity was associated with increasing phylogenetic relatedness, it related negatively with body size similarity. Further, aggregation in spectral evenness was associated with a decrease of vegetation heterogeneity, contrary to expectations based on the acoustic adaptation hypothesis.

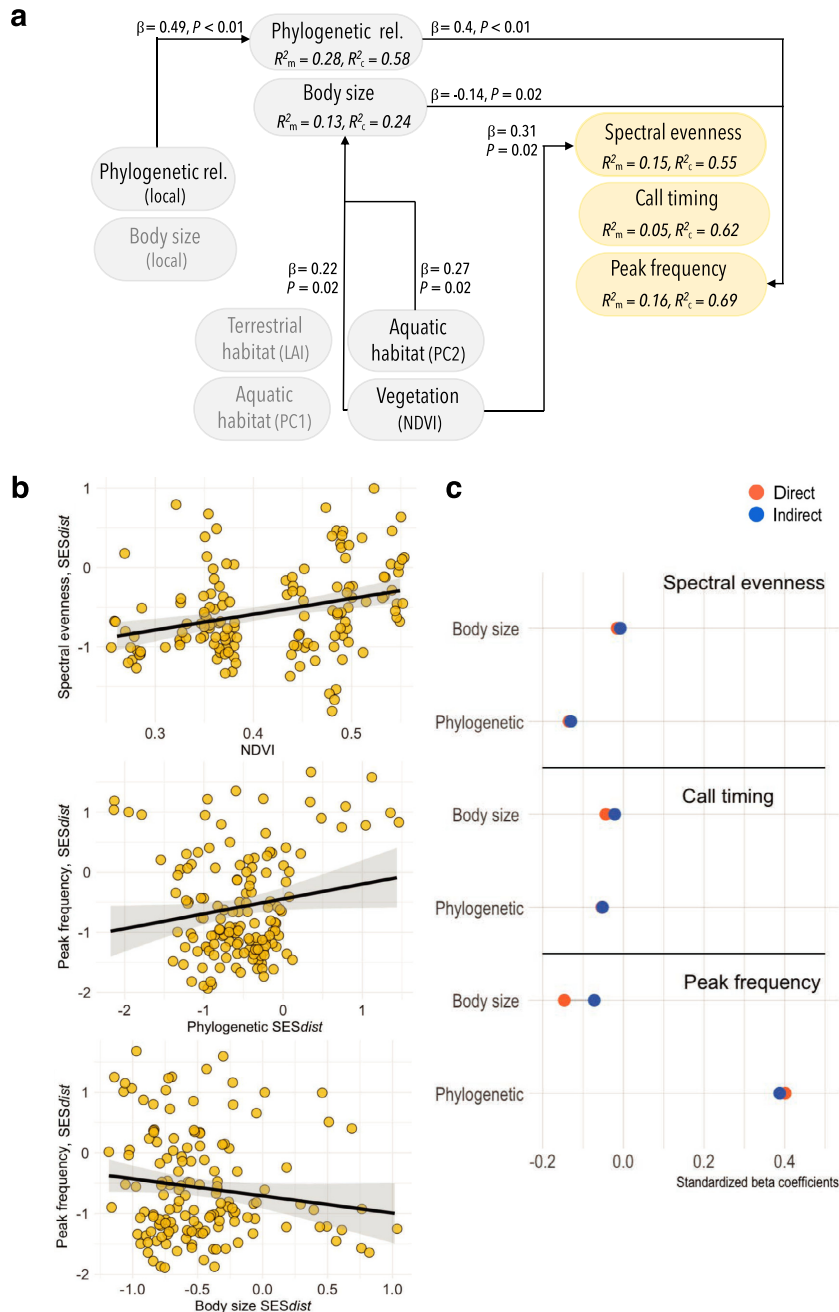


FIG. 4. Structural equation models (SEMs) fitted on the distributional patterns of acoustic traits (spectral evenness, call timing, and peak frequency) of anuran signaling assemblages in south Pantanal wetlands of Brazil. (a) Paths representing relationships with  $P < 0.05$  among the specific predictor (gray) and response (yellow) variables (variables in gray letters did not affect response variables), and their standardized beta coefficients to equivalent units, allowing comparison of the relative magnitude of different paths. (b) Relationships between acoustic traits and predictors with paths  $< 0.05$  in SEMs. (c) Standardized beta coefficients of the direct effects (orange dots) of body size similarities and phylogenetic relatedness on the variability of each acoustic trait and indirect effects (blue dots) mediated by their correspondent distributional patterns in local assemblages, and through environmental heterogeneity variables.

Altogether, we found little support for the traditional hypotheses of the drivers of the acoustic space for signaling anurans. Instead, we explain the observed trends of aggregation in the acoustic space in light of species

sorting into assemblages upon public information use and phylogenetic niche conservatism. Our findings underscore the importance to address between-assemblage variation in the acoustic space to improve



our understanding of the role of ecological and sensory-based processes that has seldom been considered (Chek et al. 2003).

When the ecological context of assemblages was considered, detecting the correlates of between-assemblage variability of acoustic traits provided additional evidence to understand the tendency toward aggregated acoustic space. The positive relationship between phylogenetic and peak frequency similarities could be a side effect of phylogenetic niche conservatism, wherein community assembly would be mediated by ecological traits correlated with the acoustic ones. Nonetheless, we found no support for environmental filtering acting on the phylogenetic component of signaling assemblages given the lack of association between environmental heterogeneity and phylogenetic relatedness. Conversely, we found similarity in body size of assemblages, which is a trait largely associated with diet and habitat preferences (Womack and Bell 2020), to relate to the structure of aquatic habitat and vegetation heterogeneity. But the indirect effect of environmental filtering on the acoustic space through selection on body size was negligible compared to the direct effect of body size alone, indicating a weak indirect role of environmental filtering. Altogether, we found no evidence that the distribution of the spectral component of assemblages emerges as a by-product of environmental selection.

Species interaction can be mediated by differences in ecological and acoustic traits and consequently, influence the sorting of co-signaling species. Despite the predominant non-dispersed acoustic space, the decreasing aggregation with increasing phylogenetic differences could argue for few particular cases where species would be sorted in communities with lower spectral overlap (Chek et al. 2003). Conversely, an extended communication network between species is expected to promote the assembly of species with similar acoustic and phylogenetic relationships (Tobias et al. 2014). Since species with similar signaling strategies are more likely to exchange information, assemblages relying on social information would have similar signaling patterns (Goodale et al. 2010, Tobias et al. 2014). Theory predicts the net benefit of information use to counteract the potential of negative interactions among species (Gil et al. 2019), and thus, public information use in communication networks would potentially influence the ecological overlap among co-signaling species.

Through the lens of social information use, the assembly of species with different body size (lower ecological overlap) and higher similarity in peak frequency (higher acoustic perception) and ecological requirements (phylogenetic relatedness) would have to offset the competitive potential among co-signaling species. Social information can provide reliable hints for predator avoidance (Schmidt et al. 2010, Gil et al. 2018), and under high predation pressure, amphibians are more selective to habitat conditions and increase responsiveness to predation cues (Narayan et al. 2013, Komine et al. 2020). Anurans at

low-heterogeneous sites are prone to greater exposure to predators that rely on visual cues (Ferreira et al. 2019), and the tendency of greater similarity in spectral evenness would favor public information use. Relying on public information can be especially important for anurans in the Pantanal wetlands, where population dynamics are largely influenced by predation risk (Costa-Pereira et al. 2018). However, the literature on the influence of heterospecific information use through acoustics on the assembly of amphibian assemblages is scarce, with most examples coming from birds (Forsman et al. 2009).

Anurans elicit behavioral responses to heterospecific signals (Gerhardt 2001, Both and Grant 2012, Vélez et al. 2017) and use cues gathered inadvertently from heterospecifics to make decisions such as finding suitable breeding sites (Slabbekoorn and Bouton 2008, Buxton et al. 2015, Buxton and Sperry 2016, Vélez et al. 2017) and engaging in anti-predator behaviors (Phelps et al. 2006). Eavesdropping on species with similar acoustic signals can be especially common in anurans, as signal characteristics should approximate the tuning of the peripheral auditory system (Gerhardt 1994). Acoustic signals not only encode information that is important for conspecifics, but also announce the presence, location, and motivation of emitters (Grafe 2005, Wells and Schwartz 2007), which can increase individual awareness and enhance fitness by reducing costs to access environmental information (Valone 2007). Nevertheless, although eavesdropping on both conspecific and heterospecific signals is widespread over a variety of taxa (Simmons et al. 2003) and characterizes public social information use (Grafe 2005, Magrath et al. 2015), we acknowledge that further experimental studies exploring heterospecific stimuli in anurans will provide more understanding about the potential of communication networks in anuran assemblages.

Variation in similarity of spectral evenness was related to vegetation heterogeneity, with signaling assemblages located in less heterogeneous sites showing greater similarity in spectral evenness. The acoustic adaptation hypothesis predicts that signals are shaped for optimized transmission according to the vegetation structure of a species' habitat (Morton 1975, Ey and Fischer 2009, Erdtmann and Lima 2013), and previous findings suggest that anurans would have higher frequency modulation in heterogeneous habitats (Bosch and De la Riva 2004). In this sense, acoustic adaptation is unlikely to generate the observed variation in the acoustic space, since we found greater similarity at less heterogeneous sites.

The legacy of selective pressures on signal design in determining the acoustic space of signaling communities remains unclear, as addressing past evolutionary processes on present-day patterns requires integrative research on eco-evolutionary dynamics of species interactions, phenotypic evolution, and diversification (Weber et al. 2017). For instance, although acoustic partitioning would promote a divergent pattern in the

acoustic space, acoustic traits may have evolved in past and distinct ecological contexts that are unrelated to current competitive interactions. Additionally, our inability to detect the signature of acoustic adaptation can be a limitation of site-based approaches, which often provide a limited range of environmental conditions required to test the effects of contrasting environments on signal transmission (Carvajal-Castro and Vargas-Salinas 2016). Thus, the role of acoustic competition and adaptation as evolutionary drivers of community-wide patterns should be further explored with emerging techniques combining explicit evolutionary modeling of trait evolution (e.g., Drury et al. 2018) and historical processes involved in community assembly (Pigot and Etienne 2015).

Signaling communities have intrigued ecologists for decades, with several hypotheses being evoked to explain present-day pattern of the acoustic space: selection against signal interference and degradation (acoustic partitioning and acoustic adaptation), species sorting through environmental filtering or extended communication networks (i.e., public information use), and evolutionary constraints (phylogenetic niche conservatism and allometric constraint). We investigated the implications of these potential drivers on the differences in acoustic, ecological, and phylogenetic features of signaling assemblages across gradients of environmental heterogeneity. A tendency toward aggregation in the acoustic space is unlikely to be produced by acoustic partitioning, allometric constraints, and acoustic adaptation, and we argue that phylogenetic niche conservatism and public information use may underlie the overall pattern and the variation observed between assemblages. These findings highlight a multivariate nature of the acoustic dimension that has seldom been considered, and thus, addressing the ecological context of signaling assemblages can improve our understanding of how multiple processes can shape the acoustic space.

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## OPEN RESEARCH

Data (Sugai et al. 2021) are available in Figshare at: <https://doi.org/10.6084/m9.figshare.14229614.v1>.