

# 1 **Drivers of assemblage-wide calling activity in tropical anurans and the role** 2 **of temporal resolution**

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19 *Abstract*

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

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

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

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

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

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

49

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

## 52 **Introduction**

53 Time is a fundamental dimension of species ecological niches. Because organisms' responses  
54 and ecological patterns are scale-dependent, the distinct timescales experienced by natural  
55 communities are key to understand the effects of environmental changes on biodiversity  
56 (Dornelas *et al.* 2013; Sutherland *et al.* 2013). Nevertheless, ecological communities are often  
57 statically framed at specific spatial and temporal scales, which may potentially lead to  
58 mismatches between ecological pattern and process. In the spatial domain, communities are  
59 usually delimited by subjective criteria or habitat boundaries (Wiens 1989; Leibold & Chase  
60 2018), with spatial grain – i.e., the resolution of spatial observations – determined by the  
61 extension of sampling units. In the temporal domain, study duration is usually emphasized in  
62 detriment of the timeframe used to depict the set of interacting species – i.e., temporal  
63 resolution. However, empirical evidence indicates that species activity is largely variable and  
64 seldom constant over a diel period (McCann, Zollner & Gilbert 2017; Gaston 2019), such as  
65 distinct daily patterns of foraging (Kronfeld-Schor, Bloch & Schwartz 2013) and breeding  
66 (Schwartz & Bee 2013; Schalk & Saenz 2016). On one hand, predictable changes in species

67 activity at short timeframes may be regulated by endogenous rhythmicity mechanisms  
68 (Kronfeld-Schor & Dayan 2003; Greenfield 2015). Alternatively, exogenous factors such as  
69 climate and species interactions may determine short-term differences in species activity  
70 (Carothers & Jaksić 1984; Hodge, Arthur & Mitchell 1996). Therefore, addressing short-term  
71 variation in the activity of animal communities, similarly to spatial variation, might lead to a  
72 more complete understanding of the ecological processes acting during community assembly  
73 (Castro-Arellano *et al.* 2010; Segre *et al.* 2014; Van Allen *et al.* 2017).

74 Ecological differences among interacting species mainly occur across three  
75 fundamental dimensions: food, space, and time (MacArthur & Levins, 1964; Amarasekare  
76 2003; Kneitel & Chase 2004). Although niche overlap is rather common in ecological  
77 communities, differences between niche dimensions, including fine-temporal partitioning  
78 (Schoener 1974), have a fundamental role in promoting stable coexistence among species  
79 (Chesson 2000, Kneitel & Chase 2004). On the local scale and in the short-term, negative  
80 interactions can promote the exclusion of inferior competitors (Vellend 2016), or alternatively,  
81 species may reduce interference (e.g. for habitat-use and breeding sites) through temporal  
82 partitioning (Schoener 1974, Carothers & Jaksić 1984, Humfeld 2013). Additionally, local  
83 dynamics are also influenced by larger spatial contexts (Ricklefs 1987; Leibold & Chase 2018),  
84 and short-term dynamics (e.g. within-days) may undergo alternative trajectories at larger  
85 temporal scales (e.g. across days). For instance, favored dispersal by heterogeneous  
86 landscapes can promote an increase in the effective size of local communities (higher species  
87 richness and abundance) and reduce the stochastic component of community assembly (e.g.  
88 fluctuations in small populations; Ron, Fragman-Sapir & Kadmon 2018). However, increasing  
89 spatial heterogeneity can likewise increase the presence of sink habitats and thus reduce the  
90 competitive dominance of species (Hodge, Arthur & Mitchell 1996; Schreiber & Kelton 2005).

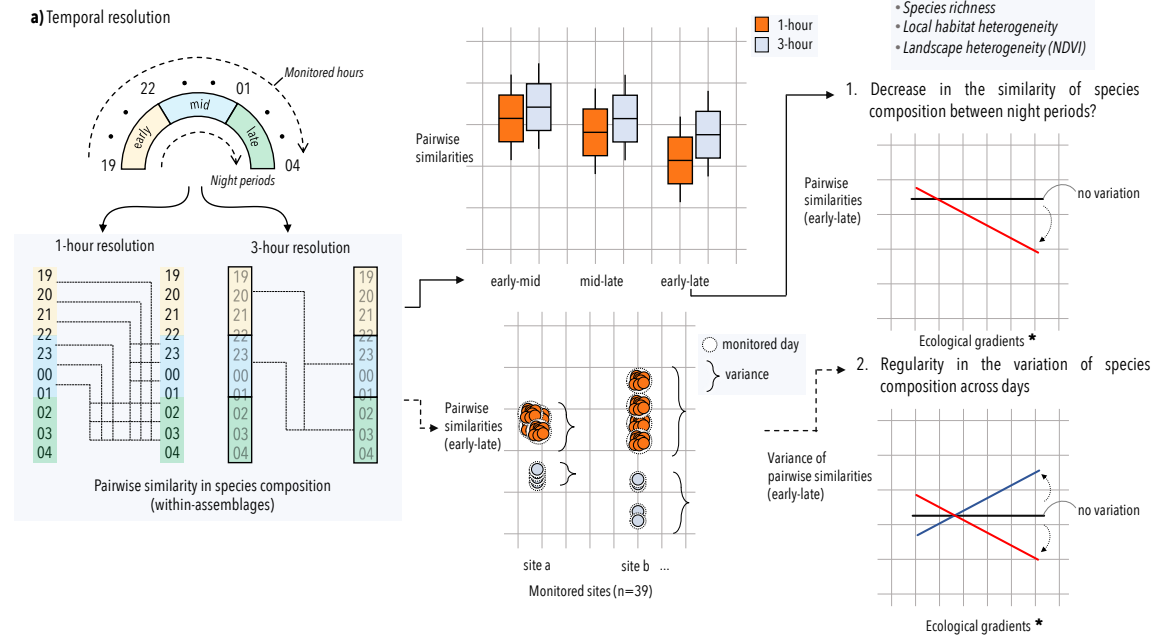
91 Therefore, understanding how communities differ in time (i.e., temporal beta-diversity;  
92 Legendre & Gauthier 2014, Baselga et al. 2015) and the drivers of community-wide activity  
93 can shed light on an interplay of short-term dynamics of ecological communities and the  
94 underlying processes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

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

108         This knowledge gap can be traced back to historically challenging conditions in  
109 addressing nocturnal phenomena (Gaston 2019), in addition to the human-observer limitation  
110 in investigating multiple sites simultaneously. Currently, modern techniques enabling passive  
111 acquisition of high-resolution data have been solving these practical issues and steadily  
112 improving our capacity to address diverse ecological phenomena (Rocchini *et al.* 2016;  
113 Gaston 2019). Amongst these developments, automated acoustic devices have facilitated the  
114 systematic collection of environmental sounds, providing new opportunities to investigate

115 multiple perspectives of animals that rely on acoustic communication (Sugai *et al.* 2019a).  
116 The “nocturnal problem” (Gaston 2019) can therefore be potentially revisited using the  
117 framework of acoustic monitoring.

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



138

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

## 149 **Methods**

### 150 ***Study area and environmental characterization***

151 We studied pond-breeding anuran assemblages in an area of approximately 100 km<sup>2</sup> located  
 152 in the southern region of the Pantanal wetlands in Brazil, Aquidauana municipality (Latitude

153 -19.534227, Longitude -56.144935; WGS-84; fig. 2a). Breeding activity takes place during  
154 the rainy season (October-April) when monthly mean temperatures range from 20.1 to 33.2  
155 °C and monthly rainfall from 96 to 231 mm (Fick & Hijmans 2017). As most tropical anurans  
156 have the highest activity levels during the peak of the rainy season (Duellman & Trueb 1994),  
157 our sampling was concentrated at the end of January 2017, which corresponded to the month  
158 of highest precipitation for that season (231 mm, Fick & Hijmans 2017). Landscapes of this  
159 southernmost region are influenced by the neighboring Cerrado (tropical savanna) and  
160 include grasslands, open wood savanna, and forested woodland (Evans & Costa 2013).  
161 Permanent bodies of standing water used by anurans are embedded among patches of these  
162 vegetation formations and have their low-lying adjacent areas composed of seasonally  
163 flooded grasslands that often inundate during the rainy season (Prado, Uetanabaro & Haddad  
164 2005). The aquatic vegetation of these freshwater water bodies comprises erectophile grass-  
165 like plants from Cyperaceae and Typhaceae families, and floating emergent plants from  
166 Pontederiaceae, Araceae, Salviniaceae, and Nymphaeaceae families (Pott & Pott 2000, Evans &  
167 Costa 2013, Delatorre et al. 2019).

168         We selected sampling sites using a geographic information system to stratify localities  
169 according to landscape heterogeneity. First, we manually mapped all ponds in the study area  
170 and selected one point per pond, located on the shore and distant at least 1 km apart of each  
171 other (n = 72). We then calculated the Normalized Difference Vegetation Index – NDVI  
172 (Rouse *et al.* 1974) using RapidEye3A satellite images (5-meter pixel size, RapidEye AG 2011)  
173 and extracted average NDVI values for 200-meter radius buffers (125,6 m<sup>2</sup>) centered on each  
174 point. Finally, we ordinated all 72 sites based on NDVI values and selected 39 sites  
175 representing the entire range of average NDVI, *i.e.* better captured the gradient of vegetation  
176 heterogeneity; from fully forested to fully open grasslands. Landscape heterogeneity was



177 represented by NDVI values since forested areas prevent anurans from overheating and  
178 dehydration during daylight and decrease resistance for movement among habitat patches  
179 (Bowler & Benton 2005; Buskirk 2012; Silva *et al.* 2012).

180         These 39 sites were located on freshwater ponds with mean size of  $9.07 \pm 8.65$  SD  
181 hectares. To characterize the breeding sites, we registered the components of the terrestrial  
182 and aquatic terrains. From a central point established by the closest distance between the  
183 recorder and the water margins (5 to 10 meters), we distributed one transect perpendicular to  
184 the margin of the pond every 3 meters, with 10 transect for each side of the central point,  
185 totalizing 20 transects. Each transect was 6-meter in length, with 3 meters towards the outside  
186 (terrestrial) and 3 meters towards the inside of the pond (aquatic), covering approximately  
187  $90\text{m}^2$  of each terrestrial and aquatic habitat. In each transect, we positioned a straight  
188 reference line and measured, for the terrestrial side, the length (cm) occupied by bare ground  
189 and shrub vegetation along the line. Additionally, at each 1-meter interval, we measured the  
190 Leaf Area Index (LAI - the ratio of foliage area to ground area; Bréda 2003) as a proxy of  
191 canopy openness. As the vegetation type surrounding the freshwater ponds are predominantly  
192 grasslands and open wood savanna, LAI was used here to represent the density (openness) of  
193 the short-stratum grassy/herbaceous terrain. We measured LAI with a LAI-2200C Plant  
194 Canopy Analyzer model (LI-COR Biosciences 1992) using a  $45^\circ$  forward view cap. For the  
195 aquatic side, we measured the length (cm) occupied by free water surface (i.e. no vegetation  
196 above the water surface), aquatic vegetation above the water surface (i.e. floating and  
197 emergent aquatic plants), and the flooded vegetation from seasonal grasslands contouring the  
198 ponds, being represented by two vertical strata of grassy vegetation ( $< 20$  cm and  $> 20$  cm,  
199 with the later also comprising emergent aquatic vegetation; Delatorre *et al.* 2015), and flooded  
200 shrub vegetation. Additionally, at each 1-meter interval, we measured pond depth. The length

201 occupied by each variable was summed, except for LAI and pond depth, which were  
202 averaged (mean depth  $1 \pm 0.46$  meters). All variables for the terrestrial and aquatic habitats  
203 were standardized to zero mean and unit variance.

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

### 216 ***Anuran assemblages***

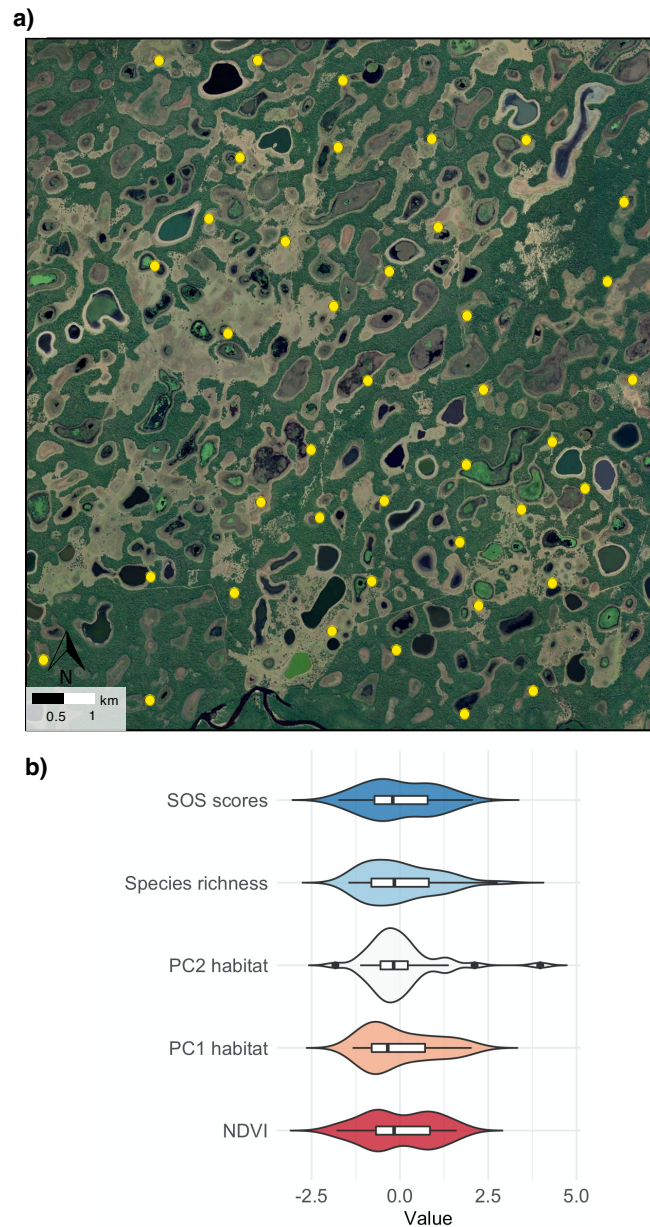
217 We used passive acoustic monitoring to record anuran calling activity for 3 to 5 consecutive  
218 days on each site using 22 automated audio recorders (four SM4, fifteen SM3, and two SM2  
219 models from Wildlife Acoustics) that were rotated among sites during a total period of 10 days  
220 (2017 January, 18th to 27th). We attached recorders on trees or wooden stakes distant no  
221 more than 10 meters from the monitored pond, at approximately 1.5 meters height, to improve  
222 sound recordings. Our recording schedule consisted of 2 minutes of stereo recording every  
223 20 minutes from 19:00 h to 4:00 h (UTC-4), to exclude the hours with bird and invertebrate  
224 overlapping sounds around sunset and sunrise. Sounds were recorded at a rate of 44.1 kHz

225 and 16-bit audio depth (uncompressed WAV format), with a gain of 6 dB and 12 dB on each  
226 channel. Anuran advertisement calls were detected and identified by the main author using  
227 visual inspection of spectrograms (window size of 512, Hamming window) and aural  
228 recognition in Audacity software (Audacity Team 2018). Call parameters were quantified with  
229 Raven Pro 1.4 (Bioacoustics Research Program 2014) and compared with reference calls for  
230 dubious vocalizations.

231 After identifying all species calling from 1900-0400 hours, we determined the  
232 composition of species in each signaling assemblage considering 1-hour and 3-hour time  
233 periods. Night activity was divided into three periods, namely *early* (1900 to 2200), *mid* (2200  
234 to 0100), and *late* (0100 to 0400) periods. For each site, we calculated the similarity in species  
235 composition between night periods using both 1-hour and 3-hour intervals, on each day (fig.  
236 1a). For the 1-hour resolution, we calculated hour-to-hour compositional similarity and coded  
237 the respective pair of night periods (within and between early, mid, and late). For the 3-hour  
238 resolution, pairwise compositional similarity corresponded to the combinations between  
239 early, mid, and late periods of the night. Because we were interested in the nightly variation  
240 determined by the between-period differences (early-mid, mid-late, early-late), we excluded  
241 within-period similarities. We calculated the Jaccard coefficient ( $s$ ) to represent similarity, an  
242 index broadly used to represent spatial beta diversity (Jost, Chao & Chazdon 2010; Baselga et  
243 al. 2015) using R package *vegan* (Oksanen et al. 2018). Because the function “vegdist” in  
244 *vegan* calculates Jaccard (and other coefficients) as dissimilarity, to facilitate interpretation, we  
245 converted it to express similarity values ( $1-s_{ij}$ ), where 1 indicates maximum similarity in the  
246 composition of vocal active species.

247 Species sharing recent ancestry tend to show similar ecological requirements given  
248 niche conservatism (Wiens & Graham 2005). To represent the degree of similarity among

249 coexisting species, we calculated the specific overrepresentation score (SOS), a measure that  
250 represents how specific lineages contribute to the distribution of species across communities  
251 (Borregaard *et al.* 2014). First, using a comprehensive time-calibrated phylogenetic tree of  
252 amphibians (Pyron & Wiens 2011) pruned to the species found in the study area, we  
253 calculated if specific sister lineages pairs contributed more to the phylogenetic structure and  
254 species co-occurrence than expected by a null model (geographic node divergence – GND;  
255 Borregaard *et al.* 2014). The node between Hylidae (except for Phyllomedusidae) and  
256 Leptodactylidae showed the highest GND score (0.5, fig. S2), and we thus calculated SOS  
257 values considering this specific node. SOS are the standardized effect sizes from the observed  
258 species richness of each sister lineage referenced to a null model that breaks the phylogenetic  
259 dominance of this lineage pair (using the *quasiswamp* algorithm; Borregaard *et al.* 2014). We  
260 used all species registered at each site to calculate SOS, with positive and negative values  
261 representing assemblages with higher overrepresentation of Hylidae and Leptodactylidae  
262 species, respectively. Therefore, more extreme values represented assemblages with higher  
263 ecological similarities.



264

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

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

### 273 **Analyses**

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

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

303 To test if variation in nightly compositional changes across days was influenced by the  
304 distinct ecological drivers, we first calculated the variance of all compositional similarities  
305 from the early-late period for all days per site. Then, we built different general linear models  
306 representing a) global model with all predictors, b) local heterogeneity only (PC1 and PC2), c)  
307 landscape heterogeneity (NDVI), d) ecological context of assemblages (species richness and  
308 SOS), and e) a null model with the intercept only. Multicollinearity was low for the full models  
309 (1-hour model VIF = 1.35, 3-hour model VIF = 1.41). We ranked these models using AICc  
310 and further determined if adding a quadratic term lead to differences in the models (using  
311 dAICc). We used a log transformation to ensure homoscedasticity of the residuals and  
312 evaluated Q-Q residual plots to check normality assumptions.

313 Additionally, to understand the combined importance of habitat structure and  
314 ecological context across local assemblages (i.e., metacommunity), we used the incidence of  
315 all anuran species recorded at each site and applied a redundancy analysis (RDA) to determine  
316 the amount of variation explained by phylogenetic relatedness (SOS values), local vegetation  
317 heterogeneity (first two PC axes on aquatic and terrestrial habitat variables), landscape

318 heterogeneity (NDVI), and species richness. We used an ANOVA-like permutation test  
319 ( $\times 1000$ ) to assess model significance with the *vegan* package (Oksanen *et al.* 2018) in R  
320 software version 4.0.2 (R Core Team 2020).

## 321 **Results**

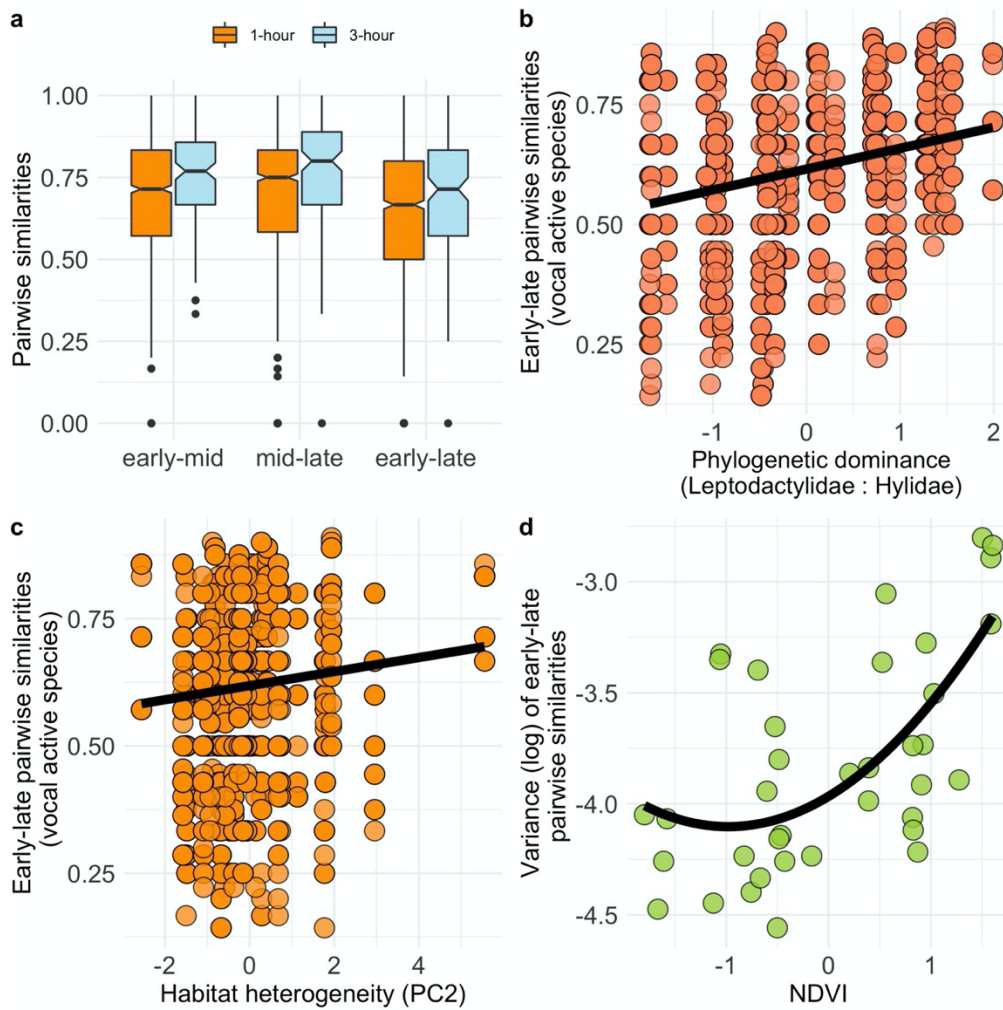
322 We recorded 24 anuran species distributed in 4 families, with Hylidae ( $n = 12$ ) and  
323 Leptodactylidae ( $n = 9$ ) being the most representative families (tab. S2). Species richness varied  
324 from 6 to 19 species per site ( $\bar{x} = 10.5 \pm 3$  SD), while hourly species richness ranged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

335 The compositional similarity of vocal active species between early-late nocturnal  
336 periods was positively related to phylogenetic relatedness (SOS scores) and the PC2  
337 representing local habitat heterogeneity ( $R^2m = 0.11$ ,  $R^2c = 0.6$ ; tab. 2). Specifically, high  
338 compositional similarities were associated with an increase in the overrepresentation of  
339 species from the family Hylidae (SOS scores,  $\beta$  1-hour =  $0.05$  and 95% CI  $[0.02, 0.07]$ ; fig.  
340 3b; tab. 1), and an increase in vegetation heterogeneity on the terrestrial terrain of breeding  
341 habitats (PC2- local habitat;  $\beta$  1-hour =  $0.03$  and 95% CI  $[0.01, 0.05]$ ; fig. 3c; tab. 1). However,



342 these relationships were observed only for compositional similarities calculated at the 1-hour  
343 resolution (tab. 1). The nMDS ordination of sites and night periods of activity shows varying  
344 degrees of variability in the composition of vocal active species between early and late periods  
345 (fig. 4a).

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



353

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

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

365 **Table 1.** Model selection (against a null model) and coefficient of determination of general  
 366 linear mixed models fitted on (1) compositional similarities (1- Jaccard dissimilarity  
 367 coefficient, 1-hour and 3-hour temporal resolutions) of vocal active anuran assemblages  
 368 with combinations of night periods as fixed effect (early: 1900, 2000, 2100; mid: 2200,  
 369 2300, 0000; late: 0100, 0200, 0300, UTC-4), and on (2) compositional similarity  
 370 between early-late period with phylogenetic relatedness of assemblages (SOS scores),  
 371 species richness, PC1 and PC2 representing local habitat structure, and landscape  
 372 heterogeneity (NDVI) as fixed effects. Monitored day and site were included as random  
 373 effects. R<sup>2</sup>m: marginal r-squared; R<sup>2</sup>c: conditional r-squared. Best models are highlighted in  
 374 bold.

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

375

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

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

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

384

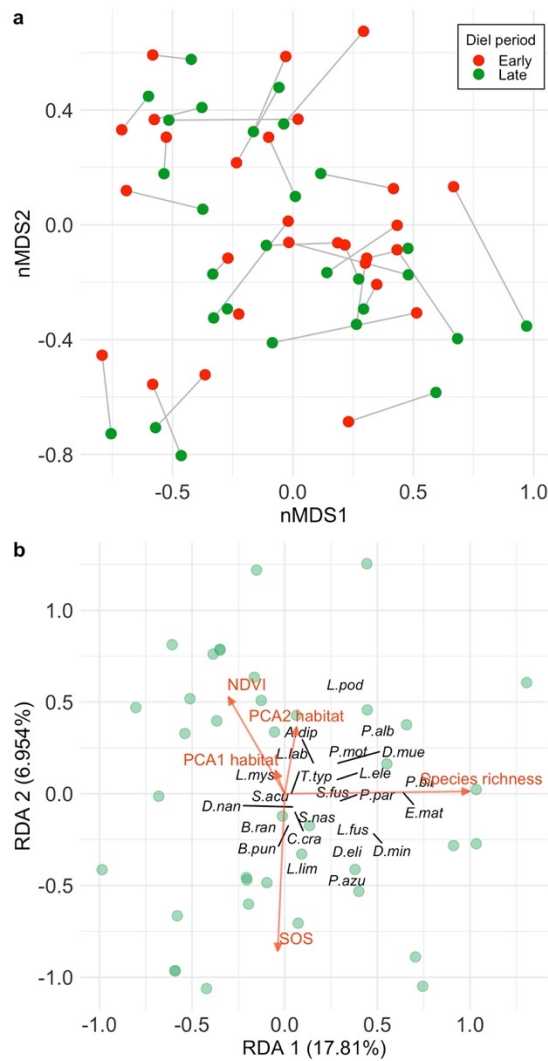
385 **Table 3.** Ranking of models fitted on the variance (log) of compositional similarities for 1-hour  
 386 and 3-hour temporal resolutions, considering early-late night periods for all days. Models were  
 387 ranked using AICc and comprised i) landscape heterogeneity (NDVI), ii) ecological context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

	dAICc	df	weight
<i>1-hour</i> ~ <b>NDVI</b>	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
	<b>Null model</b>	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

391

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



398

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

408 **Discussion**

409 The scale dependence of ecological phenomena requires ascertaining the spatial and  
410 temporal framings of ecological communities (Soininen 2010; Van Allen *et al.* 2017; Viana &  
411 Chase 2019). Although ecologists have largely neglected fine resolution timescales (Estes *et*  
412 *al.* 2018), our closer look at the temporal axis of tropical anuran assemblages unveiled that  
413 variation in species activity is influenced by the environmental structure (both local and  
414 landscape heterogeneity) and the phylogenetic relatedness of assemblages. However, these  
415 relationships were found for the 1-hour temporal resolution of species activity but not for the  
416 3-hour resolution, indicating that even small changes in temporal resolution may lead to  
417 scaling issues. We discuss our findings in the light of potential trade-offs between ecological  
418 overlap among coexisting species and temporal and spatial partitioning across the  
419 gradients of local and landscape heterogeneity.

420         Similarity in the composition of vocal active species between night periods was higher  
421 at localities with more heterogeneous habitats and in assemblages overrepresented by species  
422 of the family Hylidae, which typically use the vertical stratum of vegetation as micro-habitat.  
423 Accordingly, high complexity in the vertical stratum of vegetation reduces spatial overlap for  
424 semi-terrestrial and arboreal species (Hödl 1977; Silva, Gibbs & Rossa-Feres 2011), improving  
425 chances for species to acoustically communicate and find mates with the benefit of reduced  
426 negative interactions (Kronfeld-Schor & Dayan 2003; Gaston 2019). Also, a decay in  
427 compositional similarity between night periods was observed in localities with low  
428 vegetational heterogeneity and overrepresented by species of the family Leptodactylidae,  
429 composed predominantly of terrestrial species lacking adaptations to perch in vertical  
430 structures. These two contexts may increase chances for direct species interactions when  
431 searching for calling and breeding sites (Hödl 1977, Borzée *et al.* 2016), and one possibility  
432 is that deterministic exclusion of competing species through the night could drive the decay

433 in compositional similarity, with the persistence of few dominant species. However, we were  
434 unable to detect a clear pattern of lower species richness over diel periods, as would be  
435 presumably expected in such circumstances (fig. S4). Conversely, temporal patterns of anuran  
436 activity may be regulated by distinct strategies in response to resource availability and  
437 competition (McCauley et al. 2000, Humfeld 2013). In this sense, a decay in nightly  
438 compositional similarity could reflect temporal partitioning among species with similar  
439 ecological requirements in localities with limited potential for microhabitat partitioning.  
440 Further, we also acknowledge that a wider variation in microclimatic factors in these less  
441 heterogeneous sites could also account for the observed decay in nightly activity (Saenz et al.  
442 2006; Llusia et al. 2013), although we were unable to address these factors. Altogether, the  
443 variation in night activity of anuran assemblages indicates potential trade-offs between  
444 microhabitat and temporal partitioning, being consistent with a role of niche complementary  
445 on the structuring of ecological communities (Schoener 1974; Mason *et al.* 2008).

446 Anuran assemblages located at sites with increasing landscape heterogeneity (NDVI),  
447 ranging from open grasslands to areas with increased forest cover, showed higher variability  
448 in nightly compositional similarities across the monitored days. For amphibians, landscape  
449 structure has a large influence on organisms' movement into breeding sites and on their  
450 maintenance during the interlude of calling activity and interbreeding season (Becker *et al.*  
451 2010). For instance, higher solar radiation in open grassland compared to closed canopy sites  
452 can hinder the persistence and movement of species unable to cope with intense evaporative  
453 water loss (Rothermel 2004). Landscape heterogeneity indeed contributed to explaining the  
454 spatial variation in species composition observed at the metacommunity scale of the anuran  
455 assemblages we investigated. In this context, low-heterogeneous landscapes may emphasize  
456 the role of environmental filtering in sorting out species with low environmental tolerance and



457 dispersal capability, and the dynamics resulting from the same set of species sorted into these  
458 environments may relate to the low variability in nightly compositional similarities observed  
459 across days. Conversely, an increase in landscape heterogeneity and forest cover reduces  
460 overheating and desiccation during daylight, which favors spatial dynamics by decreasing  
461 movement resistance among habitat patches and within species home range (Bowler &  
462 Benton 2005; Buskirk 2012; Silva *et al.* 2012). Since chorusing formations start with a few  
463 early individuals establishing spatial dominance, the order of species arrival may constraint  
464 opportunities for late arrivals, and communities may undergo distinct dynamics over a  
465 nocturnal activity (Fukami 2015). In this sense, spatial dynamics and priority effects may  
466 increase stochasticity on the assembly of communities and counteract competitive  
467 interactions at fine scales (Amarasekare 2003). Previous findings of large compositional  
468 variation of amphibians have underscored a role of stochasticity on the assembly of  
469 communities (Richter-Boix, Llorente & Montori 2007; Werner *et al.* 2007), and our findings  
470 suggest that increasing landscape heterogeneity may indirectly increase the effects of spatial-  
471 related stochastic processes on signaling anuran assemblages.

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

481 Gottsberger & Gruber 2004; Heinermann et al. 2015; Lopes et al. 2011; Schalk & Saenz  
482 2016), community-wide approaches remained elusive (Ulloa *et al.* 2019, Dubos et al. 2020,  
483 Guerra *et al.* 2020). Considering our findings on the influence of habitat heterogeneity and  
484 species interactions on nightly compositional variation of anuran assemblages, we argue that  
485 future studies should take into consideration the contribution of ecological contexts in species  
486 calling activity, in addition to abiotic factors such as temperature and rainfall. Potential effects  
487 of heterospecifics in calling behavior have mainly been investigated in light of acoustic  
488 communication, with species eventually altering signaling parameters or behavior when  
489 exposed to heterospecific calls (Phelps, Rand & Ryan 2006; Both & Grant 2012), while the  
490 influence of species interactions on calling activity still remains to be elucidated. Therefore,  
491 addressing a range of conditions on which potential interactions may occur, *i.e.* distinct  
492 habitats and combinations of competing species, may increase our understanding of the  
493 acoustic communication in multi-species systems.

494 Our findings highlight the importance of temporal scaling effects in inferring  
495 community assembly processes. In the spatial domain, larger sampling units enable more  
496 individuals and species to be recorded, while environmental variation is often described with  
497 coarser resolution and thus less detailed (Wiens 1989). For this reason, a mismatch between  
498 the resolution used to describe both response and predictor variables often leads to lower  
499 explanation power of species occupancy (Barton *et al.* 2013, Sugai *et al.* 2019b) and therefore,  
500 a perceived weaker importance of the environment in explaining community structure (Viana  
501 & Chase 2019). Similarly, mismatches can also emerge with the temporal resolution used to  
502 describe ecological communities. Considering that competitive interactions and predation  
503 pressure are important determinants of diel species activity (Kronfeld-Schor, Bloch & Schwartz  
504 2013, McCann et al. 2017), disregarding diel differences in animal activity within

505 communities leads to a poorer representation of co-occurring species. Consequently, the  
506 temporal resolution used may result in an ecological pattern unrelated to the actual  
507 mechanisms driving community assembly (Gaston 2019).

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

#### 518 **Authors' contribution**

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

#### 523 **Data availability statement**

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

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