Drivers of assemblage-wide calling activity in tropical anurans and the role of temporal resolution

Larissa S. M. Sugai*[1,2], Thiago S. F. Silva[1,3], Diego Llusia[2,4,5+], Tadeu Siqueira[1+]

[1] Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro, 13506–900, São Paulo, Brazil.

[2] Terrestrial Ecology Group, Departamento de Ecología, Universidad Autónoma de Madrid, C/ Darwin, 2, 28049, Ciudad Universitaria de Cantoblanco, Facultad de Ciencias, Edificio de Biología, C–211, Madrid, Spain.

[3] Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA

[4] Centro de Investigación en Biodiversidad y Cambio Global, Universidad Autónoma de Madrid, C/ Darwin 2, E-28049, Ciudad Universitaria de Cantoblanco, Madrid, Spain.

[5] Laboratório de Herpetologia e Comportamento Animal, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Campus Samambaia, CEP 74001–970, Goiânia, Goiás, Brazil.

[+] These two authors contributed equally

*corresponding author: lariagus@gmail.com

Abstract

1. Temporal scale in animal communities is often associated with seasonality, despite the large variation in species activity during a diel cycle. A gap thus remains in understanding the dynamics of short-term activity in animal communities.

2. Here we assessed calling activity of tropical anurans and addressed how species composition varied during night activity in assemblages along gradients of local and landscape environmental heterogeneity.

3. We investigated 39 anuran assemblages in the Pantanal wetlands (Brazil) with passive acoustic monitoring during the peak of one breeding season and first determined changes in species composition between night periods (early, mid, and late) using two temporal resolutions (1-hour and 3-hour intervals). Then, we addressed the role of habitat structure (local and landscape heterogeneity variables from field-based and remote sensing metrics) and ecological context (species richness and phylogenetic relatedness) in determining changes in species composition (i) between night periods and (ii) across days.

4. Nocturnal calling activity of anuran assemblages varied more within the 1-hour resolution than the 3-hour resolution. Differences in species composition between early and late-night periods were related to local habitat structure and phylogenetic relatedness, while a low variation in compositional changes across days was associated with low-heterogeneous landscapes. None of these relationships were observed using the coarser temporal resolution (3-hour).

5. Our findings on the variation of calling activity in tropical anuran assemblages suggest potential trades-off mediated by fine-temporal partitioning. Local and landscape heterogeneity may provide conditions for spatial partitioning, while the relatedness

among co-signaling species provides cues on the ecological overlap of species with similar requirements. These relationships suggest a role of niche dimensional complementarity on the structuring of these anuran assemblages over fine temporal scales. We argue that fine-temporal differences between species in breeding activity can influence the outcome of species interaction and that addressing temporal scaling issues can improve our understanding of dynamics of animal communities.

Keywords: acoustic monitoring, calling activity, beta diversity, community dynamics, Pantanal wetlands, scaling, temporal ecology.

Introduction

Time is a fundamental dimension of species ecological niches. Because organisms' responses and ecological patterns are scale-dependent, the distinct timescales experienced by natural communities are key to understand the effects of environmental changes on biodiversity (Dornelas *et al.* 2013; Sutherland *et al.* 2013). Nevertheless, ecological communities are often statically framed at specific spatial and temporal scales, which may potentially lead to mismatches between ecological pattern and process. In the spatial domain, communities are usually delimited by subjective criteria or habitat boundaries (Wiens 1989; Leibold & Chase 2018), with spatial grain – i.e., the resolution of spatial observations – determined by the extension of sampling units. In the temporal domain, study duration is usually emphasized in detriment of the timeframe used to depict the set of interacting species – i.e., temporal resolution. However, empirical evidence indicates that species activity is largely variable and seldom constant over a diel period (McCann, Zollner & Gilbert 2017; Gaston 2019), such as distinct daily patterns of foraging (Kronfeld-Schor, Bloch & Schwartz 2013) and breeding (Schwartz & Bee 2013; Schalk & Saenz 2016). On one hand, predictable changes in species activity at short timeframes may be regulated by endogenous rhythmicity mechanisms (Kronfeld-Schor & Dayan 2003; Greenfield 2015). Alternatively, exogenous factors such as climate and species interactions may determine short-term differences in species activity (Carothers & Jaksić 1984; Hodge, Arthur & Mitchell 1996). Therefore, addressing short-term variation in the activity of animal communities, similarly to spatial variation, might lead to a more complete understanding of the ecological processes acting during community assembly (Castro-Arellano *et al.* 2010; Segre *et al.* 2014; Van Allen *et al.* 2017).

Ecological differences among interacting species mainly occur across three fundamental dimensions: food, space, and time (MacArthur & Levins, 1964; Amarasekare 2003; Kneitel & Chase 2004). Although niche overlap is rather common in ecological communities, differences between niche dimensions, including fine-temporal partitioning (Schoener 1974), have a fundamental role in promoting stable coexistence among species (Chesson 2000, Kneitel & Chase 2004). On the local scale and in the short-term, negative interactions can promote the exclusion of inferior competitors (Vellend 2016), or alternatively, species may reduce interference (e.g. for habitat-use and breeding sites) through temporal partitioning (Schoener 1974, Carothers & Jaksić 1984, Humfeld 2013). Additionally, local dynamics are also influenced by larger spatial contexts (Ricklefs 1987; Leibold & Chase 2018), and short-term dynamics (e.g. within-days) may undergo alternative trajectories at larger temporal scales (e.g. across days). For instance, favored dispersal by heterogeneous landscapes can promote an increase in the effective size of local communities (higher species richness and abundance) and reduce the stochastic component of community assembly (e.g. fluctuations in small populations; Ron, Fragman-Sapir & Kadmon 2018). However, increasing spatial heterogeneity can likewise increase the presence of sink habitats and thus reduce the competitive dominance of species (Hodge, Arthur & Mitchell 1996; Schreiber & Kelton 2005).

Therefore, understanding how communities differ in time (i.e., temporal beta-diversity; Legendre & Gauthier 2014, Baselga et al. 2015) and the drivers of community-wide activity can shed light on an interplay of short-term dynamics of ecological communities and the underlying processes across scales (Dubos et al. 2020).

Tropical anuran assemblages are excellent models to address short-term dynamics of species activity. The aggregated breeding activity in the rainy season (Hödl 1977) gathers several species in communal water bodies, especially for species with aquatic oviposition (Duellman & Trueb 1994), forming a potential competition arena for calling and spawning sites (Schwartz & Bee 2013, Ulloa *et al.* 2019). The composition of species in these sites is influenced by the structural heterogeneity of breeding habitats, where species advertise calls to attract mates (Sugai *et al.* 2019b). Additionally, landscape context influences species persistence (e.g. by maintaining low levels of desiccation in forested patches) and dispersal dynamics underlying variation in the composition of assemblages (Werner *et al.* 2007; Signorelli *et al.* 2016). Nonetheless, short-term variation in species activity has been mainly addressed with respect to meteorological and social factors (Oseen & Wassersug 2002; Saenz et al. 2006, Llusia *et al.* 2013; Schalk & Saenz 2016, Dubos et al. 2020, Guerra et al. 2020) and the role of ecological processes driving such dynamics remain largely unexplored.

This knowledge gap can be traced back to historically challenging conditions in addressing nocturnal phenomena (Gaston 2019), in addition to the human-observer limitation in investigating multiple sites simultaneously. Currently, modern techniques enabling passive acquisition of high-resolution data have been solving these practical issues and steadily improving our capacity to address diverse ecological phenomena (Rocchini *et al.* 2016; Gaston 2019). Amongst these developments, automated acoustic devices have facilitated the systematic collection of environmental sounds, providing new opportunities to investigate multiple perspectives of animals that rely on acoustic communication (Sugai *et al.* 2019a). The "nocturnal problem" (Gaston 2019) can therefore be potentially revisited using the framework of acoustic monitoring.

Here, we used acoustic monitoring to investigate variation in night activity of tropical anuran assemblages across distinct ecological gradients. Based on the incidence of vocal active species, we first assessed whether species composition varied through different night periods (early, mid, and late) using two temporal resolutions (1-hour and 3-hour intervals, fig. 1a–b). We then assessed if changes in species composition between night periods was associated with gradients representing habitat structure (local and landscape habitat heterogeneity) and the ecological context (species richness and phylogenetic relatedness, here used as a proxy of ecological similarities, fig. 1c.1). We also assessed if the regularity of nightly variation in species composition across monitored days (i.e., variance of temporal beta diversity fig. 1c.2) was influenced by the same potential drivers. We expected that an increase in the competitive potential of different species within the assemblage (higher species richness and phylogenetic relatedness) would promote deterministic exclusion of species across the night and thus decrease the similarity in species composition between night periods. Moreover, we expected that an increase in habitat heterogeneity (local and landscape) would increase potential for spatial partitioning and thus maintain similar species composition between night periods. We used the two temporal resolutions (1-hour and 3-hour intervals) to determine if the above expectations hold across temporal resolutions. Further, we assessed the contribution of the habitat and ecological gradients to the spatial variation of all species registered at each site to address their importance at the metacommunity scale.

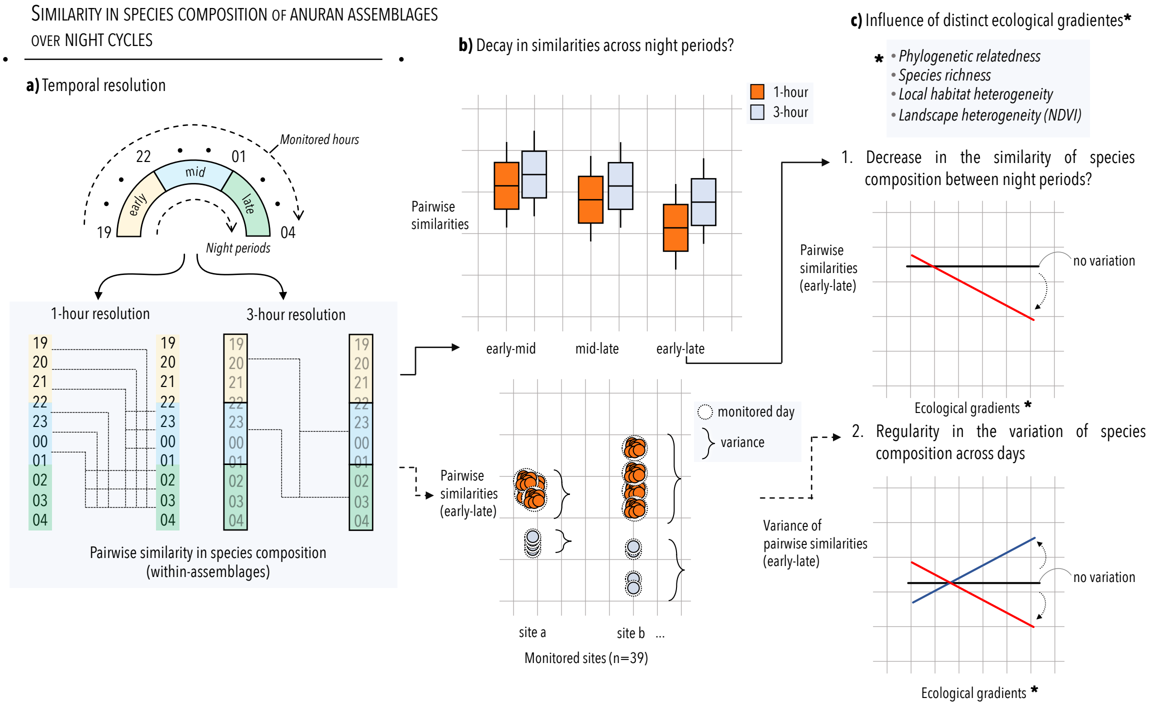

Figure 1. Conceptual scheme depicting (a) temporal resolution: incidence of vocal active species registered for 2 minutes each 20 minutes over the early, mid, and late periods of the night (1900 h to 0400 hours, UTC-4) and summarized with two temporal resolutions: 1-hour and 3-hour intervals. Similarity in species composition was computed for pairwise combinations of temporal units within a night cycle. (b) We investigated if species composition differed between night periods using the two temporal resolutions. Second, we addressed the potential role of distinct ecological processes on the variation of species composition in nightly activity by fitting relationships on (c.1) the differences in species composition from the early-late night period and (c.2) the variance of such differences across the different monitored days.

Methods

Study area and environmental characterization

We studied pond-breeding anuran assemblages in an area of approximately 100 km² located in the southern region of the Pantanal wetlands in Brazil, Aquidauana municipality (Latitude

-19.534227, Longitude -56.144935; WGS-84; fig. 2a). Breeding activity takes place during the rainy season (October-April) when monthly mean temperatures range from 20.1 to 33.2 °C and monthly rainfall from 96 to 231 mm (Fick & Hijmans 2017). As most tropical anurans have the highest activity levels during the peak of the rainy season (Duellman & Trueb 1994), our sampling was concentrated at the end of January 2017, which corresponded to the month of highest precipitation for that season (231 mm, Fick & Hijmans 2017). Landscapes of this southernmost region are influenced by the neighboring Cerrado (tropical savanna) and include grasslands, open wood savanna, and forested woodland (Evans & Costa 2013). Permanent bodies of standing water used by anurans are embedded among patches of these vegetation formations and have their low-lying adjacent areas composed of seasonally flooded grasslands that often inundate during the rainy season (Prado, Uetanabaro & Haddad 2005). The aquatic vegetation of these freshwater water bodies comprises erectophile grass-like plants from Cyperaceae and Typhaceae families, and floating emergent plants from Pontederiaceae, Araceae, Salviniaceae, and Nymphaceae families (Pott & Pott 2000, Evans & Costa 2013, Delatorre et al. 2019).

We selected sampling sites using a geographic information system to stratify localities according to landscape heterogeneity. First, we manually mapped all ponds in the study area and selected one point per pond, located on the shore and distant at least 1 km apart of each other (n = 72). We then calculated the Normalized Difference Vegetation Index – NDVI (Rouse *et al.* 1974) using RapidEye3A satellite images (5-meter pixel size, RapidEye AG 2011) and extracted average NDVI values for 200-meter radius buffers (125,6 m^2) centered on each point. Finally, we ordinated all 72 sites based on NDVI values and selected 39 sites representing the entire range of average NDVI, *i.e.* better captured the gradient of vegetation heterogeneity; from fully forested to fully open grasslands. Landscape heterogeneity was represented by NDVI values since forested areas prevent anurans from overheating and dehydration during daylight and decrease resistance for movement among habitat patches (Bowler & Benton 2005; Buskirk 2012; Silva *et al.* 2012).

These 39 sites were located on freshwater ponds with mean size of 9.07 ± 8.65 SD hectares. To characterize the breeding sites, we registered the components of the terrestrial and aquatic terrains. From a central point established by the closest distance between the recorder and the water margins (5 to 10 meters), we distributed one transect perpendicular to the margin of the pond every 3 meters, with 10 transect for each side of the central point, totalizing 20 transects. Each transect was 6-meter in length, with 3 meters towards the outside (terrestrial) and 3 meters towards the inside of the pond (aquatic), covering approximately $90m^2$ of each terrestrial and aquatic habitat. In each transect, we positioned a straight reference line and measured, for the terrestrial side, the length (cm) occupied by bare ground and shrub vegetation along the line. Additionally, at each 1-meter interval, we measured the Leaf Area Index (LAI - the ratio of foliage area to ground area; Bréda 2003) as a proxy of canopy openness. As the vegetation type surrounding the freshwater ponds are predominantly grasslands and open wood savanna, LAI was used here to represent the density (openness) of the short-stratum grassy/herbaceous terrain. We measured LAI with a LAI-2200C Plant Canopy Analyzer model (LI-COR Biosciences 1992) using a 45° forward view cap. For the aquatic side, we measured the length (cm) occupied by free water surface (i.e. no vegetation above the water surface), aquatic vegetation above the water surface (i.e. floating and emergent aquatic plants), and the flooded vegetation from seasonal grasslands contouring the ponds, being represented by two vertical strata of grassy vegetation (< 20 cm and > 20 cm, with the later also comprising emergent aquatic vegetation; Delatorre et al. 2015), and flooded shrub vegetation. Additionally, at each 1-meter interval, we measured pond depth. The length occupied by each variable was summed, except for LAI and pond depth, which were averaged (mean depth 1 ± 0.46 meters). All variables for the terrestrial and aquatic habitats were standardized to zero mean and unit variance.

To represent the heterogeneity of the breeding sites with reduced dimensionality, we performed a principal component analysis (PCA) on the variables representing the aquatic and terrestrial habitats with R package *FactoMineR* (Le, Josse & Husson 2008). We used the first two PC axes (28 and 21.2% of variation, fig 2b) to represent two gradients of habitat vegetation heterogeneity. The first axis (PC1) represented a gradient of vegetational heterogeneity on the aquatic habitat that ranges from flooded grasslands to typical permanent ponds. Sites with positive scores were positively associated with aquatic vegetation and free water surface whereas sites with negative scores were positively associated with high-stratum grassy vegetation (grass > 20cm). The second axis (PC2) represented a gradient of increasing heterogeneity on the terrestrial habitat. Sites with positive scores were associated with the presence of shrub vegetation both on the terrestrial and aquatic sides and with increased density of the grassy/herbaceous vegetation on the terrestrial terrain (LAI) (tab. S1, fig. S1).

Anuran assemblages

We used passive acoustic monitoring to record anuran calling activity for 3 to 5 consecutive days on each site using 22 automated audio recorders (four SM4, fifteen SM3, and two SM2 models from Wildlife Acoustics) that were rotated among sites during a total period of 10 days (2017 January, 18th to 27th). We attached recorders on trees or wooden stakes distant no more than 10 meters from the monitored pond, at approximately 1.5 meters height, to improve sound recordings. Our recording schedule consisted of 2 minutes of stereo recording every 20 minutes from 19:00 h to 4:00 h (UTC-4), to exclude the hours with bird and invertebrate overlapping sounds around sunset and sunrise. Sounds were recorded at a rate of 44.1 kHz and 16-bit audio depth (uncompressed WAV format), with a gain of 6 dB and 12 dB on each channel. Anuran advertisement calls were detected and identified by the main author using visual inspection of spectrograms (window size of 512, Hamming window) and aural recognition in Audacity software (Audacity Team 2018). Call parameters were quantified with Raven Pro 1.4 (Bioacoustics Research Program 2014) and compared with reference calls for dubious vocalizations.

After identifying all species calling from 1900-0400 hours, we determined the composition of species in each signaling assemblage considering 1-hour and 3-hour time periods. Night activity was divided into three periods, namely *early* (1900 to 2200), *mid* (2200 to 0100), and *late* (0100 to 0400) periods. For each site, we calculated the similarity in species composition between night periods using both 1-hour and 3-hour intervals, on each day (fig. 1a). For the 1-hour resolution, we calculated hour-to-hour compositional similarity and coded the respective pair of night periods (within and between early, mid, and late). For the 3-hour resolution, pairwise compositional similarity corresponded to the combinations between early, mid, and late periods of the night. Because we were interested in the nightly variation determined by the between-period differences (early-mid, mid-late, early-late), we excluded within-period similarities. We calculated the Jaccard coefficient (s) to represent similarity, an index broadly used to represent spatial beta diversity (Jost, Chao & Chazdon 2010; Baselga et al. 2015) using R package *vegan* (Oksanen *et al.* 2018). Because the function "vegdist" in *vegan* calculates Jaccard (and other coefficients) as dissimilarity, to facilitate interpretation, we converted it to express similarity values ($1\text{-}s_{ij}$), where 1 indicates maximum similarity in the composition of vocal active species.

Species sharing recent ancestry tend to show similar ecological requirements given niche conservatism (Wiens & Graham 2005). To represent the degree of similarity among coexisting species, we calculated the specific overrepresentation score (SOS), a measure that represents how specific lineages contribute to the distribution of species across communities (Borregaard *et al.* 2014). First, using a comprehensive time-calibrated phylogenetic tree of amphibians (Pyron & Wiens 2011) pruned to the species found in the study area, we calculated if specific sister lineages pairs contributed more to the phylogenetic structure and species co-occurrence than expected by a null model (geographic node divergence – GND; Borregaard *et al.* 2014). The node between Hylidae (except for Phyllomedusidae) and Leptodactylidae showed the highest GND score (0.5, fig. S2), and we thus calculated SOS values considering this specific node. SOS are the standardized effect sizes from the observed species richness of each sister lineage referenced to a null model that breaks the phylogenetic dominance of this lineage pair (using the *quasiswamp* algorithm; Borregaard *et al.* 2014). We used all species registered at each site to calculate SOS, with positive and negative values representing assemblages with higher overrepresentation of Hylidae and Leptodactylidae species, respectively. Therefore, more extreme values represented assemblages with higher ecological similarities.

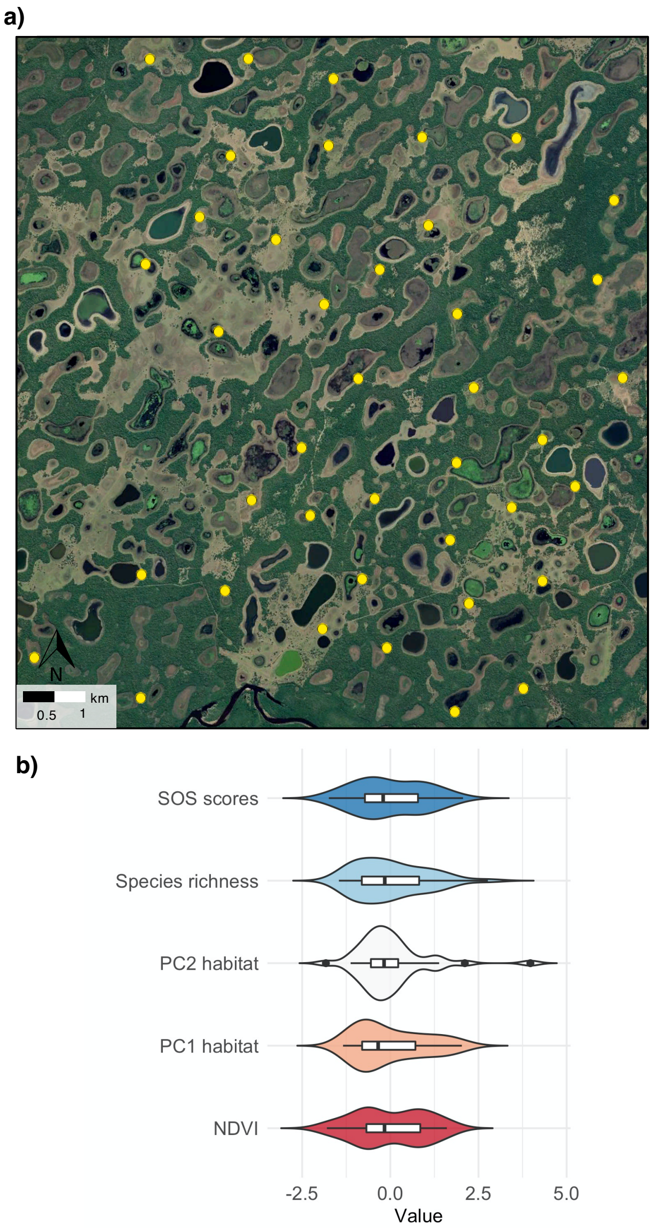

Figure 2. Study region and (a) spatial distribution of the 39 monitored sites used by anuran assemblages in south Pantanal wetlands, Brazil, and (b) frequency distribution of the variables (standardized to zero mean and unit variance) representing ecological context and environmental structure: phylogenetic relatedness (SOS scores), species richness, habitat structure represented by two principal component axes summarizing aquatic and terrestrial variables, and landscape heterogeneity. Boxplots represent the median, 25% and 75%

quantiles (white box) and min-max values (whiskers) are surrounded by violin plots (kernel density plots representing the probability density).

Analyses

To test if species composition differed across night periods, we fitted a general linear mixed model (GLMM) on compositional similarity for each time resolution (1-hour and 3-hour intervals), using the associated combination of night period (three levels: early-mid, mid-late, and early-late) as fixed factor, and site (n=39) and monitored day (10 distinct days) as random factors. We checked normality and homoscedasticity through visual examination of residuals and probability plots (Q-Q plots) and ranked them with models with null intercept effect only and random effects using Akaike Information Criterion (Burnham and Anderson, 2002) corrected for small sample sizes (AICc). Confidence intervals for model coefficients were estimated by computing likelihood profiles using package *lme4* (Bates *et al.* 2015). Models with delta AIC (dAICc) <2 were considered equally plausible and variables which corresponding 95% confidence interval (CI) did not include zero were considered significant. We estimated the coefficient of determination (R^2) for the mixed models based on Nakagawa, Johnson and Schielzeth (2017), where the marginal coefficient (R^2 m) refers to the variation explained by fixed effects, and the conditional coefficient (R^2 c) consider both fixed and random structures. As a visual display of overall nightly variation in species composition, we applied a non-metric multidimensional scaling (nMDS) on the composition of vocal active species on the early- and the late night-periods at each day and site. Then, we plotted the centroid of each site and combination of night period. Low variation in species composition between early and late periods would be represented by short distances between the periods.

To assess if changes in species composition in a night cycle were influenced by gradients representing habitat structure (local and landscape habitat heterogeneity, fig 2b) and the ecological context (species richness and SOS scores considering all species registered at each site, fig 2b), we fitted a GLMM on the compositional similarity for the early-late period and used the first two PC axes representing habitat structure, NDVI, species richness, and SOS scores as fixed factors, and site and monitoring day as random factors. Models were built for both temporal resolutions and ranked with AICc, including a model with null intercept effect only, and the same abovementioned procedures were used to check residual normality and to estimate the confidence intervals and R^2.

To test if variation in nightly compositional changes across days was influenced by the distinct ecological drivers, we first calculated the variance of all compositional similarities from the early-late period for all days per site. Then, we built different general linear models representing a) global model with all predictors, b) local heterogeneity only (PC1 and PC2), c) landscape heterogeneity (NDVI), d) ecological context of assemblages (species richness and SOS), and e) a null model with the intercept only. Multicollinearity was low for the full models (1-hour model VIF = 1.35, 3-hour model VIF = 1.41). We ranked these models using AICc and further determined if adding a quadratic term lead to differences in the models (using dAICc). We used a log transformation to ensure homoscedasticity of the residuals and evaluated Q-Q residual plots to check normality assumptions.

Additionally, to understand the combined importance of habitat structure and ecological context across local assemblages (i.e., metacommunity), we used the incidence of all anuran species recorded at each site and applied a redundancy analysis (RDA) to determine the amount of variation explained by phylogenetic relatedness (SOS values), local vegetation heterogeneity (first two PC axes on aquatic and terrestrial habitat variables), landscape heterogeneity (NDVI), and species richness. We used an ANOVA-like permutation test (x1000) to assess model significance with the *vegan* package (Oksanen *et al.* 2018) in R software version 4.0.2 (R Core Team 2020).

Results

We recorded 24 anuran species distributed in 4 families, with Hylidae (n = 12) and Leptodactylidae (n = 9) being the most representative families (tab. S2). Species richness varied from 6 to 19 species per site ($\bar{x} = 10.5 \pm 3$ SD), while hourly species richness ranged from a mean of 5.14 to 5.78 species ($\bar{x} = 5.48 \pm 2.1$ SD, fig. S3). Overall, mean similarity in species composition was higher between early-mid and mid-late periods, both at the 1-hour (early-mid: 0.69 ± 0.19 SD, mid-late: 0.71 ± 0.2 SD, early-late: 0.64 ± 0.2 SD) and 3-hour resolutions (early-mid: 0.77 ± 0.16 SD, mid-late: 0.78 ± 0.16 SD, early-late: 0.71 ± 0.18 SD, fig. 3a). However, as shown by GLMM, differences in compositional similarity between night periods were poorly explained by the fixed factors (i.e., combinations of nocturnal periods; $R^2c < 0.04$), with the highest variation attributed to random factors both for the 1-hour and 3-hour resolutions ($R^2c > 0.42$; tab. 1). A decay in compositional similarity was observed only for the combination of early-late periods (β 1-hour = -0.05 and 95% CI [-0.06, -0.04]; β 3-hour = -0.06 and 95% CI [-0.09, -0.03]).

The compositional similarity of vocal active species between early-late nocturnal periods was positively related to phylogenetic relatedness (SOS scores) and the PC2 representing local habitat heterogeneity ($R^2m = 0.11$, $R^2c = 0.6$; tab. 2). Specifically, high compositional similarities were associated with an increase in the overrepresentation of species from the family Hylidae (SOS scores, β 1-hour = 0.05 and 95% CI [0.02, 0.07]; fig. 3b; tab. 1), and an increase in vegetation heterogeneity on the terrestrial terrain of breeding habitats (PC2- local habitat; β 1-hour = 0.03 and 95% CI [0.01, 0.05]; fig. 3c; tab. 1). However, these relationships were observed only for compositional similarities calculated at the 1-hour resolution (tab. 1). The nMDS ordination of sites and night periods of activity shows varying degrees of variability in the composition of vocal active species between early and late periods (fig. 4a).

The models including landscape heterogeneity (NDVI) with and without the quadratic term were considered equally plausible models explaining the variability of nightly similarities across days, for the 1-hour resolution (tab. 2). The model with a quadratic term ($R^2 = 0.25$, $p=0.005$; fig. 3d) indicates that assemblages with similar variation of compositional similarity across different days were located in more heterogeneous landscapes (higher NDVI). Model ranking using the 3-hour resolution indicates that the fit with NDVI is not different from an effect from a null model (tab.2).

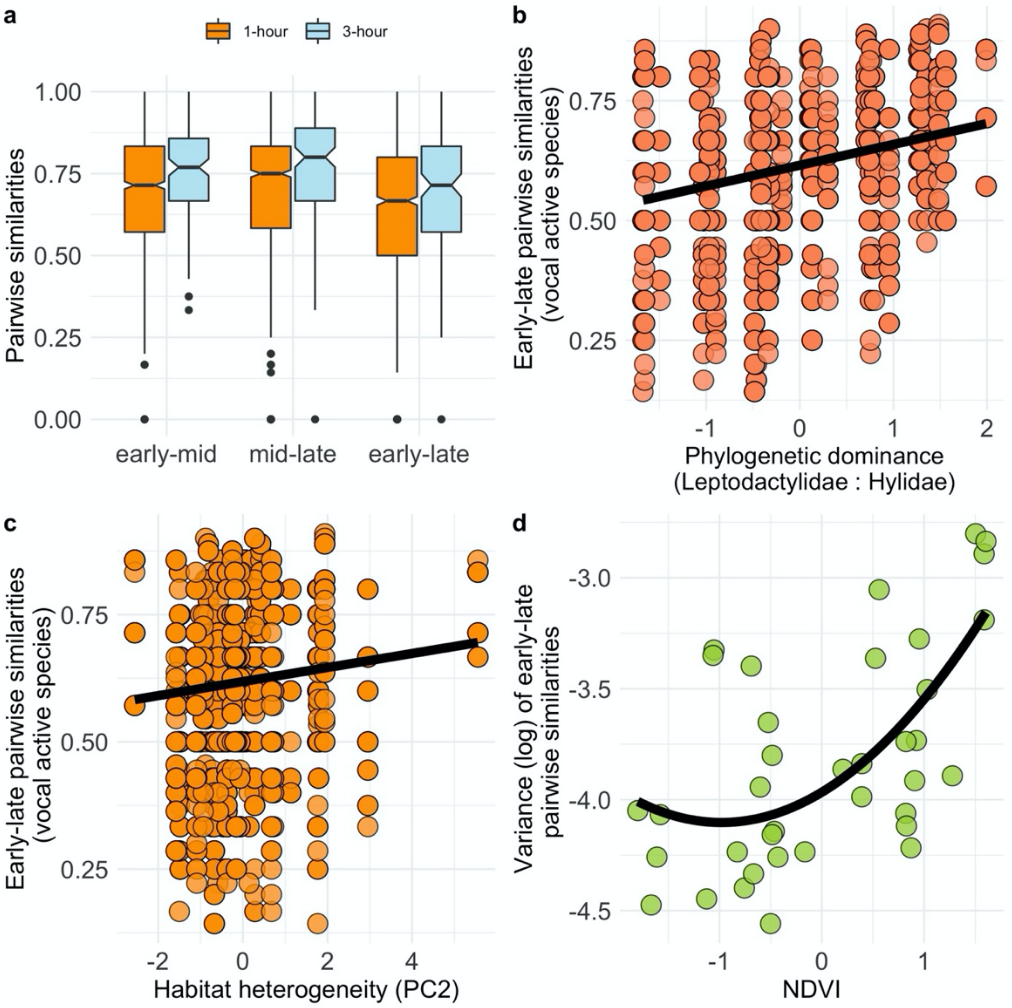

Figure 3. (a) Similarity in species composition between night periods using two temporal resolutions (1-hour and 3-hour intervals). General linear mixed models fit on the compositional similarity between early-late periods for all days at the 1-hour resolution show an association with (b) overrepresentation of species from the family Hylidae (SOS positive values) in assemblages and (c) a PCA axis representing terrestrial vegetational heterogeneity on the breeding sites. Using Akaike Information Criteria, we ranked five potential models (general linear models) explaining the variance of compositional similarity between early-late periods in all days: landscape heterogeneity (NDVI), habitat structure (PC1 + PC2), and ecological context (species richness and SOS scores), and found (d) a positive relationship of

the variance of compositional similarity between early-late periods for all days and landscape heterogeneity (NDVI).

Table 1. Model selection (against a null model) and coefficient of determination of general linear mixed models fitted on (1) compositional similarities (1- Jaccard dissimilarity coefficient, 1-hour and 3-hour temporal resolutions) of vocal active anuran assemblages with combinations of night periods as fixed effect (early: 1900, 2000, 2100; mid: 2200, 2300, 0000; late: 0100, 0200, 0300, UTC-4), and on (2) compositional similarity between early-late period with phylogenetic relatedness of assemblages (SOS scores), species richness, PC1 and PC2 representing local habitat structure, and landscape heterogeneity (NDVI) as fixed effects. Monitored day and site were included as random effects. R^2m: marginal r-squared; R^2c: conditional r-squared. Best models are highlighted in bold.

	deltaAICc	AICc	df	weight	R^2m	R^2c
(1) Compositional similarity ~ night periods						
1-hour null	117.2	-2583.5	4	<0.001		
1-hour	0	-2700.7	6	1	0.02	0.42
3-hour null	20	-355.4	4	<0.001		
3-hour	0	-375.4	6	1	0.04	0.53
(2) Early-late compositional similarity ~ drivers						
1-hour null	2.6	-1269.8	4	0.22	0.11	0.48
1-hour	0	-1272.4	9	0.78		
3-hour null	0	-673.7		0.901	0.08	0.53
3-hour	4.4	-669.2		0.09		

Table 2. Model coefficients from general linear mixed models fitted on (1) compositional similarities (1-hour and 3-hour temporal resolutions) of vocal active anuran assemblages with combinations of night periods as fixed effect, and on (2) compositional similarity between early-late period with phylogenetic relatedness of assemblages (SOS scores),

species richness, PC1 and PC2 representing local habitat structure, and landscape heterogeneity (NDVI) as fixed effects. Monitored day and site were included as random effects. LCI: lower confidence interval; UCI: upper confidence interval [95%]. Significant results are highlighted in bold.

	t-value	beta	LCI	UCI
(1) Compositional similarity ~ night periods				
1-hour				
Intercept (early-mid)	59.8	-0.69	0.67	0.71
mid-late	**3.2**	**0.02**	**0.01**	**0.03**
early-late	**-8.4**	**-0.05**	**-0.06**	**-0.04**
3-hour				
Intercept (early-mid)	52.8	0.77	0.74	0.79
mid-late	1	0.01	-0.01	0.04
early-late	**-4.4**	**-0.06**	**-0.09**	**-0.03**
(2) Early-late compositional similarity ~ drivers				
1-hour				
Intercept	10.7	0.7	0.57	0.83
PC1-Habitat heterogeneity	0.7	0.01	-0.01	0.03
PC2-Habitat heterogeneity	**2.6**	**0.03**	**0.01**	**0.06**
SOS scores	**2.6**	**0.05**	**0.01**	**0.09**
NDVI	0.4	0.01	-0.03	0.05
Species richness	-1	-0.01	-0.02	0.01

Table 3. Ranking of models fitted on the variance (log) of compositional similarities for 1-hour and 3-hour temporal resolutions, considering early-late night periods for all days. Models were ranked using AICc and comprised i) landscape heterogeneity (NDVI), ii) ecological context of assemblages (SOS scores and species richness), iii) local habitat structure (PC1 and PC2), iv) a global model containing all variables, and a v) null model with intercept only. Significant results are highlighted in bold.

		dAICc	df	weight
1-hour	**~ NDVI**	0	3	0.867
	~ SOS + species richness	5.2	4	0.063
	Null model	5.9	2	0.045
	Global model	7.5	7	0.021

	~ PC1 + PC2 (habitat structure)	10.8	4	0.004
1-hour	**~ NDVI + ~ NDVI2**	0	4	0.59
	~ NDVI	0.7	3	0.41
3-hour	**~ NDVI**	0	3	0.48
	Null model	1.3	2	0.245
	Global model	2.2	7	0.161
	~ PC1 + PC2 (habitat structure)	3.3	4	0.09
	~ SOS + species richness	6	4	0.023

Spatial variation in assemblage composition was partially explained by the predictors representing distinct ecological gradients ($R^2 = 0.34$, $p = 0.001$; fig. 4a, tab. S3). Specifically, three orthogonal axes of explanatory variables could be distinguished, with species richness showing a positive association with the first RDA axis, SOS scores showing a negative association with the second RDA axis, and NDVI (and PC1 and PC2 to a lesser degree) showing a positive association with the second RDA axis (fig. 4b).

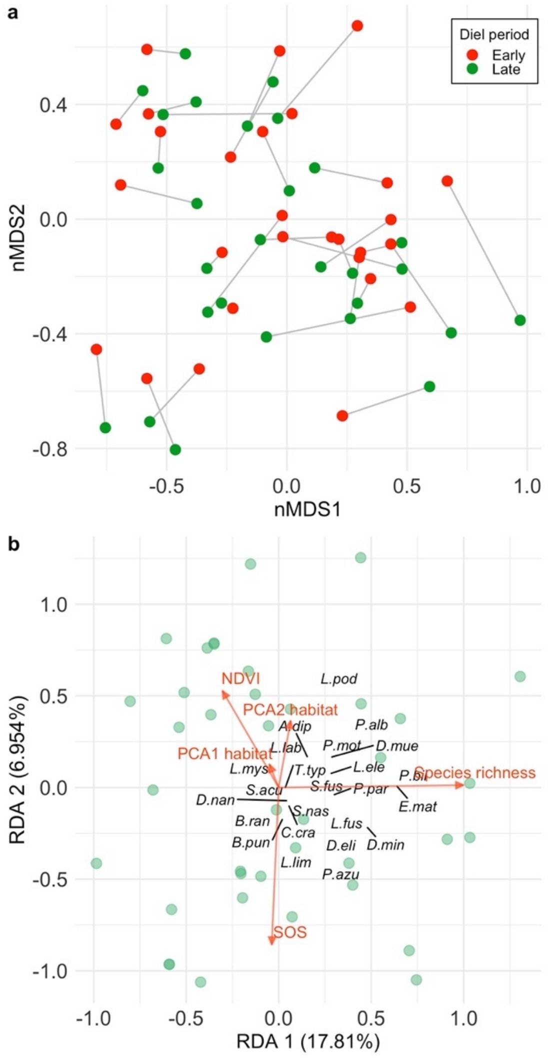

Figure 4. (a) A non-metric multidimensional scaling for the combination of species registered on early and late periods at each site, depicting overall short-term variability in species composition (species names are listed in table S2). Points indicate the centroid of species composition on each site and period. (b) Two first axes of a redundancy analysis (RDA) using total species incidence per site and phylogenetic relatedness (SOS scores), local habitat heterogeneity (first two PC axes on habitat variables), landscape heterogeneity (NDVI), and total species richness. Dots represent sites ordinated according to their compositional similarities and angle between arrows (environmental and ecological gradients) and response variables (species) indicate their linear correlation.

Discussion

The scale dependence of ecological phenomena requires ascertaining the spatial and temporal framings of ecological communities (Soininen 2010; Van Allen *et al.* 2017; Viana & Chase 2019). Although ecologists have largely neglected fine resolution timescales (Estes *et al.* 2018), our closer look at the temporal axis of tropical anuran assemblages unveiled that variation in species activity is influenced by the environmental structure (both local and landscape heterogeneity) and the phylogenetic relatedness of assemblages. However, these relationships were found for the 1-hour temporal resolution of species activity but not for the 3-hour resolution, indicating that even small changes in temporal resolution may lead to scaling issues. We discuss our findings in the light of potential trade-offs between ecological overlap among coexisting species and temporal and spatial partitioning across the gradients of local and landscape heterogeneity.

Similarity in the composition of vocal active species between night periods was higher at localities with more heterogeneous habitats and in assemblages overrepresented by species of the family Hylidae, which typically use the vertical stratum of vegetation as micro-habitat. Accordingly, high complexity in the vertical stratum of vegetation reduces spatial overlap for semi-terrestrial and arboreal species (Hödl 1977; Silva, Gibbs & Rossa-Feres 2011), improving chances for species to acoustically communicate and find mates with the benefit of reduced negative interactions (Kronfeld-Schor & Dayan 2003; Gaston 2019). Also, a decay in compositional similarity between night periods was observed in localities with low vegetational heterogeneity and overrepresented by species of the family Leptodactylidae, composed predominantly of terrestrial species lacking adaptations to perch in vertical structures. These two contexts may increase chances for direct species interactions when searching for calling and breeding sites (Hödl 1977, Borzée et al. 2016), and one possibility is that deterministic exclusion of competing species through the night could drive the decay in compositional similarity, with the persistence of few dominant species. However, we were unable to detect a clear pattern of lower species richness over diel periods, as would be presumably expected in such circumstances (fig. S4). Conversely, temporal patterns of anuran activity may be regulated by distinct strategies in response to resource availability and competition (McCauley et al. 2000, Humfeld 2013). In this sense, a decay in nightly compositional similarity could reflect temporal partitioning among species with similar ecological requirements in localities with limited potential for microhabitat partitioning. Further, we also acknowledge that a wider variation in microclimatic factors in these less heterogeneous sites could also account for the observed decay in nightly activity (Saenz et al. 2006; Llusia et al. 2013), although we were unable to address these factors. Altogether, the variation in night activity of anuran assemblages indicates potential trade-offs between microhabitat and temporal partitioning, being consistent with a role of niche complementary on the structuring of ecological communities (Schoener 1974; Mason *et al.* 2008).

Anuran assemblages located at sites with increasing landscape heterogeneity (NDVI), ranging from open grasslands to areas with increased forest cover, showed higher variability in nightly compositional similarities across the monitored days. For amphibians, landscape structure has a large influence on organisms' movement into breeding sites and on their maintenance during the interlude of calling activity and interbreeding season (Becker *et al.* 2010). For instance, higher solar radiation in open grassland compared to closed canopy sites can hinder the persistence and movement of species unable to cope with intense evaporative water loss (Rothermel 2004). Landscape heterogeneity indeed contributed to explaining the spatial variation in species composition observed at the metacommunity scale of the anuran assemblages we investigated. In this context, low-heterogeneous landscapes may emphasize the role of environmental filtering in sorting out species with low environmental tolerance and dispersal capability, and the dynamics resulting from the same set of species sorted into these environments may relate to the low variability in nightly compositional similarities observed across days. Conversely, an increase in landscape heterogeneity and forest cover reduces overheating and desiccation during daylight, which favors spatial dynamics by decreasing movement resistance among habitat patches and within species home range (Bowler & Benton 2005; Buskirk 2012; Silva *et al.* 2012). Since chorusing formations start with a few early individuals establishing spatial dominance, the order of species arrival may constraint opportunities for late arrivals, and communities may undergo distinct dynamics over a nocturnal activity (Fukami 2015). In this sense, spatial dynamics and priority effects may increase stochasticity on the assembly of communities and counteract competitive interactions at fine scales (Amarasekare 2003). Previous findings of large compositional variation of amphibians have underscored a role of stochasticity on the assembly of communities (Richter-Boix, Llorente & Montori 2007; Werner *et al.* 2007), and our findings suggest that increasing landscape heterogeneity may indirectly increase the effects of spatial-related stochastic processes on signaling anuran assemblages.

The nightly compositional similarity was relatively high ($\bar{x} = 0.64$ between early-late period, 1-hour resolution), indicating that a large portion of species maintains continuous calling activity throughout the night. The phenomenon of anuran chorusing may emerge with a single signaling individual whose calling activity induces competing conspecific males to start advertising, initiating a chain reaction that may last for hours (Brooke et al. 2000, Prado et al. 2005, Wells and Schwartz 2007, Llusia et al. 2013). Chorusing formation may benefit calling energetic costs by increasing attractiveness for mates to a common breeding site and minimizing predation risk (Schwartz and Bee 2013). Although chorusing attendance and diel activity patterns are widely described in species-specific studies (Bertoluci & Rodrigues 2002;

Gottsberger & Gruber 2004; Heinermann et al. 2015; Lopes et al. 2011; Schalk & Saenz 2016), community-wide approaches remained elusive (Ulloa *et al.* 2019, Dubos et al. 2020, Guerra *et al.* 2020). Considering our findings on the influence of habitat heterogeneity and species interactions on nightly compositional variation of anuran assemblages, we argue that future studies should take into consideration the contribution of ecological contexts in species calling activity, in addition to abiotic factors such as temperature and rainfall. Potential effects of heterospecifics in calling behavior have mainly been investigated in light of acoustic communication, with species eventually altering signaling parameters or behavior when exposed to heterospecific calls (Phelps, Rand & Ryan 2006; Both & Grant 2012), while the influence of species interactions on calling activity still remains to be elucidated. Therefore, addressing a range of conditions on which potential interactions may occur, *i.e.* distinct habitats and combinations of competing species, may increase our understanding of the acoustic communication in multi-species systems.

Our findings highlight the importance of temporal scaling effects in inferring community assembly processes. In the spatial domain, larger sampling units enable more individuals and species to be recorded, while environmental variation is often described with coarser resolution and thus less detailed (Wiens 1989). For this reason, a mismatch between the resolution used to describe both response and predictor variables often leads to lower explanation power of species occupancy (Barton *et al.* 2013, Sugai *et al.* 2019b) and therefore, a perceived weaker importance of the environment in explaining community structure (Viana & Chase 2019). Similarly, mismatches can also emerge with the temporal resolution used to describe ecological communities. Considering that competitive interactions and predation pressure are important determinants of diel species activity (Kronfeld-Schor, Bloch & Schwartz 201,3 McCann et al. 2017), disregarding diel differences in animal activity within communities leads to a poorer representation of co-occurring species. Consequently, the temporal resolution used may result in an ecological pattern unrelated to the actual mechanisms driving community assembly (Gaston 2019).

Theory predicts that changes in the seasonal timing of species activity alter the temporal overlap of competing species and potentially affect the strength of species interaction, either stabilizing coexistence or increasing competitive inequalities (Godoy & Levine 2014; Rudolf 2019). Our findings, however, raise the possibility that diel differences in species activity may change the magnitude of competitive interactions (Schwartz 1987; Brumm 2006, Humfeld 2013). Importantly, we found that even a small change in temporal resolution (from 1 to 3-hour resolution), was enough to prevent finding a relationship with habitat structure and ecological context (phylogenetic dominance). Therefore, using appropriate temporal resolution in breeding phenology investigations can reveal differences in species activity that account to reduce negative interactions.

Authors' contribution

LSMS and TS conceived the presented idea; LSMS, TSFS, and DLL contributed to design the study; LSMS and TSFS collected the data; LSMS performed the analysis and took the lead in writing the manuscript; all authors revised the manuscript critically; DLL and TS contributed to the writing of the manuscript.

Data availability statement

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.sf7m0cg4r (Sugai et al. 2020).

Acknowledgements

We thank the handling editor and the three reviewers for the thoughtful suggestions on the manuscript. We thank D.C. Rossa-Feres, M.C. Côrtes, V.S. Saito, and L.F. Toledo for helpful suggestions in an early version of the manuscript. We thank M.C. Ribeiro for providing some of the audio recorders through grant #2013/50421-2, São Paulo Research Foundation (FAPESP); Barranco Alto farm owners and crew for their support; R. Costa-Pereira, J.L.M.M. Sugai, G.N. Souza, P. Eveline, S. Duleba, H.S.G. Folly, L.S. Almeida for assisting in fieldwork; Rufford Foundation for Small Grant funding. LSMS and TS acknowledges grants #2015/25316-6, #2017/15772-0, and # 2019/04033-7 São Paulo Research Foundation (FAPESP); Programa Nacional de Cooperação Acadêmica (Procad) 07/2013 project 88881.068425/2014-01, and Programa de Apoio à Pós-Graduação (PROAP) 817737/2015 from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). This study was financed in part by CAPES - Finance Code 001. DLL acknowledges grant 2016-T2/AMB-1722 provided by the Comunidad de Madrid and a research project funded by the Ministerio de Economía, Industria y Competitividad (CGL2017-88764-R, MINECO/AEI/FEDER, Spain). LSMS acknowledges grant PEJ2018-004603-A. TSF Silva received a productivity grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), grant #310144/2015-9, during part of this research.

References

Amarasekare, P. (2003) Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters,* **6,** 1109-1122.

Audacity Team (2018) Audacity(R): Free audio editor and recorder. Version 2.3.1. https://audacityteam.org/

Barton, P.S., Cunningham, S.A., Manning, A.D., Gibb, H., Lindenmayer, D.B., & Didham, R.K. (2013) The spatial scaling of beta diversity. *Global Ecology and Biogeography,* **22,** 639-647.

Baselga, A., Bonthoux, S., & Balent, G. (2015). Temporal beta diversity of bird assemblages in agricultural landscapes: land cover change vs. stochastic processes. PLoS ONE, 1–14. doi:10.1371/journal.pone.0127913

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *2015,* **67,** 48.

Becker, C.G., Fonseca, C.R., Haddad, C.F.B., & Prado, P.I. (2010) Habitat split as a cause of local population declines of amphibians with aquatic larvae. *Conservation Biology,* **24,** 287-294.

Bertoluci, J., & Rodrigues, M. T. (2002). Seasonal patterns of breeding activity of Atlantic Rainforest anurans at Boracéia, Southeastern Brazil. *Amphibia-Reptilia*, **23**(2), 161–167.

Bioacoustics Research Program (2014) Raven Pro: interactive sound analysis software (Version 1.5). The Cornell Lab of Ornithology, Ithaca, NY.

Borregaard, M.K., Rahbek, C., Fjeldså, J., Parra, J.L., Whittaker, R.J., & Graham, C.H. (2014) Node-based analysis of species distributions. *Methods in Ecology and Evolution,* **5,** 1225-1235.

Borzée, A., Kim, J.Y., & Jang, Y. Asymmetric competition over calling sites in two closely related treefrog species. *Scientific Reports*, 2016, **6**, 32569.

Both, C., & Grant, T. (2012) Biological invasions and the acoustic niche: the effect of bullfrog calls on the acoustic signals of white-banded tree frogs. *Biology Letters,* **8,** 714-716.

Bowler, D.E., & Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews,* **80,** 205-225.

Burnham K.P., & Anderson D.R. (2002) Model selection and multimodel inference: a practical information- theoretic approach. Springer S, New York

Bréda, N.J.J. (2003) Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. *Journal of Experimental Botany,* **54,** 2403-2417.

Brumm, H. (2006) Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. *Journal of Comparative Physiology A,* **192,** 1279-1285.

Buskirk, J. (2012) Permeability of the landscape matrix between amphibian breeding sites. *Ecology and evolution,* **2,** 3160-3167.

Carothers, J.H., & Jaksić, F.M. (1984) Time as a niche difference: the role of interference competition. *Oikos,* **42,** 403-406.

Castro-Arellano, I., Lacher Jr, T.E., Willig, M.R., & Rangel, T.F. (2010) Assessment of assemblage-wide temporal niche segregation using null models. *Methods in Ecology and Evolution,* **1,** 311-318.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics,* **31,** 343-366.

Delatorre, M., Cunha, N., Raizer, J., & Ferreira, V.L. (2015) Evidence of stochasticity driving anuran metacommunity structure in the Pantanal wetlands. *Freshwater Biology*, **60**: 2197-2207.

Delatorre, M., da Cunha, N.L., Rodrigues, R.B., Damasceno-Júnior, G.A., & Ferreira, V.L. (2020) Trait-environment relationship of aquatic vegetation in a tropical pond complex system. *Wetlands*, **40**, 299–310.

Dornelas, M., Magurran, A.E., Buckland, S.T., Chao, A., Chazdon, R.L., Colwell, R.K., Curtis, T., Gaston, K.J., Gotelli, N.J., Kosnik, M.A., McGill, B., McCune, J.L., Morlon, H., Mumby, P.J., Øvreås, L., Studeny, A. & Vellend, M. (2013) Quantifying temporal change in biodiversity: challenges and opportunities. *Proceedings of the Royal Society B: Biological Sciences,* **280,** 20121931.

Dubos, N., Morel, L., Crottini, A., Freeman, K., Honoré, J., Lava, H., Noël J., Porton, I., Rendrirendry, G., Rosa G.M., & Andreone, F. (2020). High interannual variability of a climate driven amphibian community in a seasonal rainforest. *Biodiversity and Conservation*, **29**, 893–912.

Duellman, W.E., & Trueb, L. (1994) *Biology of amphibians*. The Johns Hopkins University Press, Baltimore, MD.

Estes, L., Elsen, P.R., Treuer, T., Ahmed, L., Caylor, K., Chang, J., Choi, J.J., & Ellis, E.C. (2018) The spatial and temporal domains of modern ecology. *Nature Ecology & Evolution,* **2,** 819-826.

Evans, T.L., & Costa, M. (2013) Landcover classification of the Lower Nhecolândia subregion of the Brazilian Pantanal Wetlands using ALOS/PALSAR, RADARSAT-2 and ENVISAT/ASAR imagery. *Remote Sensing of Environment,* **128,** 118-137.

Fick, S.E., & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology,* **37,** 4302-4315.

Fukami, T. (2015) Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics,* **46,** 1-23.

Gaston, K.J. (2019) Nighttime ecology: the "nocturnal problem" revisited. *The American Naturalist,* **193,** 481-502.

Godoy, O., & Levine, J.M. (2014) Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology,* **95,** 726-736.

Gottsberger, B., & Gruber, E. (2004) Temporal partitioning of reproductive activity in a neotropical anuran community. *Journal of Tropical Ecology,* **20,** 271-280.

Greenfield, M.D. (2015) Synchronous and alternating choruses in insects and anurans: Common mechanisms and diverse functions1. *Integrative and Comparative Biology,* **34,** 605-615.

Guerra, V., Costa, N.Q., Llusia, D., Márqueza, R., & Bastos, R.P. (2020) Nightly patterns of calling activity in anuran assemblages of the Cerrado, Brazil. *Community Ecology*, **21**, 33-42.

Heinermann, J., Rodríguez, A., Segev, O., Edmonds, D., Dolch, R., & Vences, M. (2015) Year-round activity patterns in a hyperdiverse community of rainforest amphibians in Madagascar. *Journal of Natural History*, **49**(35–36), 2213–2231.

Hodge, S., Arthur, W., & Mitchell, P. (1996) Effects of temporal priority on interspecific interactions and community development. *Oikos,* **76,** 350-358.

Humfeld, S. (2013) Condition-dependent signaling and adoption of mating tactics in an amphibian with energetic displays. *Behavioral Ecology*, **24**, 859-870.

Hödl, W. (1977) Call differences and calling site segregation in anuran species from central Amazonian floating meadows. *Oecologia,* **28,** 351-363.

Jost, L., Chao, A., & Chazdon, R.L. (2010) Compositional similarity and beta diversity. *Biological diversity: frontiers in measurement and assessment* (eds A.E. Magurran & B. McGill), pp. 66-84. Oxford University Press, Oxford, UK.

Kneitel, J.M., & Chase, J.M. (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters,* **7,** 69-80.

Kronfeld-Schor, N., Bloch, G., & Schwartz, W.J. (2013) Animal clocks: when science meets nature. *Proceedings of the Royal Society B: Biological Sciences,* **280,** 20131354.

Kronfeld-Schor, N., & Dayan, T. (2003) Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics,* **34,** 153-181.

Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software*, **25**, 1-18.

Leibold, M.A., & Chase, J.M. (2018) *Metacommunity ecology*. Princeton University Press, Princeton, NJ.

Legendre, P., & Gauthier, O. (2014) Statistical methods for temporal and space–time analysis of community composition data. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 2013-2728

LI-COR Biosciences (1992) *Lai 2000 Plant Canopy Analyzer. Operating Manual.* LI-COR Biosciences, Nebraska, USA.

Llusia, D., Márquez, R., Beltrán, J.F., Moreira, C., & do Amaral, J.P. (2013) Environmental and social determinants of anuran lekking behavior: intraspecific variation in populations at thermal extremes. *Behavioral Ecology and Sociobiology,* **67,** 493-511.

Lopez, J. A., Scarabotti, P. A., & Ghirardi, R. (2011). Seasonal patterns of abundance and recruitment in an amphibian assemblage from the Parana River floodplain. *Interciencia*, **36**(7), 538–544.

MacArthur, R., & Levins, R. (1964). Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences*, **6**, 1207-1210.

Mason, N.W.H., Lanoiselée, C., Mouillot, D., Wilson, J.B., & Argilier, C. (2008) Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. *Journal of Animal Ecology,* **77,** 661-669.

McCann, N.P., Zollner, P.A., & Gilbert, J.H. (2017) Temporal scaling in analysis of animal activity. *Ecography,* **40,** 1436-1444.

Mccauley, S. J., Bouchard, S. S., Farina, B. J., Isvaran, K., Quader, S., Wood, D. W., & St. Mary, C. M. (2000) Energetic dynamics and anuran breeding phenology: insights from a dynamic game. *Behavioral Ecology*, **11**, 429–436.

Nakagawa, S., Johnson, P.C.D., & Schielzeth, H. (2017) The coefficient of determination $R^2$and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of The Royal Society Interface,* **14,** 20170213.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Ledengre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Steven, M.H.H., Szoecs, E., & Wagner, H. (2018) vegan: Community ecology package. R package version 2.5-3.

Oseen, K.L., & Wassersug, R.J. (2002) Environmental factors influencing calling in sympatric anurans. *Oecologia,* **133,** 616-625.

Phelps, S.M., Rand, A.S., & Ryan, M.J. (2006) The mixed-species chorus as public information: túngara frogs eavesdrop on a heterospecific. *Behavioral Ecology,* **18,** 108-114.

Prado, C., Uetanabaro, M. & Haddad, ,C. (2005) Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. *Amphibia-Reptilia*, **26,** 211-221.

Pyron, A.R., & 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,** 543-583.

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RapidEye AG (2011) Satellite imagery product specifications. Version 2.1., pp. 44.

Richter-Boix, A., Llorente, G.A., & Montori, A. (2007) Structure and dynamics of an amphibian metacommunity in two regions. *Journal of Animal Ecology,* **76,** 607-618.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science,* **235,** 167-171.

Rocchini, D., Boyd, D.S., Féret, J.-B., Foody, G.M., He, K.S., Lausch, A., Nagendra, H., Wegmann, M. & Pettorelli, N. (2016) Satellite remote sensing to monitor species diversity: potential and pitfalls. *Remote Sensing in Ecology and Conservation,* **2,** 25-36.

Ron, R., Fragman-Sapir, O., & Kadmon, R. (2018) Dispersal increases ecological selection by increasing effective community size. *Proceedings of the National Academy of Sciences,* **115,** 11280-11285.

Rothermel, B.B. (2004) Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. *Ecological Applications,* **14,** 1535-1546.

Rouse, J.W.J., Haas, R.H., Schell, J.A., & Deering, D.W. (1974) Monitoring the vernal advancements and retrogradation of natural vegetation. pp. 137. NASA/GSFC, Final Report, Greenbelt, MD.

Rudolf, V.H.W. (2019) The role of seasonal timing and phenological shifts for species coexistence. *Ecology Letters,* **22,** 1324-1338.

Saenz D., Fitzgerald L.A., & Baum K.A. (2006) Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. *Herpetological Monographs*, **20**, 64-82.

Schalk, C.M., & Saenz, D. (2016) Environmental drivers of anuran calling phenology in a seasonal Neotropical ecosystem. *Austral Ecology,* **41,** 16-27.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science,* **185,** 27-39.

Schreiber, S.J., & Kelton , M. (2005) Sink habitats can alter ecological outcomes for competing species. *Journal of Animal Ecology,* **74,** 995–1004.

Schwartz, J.J. (1987) The function of call alternation in anuran amphibians: a test of three hypotheses. *Evolution,* **41,** 461-471.

Schwartz, J.J., & Bee, M.A. (2013) Anuran acoustic signal production in noisy environments. *Animal Communication and Noise* (ed. H. Brumm), pp. 91-132. Springer Berlin Heidelberg, Berlin, Heidelberg.

Segre, H., Ron, R., De Malach, N., Henkin, Z., Mandel, M., & Kadmon, R. (2014) Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. *Ecology Letters,* **17,** 1400-1408.

Signorelli, L., Bastos, R.P., De Marco, P., & With, K.A. (2016) Landscape context affects site occupancy of pond-breeding anurans across a disturbance gradient in the Brazilian Cerrado. *Landscape Ecology,* **31,** 1997-2012.

Silva, F.R., Gibbs, J.P., & Rossa-Feres, D.C. (2011) Breeding habitat and landscape correlates of frog diversity and abundance in a tropical agricultural landscape. *Wetlands,* **31,** 1079-1087.

Silva, F.R., Oliveira, T.A.L., Gibbs, J.P., & Rossa-Feres, D.C. (2012) An experimental assessment of landscape configuration effects on frog and toad abundance and diversity in tropical agro-savannah landscapes of southeastern Brazil. *Landscape Ecology,* **27,** 87-96.

Soininen, J. (2010) Species turnover along abiotic and biotic gradients: patterns in space equal patterns in time? *BioScience,* **60,** 433-439.

Sugai, L.S.M., Silva, T.S.F., Ribeiro, J.W., Jr, & Llusia, D. (2019a) Terrestrial passive acoustic monitoring: review and perspectives. *BioScience,* **69,** 15-25.

Sugai, L.S.M., Sugai, J.L.M.M., Ferreira, V.L., & Silva, T.S.F. (2019b) Satellite image texture for the assessment of tropical anuran communities. *Biotropica,* **51,** 581-590.

Sugai, L.S.M.; Silva, T.S.F.; Llusia, D.; Siqueira, T. (2020), Data from Drivers of assemblage-wide calling activity in tropical anurans and the role of temporal resolution, Dryad, Dataset, https://doi.org/10.5061/dryad.sf7m0cg4r .

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y., Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves, D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A., Wardle, D.A., & Wiegand, T. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology,* **101,** 58-67.

Ulloa, J.S., Aubin, T., Llusia, D., Courtois, É.A., Fouquet, A., Gaucher, P., Pavoine, S., & Sueur, J. (2019) Explosive breeding in tropical anurans: environmental triggers, community composition and acoustic structure. *BMC Ecology,* **19,** 28.

Van Allen, B.G., Rasmussen, N.L., Dibble, C.J., Clay, P.A., & Rudolf, V.H.W. (2017) Top predators determine how biodiversity is partitioned across time and space. *Ecology Letters,* **20,** 1004-1013.

Vellend, M. (2016) *The theory of ecological communities*. Princeton University Press, Princeton, NJ.

Viana, D.S., & Chase, J.M. (2019) Spatial scale modulates the inference of metacommunity assembly processes. *Ecology,* **100,** e02576.

Werner, E.E., Yurewicz, K.L., Skelly, D.K., & Relyea, R.A. (2007) Turnover in an amphibian metacommunity: the role of local and regional factors. *Oikos,* **116,** 1713-1725.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology,* **3,** 385-397.

Wiens, J. J., & Graham, C.H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Reviews of Ecology, Evolution, and Systematics*, **36**, 519-539.