

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

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## 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- and 3-hr 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 (a) between night periods and (b) across days.
4. Nocturnal calling activity of anuran assemblages varied more within the 1-hr resolution than the 3-hr 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 hr).
5. Our findings on the variation of calling activity in tropical anuran assemblages suggest potential trade-offs mediated by fine-temporal partitioning. Local and landscape heterogeneity may provide conditions for spatial partitioning, while the relatedness among co-signalling 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 thus, addressing temporal scaling issues can improve our understanding of the dynamics of animal communities.

**KEYWORDS**

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

**1 | INTRODUCTION**

Time is a fundamental dimension of species ecological niches. Because organisms' responses and ecological patterns are scale-dependent, the distinct time-scales 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 (Leibold & Chase, 2018; Wiens, 1989), with spatial grain—that is, 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—that is, temporal resolution. However, empirical evidence indicates that species activity is largely variable and seldom constant over a diel period (Gaston, 2019; McCann et al., 2017) such as distinct daily patterns of foraging (Kronfeld-Schor et al., 2013) and breeding (Schalk & Saenz, 2016; Schwartz & Bee, 2013). On the one hand, predictable changes in species activity at short timeframes may be regulated by endogenous rhythmicity mechanisms (Greenfield, 2015; Kronfeld-Schor & Dayan, 2003). Alternatively, exogenous factors such as climate and species interactions may determine short-term differences in species activity (Carothers & Jaksic, 1984; Hodge et al., 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).

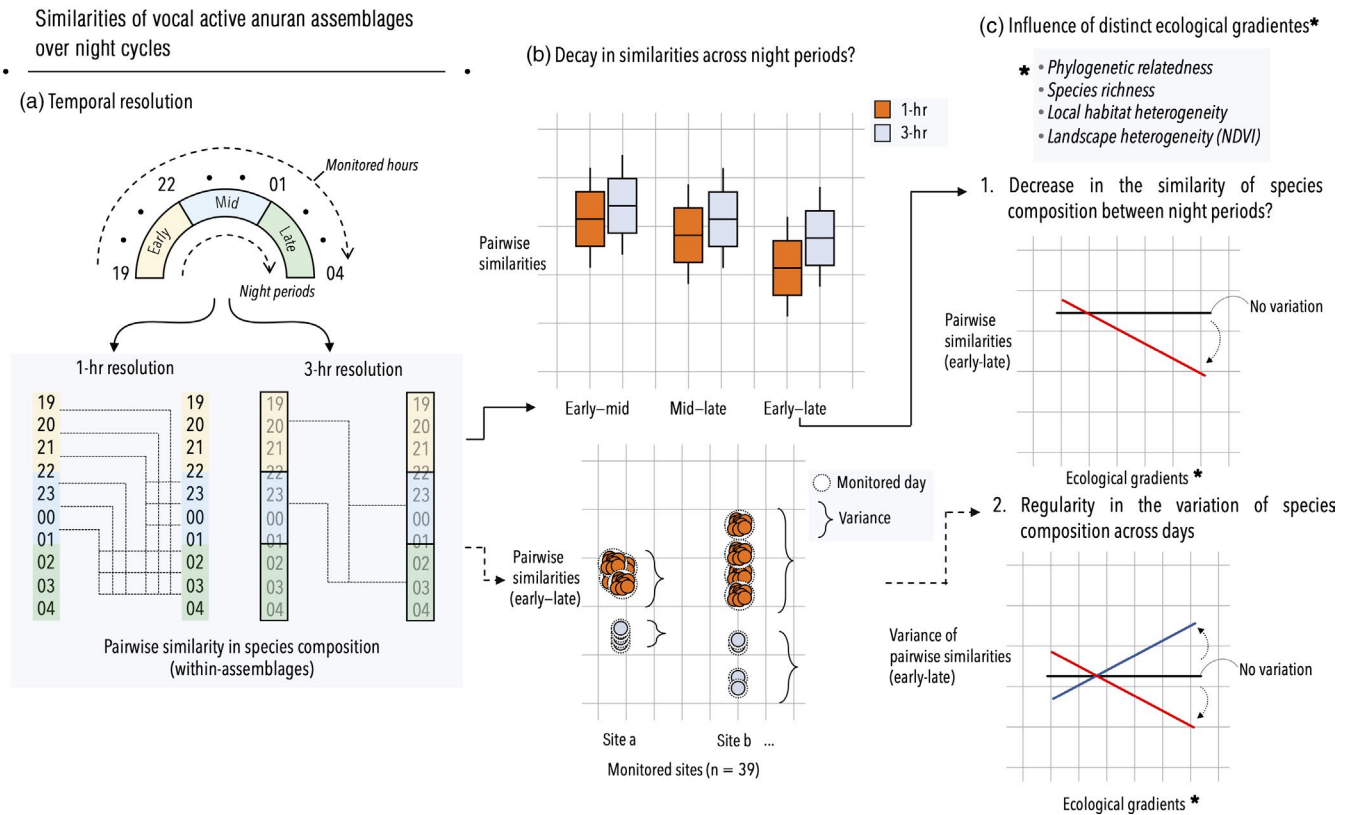
Ecological differences among interacting species mainly occur across three fundamental dimensions: food, space and time (Amarasekare, 2003; Kneitel & Chase, 2004; MacArthur & Levins, 1964). Although niche overlap is rather common in ecological communities, differences between niche dimensions, including 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 (Carothers & Jaksic, 1984; Humfeld, 2013; Schoener, 1974). Additionally, local dynamics are also influenced by larger spatial contexts (Leibold & Chase, 2018; Ricklefs, 1987), such that short-term dynamics (e.g. within days) may undergo alternative trajectories at increasing temporal scales (e.g. across days). For instance, favoured dispersal

in heterogeneous landscapes can increase the effective size of local communities (higher species richness and abundance), which reduces the stochastic component of community assembly (e.g. fluctuations in small populations; Ron et al., 2018). However, spatial heterogeneity can likewise increase the presence of sink habitats and thus reduce competitive dominance between species (Hodge et al., 1996; Schreiber & Kelton, 2005). Therefore, understanding how communities vary in time (i.e. temporal beta-diversity; Baselga et al., 2015; Legendre & Gauthier, 2014) and the drivers of community-wide activity can shed light on the contribution of short-term dynamics of ecological communities to 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., 2019). 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 (Signorelli et al., 2016; Werner et al., 2007). Nonetheless, short-term variation in species activity has been mainly addressed with respect to meteorological and social factors (Dubos et al., 2020; Guerra et al., 2020; Llusia et al., 2013; Oseen & Wassersug, 2002; Saenz et al., 2006; Schalk & Saenz, 2016) 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 (Gaston, 2019; Rocchini et al., 2016). Among 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., 2019). 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,



**FIGURE 1** Conceptual scheme depicting (a) temporal resolution: incidence of vocal active species registered for 2 min each 20 min over the early, mid and late periods of the night (19:00–04:00 hr, UTC-4) and summarized with two temporal resolutions: 1- and 3-hr intervals. Similarity in species composition was computed for pairwise combinations of temporal units within a night cycle. (b) We investigated whether 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

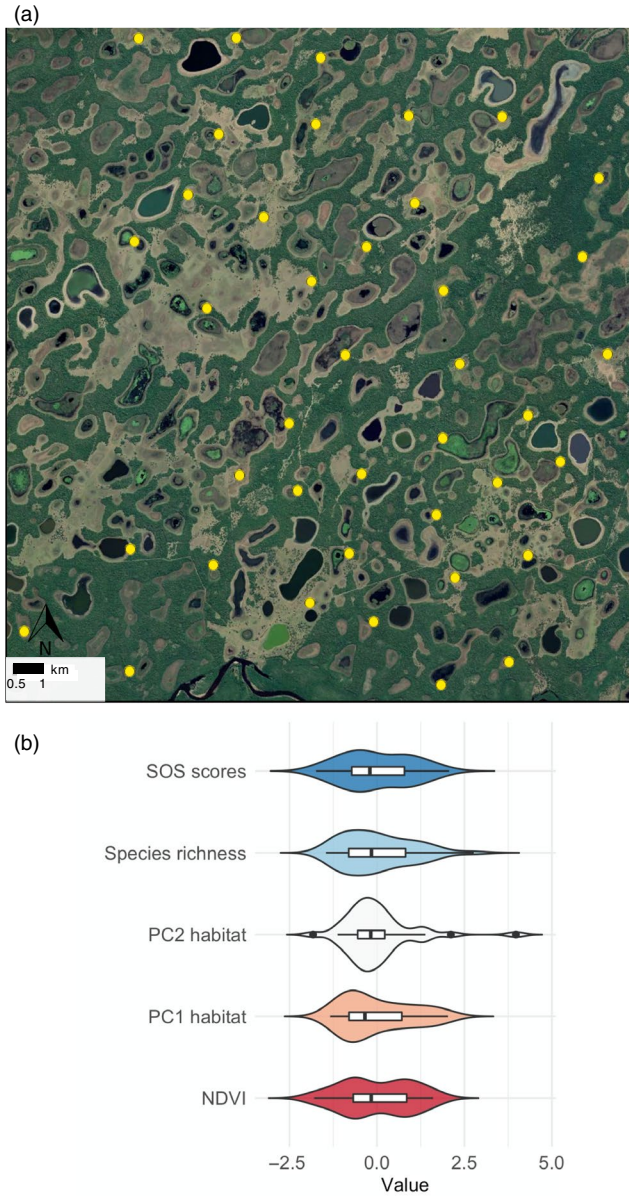
we first assessed whether species composition varied through different night periods (early, mid and late) using two temporal resolutions (1- and 3-hr intervals, Figure 1a,b). We then assessed if changes in species composition between night periods was associated with gradients representing habitat structure (local and landscape habitat heterogeneity) and the ecological context (species richness and phylogenetic relatedness, here used as a proxy of ecological similarities, Figure 1c.1). We also assessed whether the regularity of nightly variation in species composition across monitored days (i.e. variance of temporal beta diversity; Figure 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- and 3-hr intervals) to determine whether the above expectations hold across temporal resolutions. Furthermore, 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.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and environmental characterization

We studied pond-breeding anuran assemblages in an area of approximately 100 km<sup>2</sup> located in the southern region of the Pantanal wetlands in Brazil, Aquidauana municipality (Latitude -19.534227, Longitude -56.144935; WGS-84; Figure 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 neighbouring 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



**FIGURE 2** (a) Study region and 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 (NDVI). 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)

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 et al., 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

Nymphaeaceae families (Delatorre et al., 2020; Evans & Costa, 2013; Pott & Pott, 2000).

We used a geographical information to stratify sampling sites over a gradient of landscape heterogeneity. First, we manually mapped all ponds in the study area and randomly selected one location 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-m pixel size, RapidEye AG, 2011) and extracted average NDVI values for 200-m radius buffers ( $125.6 \text{ m}^2$ ) centred on each location. Finally, we ordinated all 72 sites based on NDVI values and selected 39 sites representing the entire range of average NDVI, that is, better captured the gradient of vegetation heterogeneity; from fully forested to fully open grasslands. Because 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), we used NDVI to represent Landscape heterogeneity.

These 39 sites were located on freshwater ponds with mean size of  $9.07 \pm 8.65 \text{ SD}$  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 audio recorder and the water margins (5–10 m), we distributed one transect perpendicular to the margin of the pond every 3 m, with 10 transect for each side of the central point, totaling 20 transects. Each transect was 6 m in length, with 3 m towards the outside (terrestrial) and 3 m towards the inside of the pond (aquatic), covering approximately  $90 \text{ m}^2$  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-m 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  $45^\circ$  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-m interval, we measured pond depth. The length occupied by each variable was summed, except for LAI and pond depth, which were averaged (mean depth  $1 \pm 0.46 \text{ m}$ ). 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 (Lê et al., 2008)



). We used the first two PC axes (28% and 21.2% of variation, Figure 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 > 20 cm). 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; Table S1; Figure S1).

## 2.2 | Anuran assemblages

We used passive acoustic monitoring to record anuran calling activity for 3–5 consecutive days on each site using 21 automated audio recorders (4 SM4, 15 SM3 and 2 SM2 models from Wildlife Acoustics) that were rotated among sites during a total period of 10 days (18th–27th January 2017). We attached recorders on trees or wooden stakes distant no more than 10 m from the monitored pond, at approximately 1.5 m height, to improve sound recordings. Our recording schedule consisted of 2 min of stereo recording every 20 min from 19:00 to 4:00 hr (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 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 19:00 to 04:00 hr, we determined the composition of species in each signalling assemblage considering 1- and 3-hr time periods. Night activity was divided into three periods, namely *early* (19:00–22:00), *mid* (22:00–01:00) and *late* (01:00–04:00) periods. For each site, we calculated the similarity in species composition between night periods using both 1- and 3-hr intervals, on each day (Figure 1a). For the 1-hr 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-hr 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 between-period differences (early-mid, mid-late and 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 (Baselga et al., 2015; Jost et al., 2010) 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 ( $1 - s_{ij}$ ), 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 ecological 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 whether specific sister lineage pairs contributed more to the phylogenetic structure and species co-occurrence than expected by a null model (geographical node divergence—GND; Borregaard et al., 2014). The node between Hylidae (except for Phyllomedusidae) and Leptodactylidae showed the highest GND score (0.5; Figure 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.

## 2.3 | Analyses

To test whether species composition differed across night periods, we fitted a general linear mixed model (GLMM) on compositional similarity for each time resolution (1- and 3-hr 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 & 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 ( $\Delta AICc$ ) < 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 et al. (2017), where the marginal coefficient ( $R_m^2$ ) refers to the variation explained by fixed effects, and the conditional coefficient ( $R_c^2$ ) 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 whether changes in species composition in a night cycle were influenced by environmental gradients representing habitat structure (local and landscape habitat heterogeneity and the ecological context (species richness and SOS scores considering all species registered at each site), 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  $R^2$ .

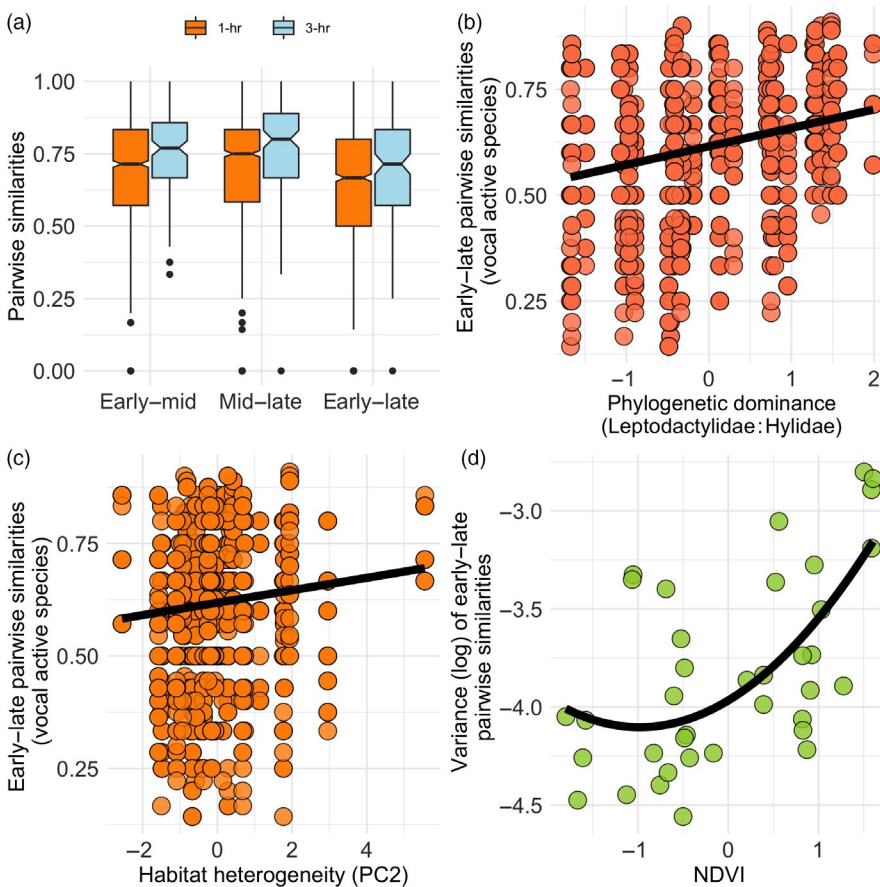
To test whether variation in nightly compositional changes across days was influenced by the distinct ecological drivers, we first calculated the variance of all compositional similarities from the early-late period for all days per site. Then, we built different general linear models representing (a) 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-hr model VIF = 1.35, 3-hr model VIF = 1.41). We ranked these models using AICc and further determined whether 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. meta-community), 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 ( $\times 1,000$ ) to assess model significance with the *VEGAN* package (Oksanen et al., 2018) in R software version 4.0.2 (R Core Team, 2020).

### 3 | RESULTS

We recorded 24 anuran species distributed in four families, with Hylidae ( $n = 12$ ) and Leptodactylidae ( $n = 9$ ) being the most representative families (Table 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, Figure S3). Overall, mean similarity in species composition was higher between early-mid and mid-late periods, both at the 1-hr (early-mid:  $0.69 \pm 0.19$  SD, mid-late:  $0.71 \pm 0.2$  SD and early-late:  $0.64 \pm 0.2$  SD) and 3-hr resolutions (early-mid:  $0.77 \pm 0.16$  SD, mid-late:  $0.78 \pm 0.16$  SD and early-late:  $0.71 \pm 0.18$  SD, Figure 3a).



**FIGURE 3** (a) Similarity in species composition between night periods using two temporal resolutions (1- and 3-hr intervals). General linear mixed models fit on the compositional similarity between early-late periods for all days at the 1-hr 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- and 3-hr temporal resolutions) of vocal active anuran assemblages with combinations of night periods as fixed effect (early: 19:00, 20:00, 21:00; mid: 22:00, 23:00, 00:00; late: 01:00, 02:00, 03:00, 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.  $R_m^2$ , marginal *r*-squared;  $R_c^2$ , conditional *r*-squared. Best models are highlighted in bold

	deltaAICc	AICc	df	weight	$R_m^2$	$R_c^2$
(1) Compositional similarity ~ night periods						
1-hr null	117.2	-2,583.5	4	<0.001		
<b>1-hr</b>	<b>0</b>	<b>-2,700.7</b>	<b>6</b>	<b>1</b>	<b>0.02</b>	<b>0.42</b>
3-hr null	20	-355.4	4	<0.001		
<b>3-hr</b>	<b>0</b>	<b>-375.4</b>	<b>6</b>	<b>1</b>	<b>0.04</b>	<b>0.53</b>
(2) Early-late compositional similarity ~ drivers						
1-hr null	2.6	-1,269.8	4	0.22	0.11	0.48
<b>1-hr</b>	<b>0</b>	<b>-1,272.4</b>	<b>9</b>	<b>0.78</b>		
<b>3-hr null</b>	<b>0</b>	<b>-673.7</b>	<b>3</b>	<b>0.901</b>	<b>0.08</b>	<b>0.53</b>
3-hr	4.4	-669.2	8	0.09		

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;  $R_c^2 < 0.04$ ), with the highest variation attributed to random factors both for the 1- and 3-hr resolutions ( $R_c^2 > 0.42$ ; Table 1). A decay in compositional similarity was observed only for the combination of early-late periods for both temporal resolutions ( $\beta$  1-hr = -0.05 and 95% CI [-0.06, -0.04];  $\beta$  3-hr = -0.06 and 95% CI [-0.09, -0.03], Table 2).

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 ( $R_m^2 = 0.11$ ,  $R_c^2 = 0.6$ ; Table 1). Specifically, high compositional similarities were associated with an increase in the over-representation of species from the family Hylidae (SOS scores,  $\beta$  1-hr = 0.05 and 95% CI [0.01, 0.09]; Figure 3b; Table 2), and an increase in vegetation heterogeneity on the terrestrial terrain of breeding habitats (PC2- local habitat;  $\beta$  1-hr = 0.03 and 95% CI [0.01, 0.06]; Figure 3c; Table 2). However, these relationships were observed only for compositional similarities calculated at the 1-hr resolution (Table 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 (Figure 4a).

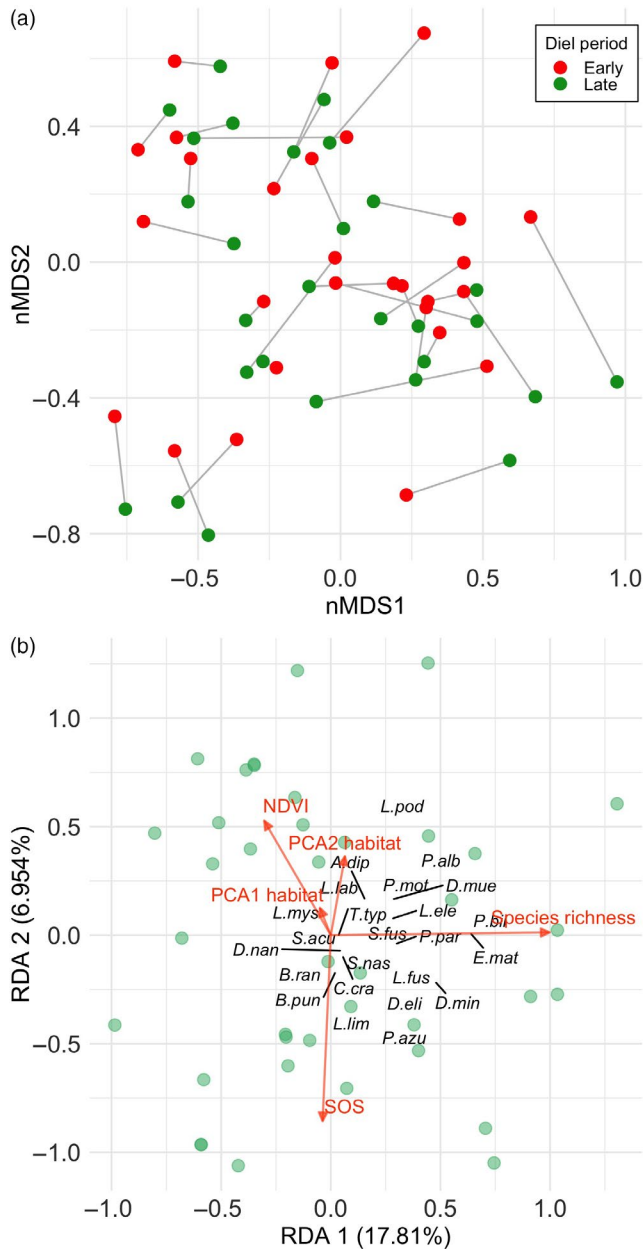
The models including landscape heterogeneity (NDVI) with and without the quadratic term were considered equally plausible models explaining the variability of nightly similarities across days, for the 1-hr resolution (Table 3). The model with a quadratic term ( $R^2 = 0.25$ ,  $p = 0.005$ ; Figure 3d) 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-hr resolution indicates that the fit with NDVI is not different from an effect from a null model (Table 3).

Spatial variation in assemblage composition was partially explained by the predictors representing distinct ecological gradients

**TABLE 2** Model coefficients from general linear mixed models fitted on (a) compositional similarities (1- and 3-hr temporal resolutions) of vocal active anuran assemblages with combinations of night periods as fixed effect, and on (b) 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-hr				
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>
3-hr				
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				
1-hr				
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

( $R^2 = 0.34$ ,  $p = 0.001$ ; Figure 4a, Table S3). Specifically, three orthogonal axes of explanatory variables could be distinguished, with species richness showing a positive association with the



**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

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 (Figure 4b).

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

	dAICc	df	Weight
<b>1-hr</b>			
~NDVI	<b>0</b>	<b>3</b>	<b>0.867</b>
~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
<b>1-hr</b>			
~NDVI + ~NDVI2	<b>0</b>	<b>4</b>	<b>0.59</b>
~NDVI	<b>0.7</b>	<b>3</b>	<b>0.41</b>
<b>3-hr</b>			
~NDVI	<b>0</b>	<b>3</b>	<b>0.48</b>
Null model	<b>1.3</b>	<b>2</b>	<b>0.245</b>
Global model	2.2	7	0.161
~PC1 + PC2 (habitat structure)	3.3	4	0.09
~SOS + species richness	6	4	0.023

## 4 | 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-time-scales (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-hr temporal resolution of species activity but not for the 3-hr 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 et al., 2011), improving chances for species to acoustically communicate and find mates with the benefit of reduced negative interactions (Gaston, 2019; Kronfeld-Schor & Dayan, 2003). 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 (Borzée et al., 2016; Hödl, 1977), 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 (Figure S4). Conversely, temporal patterns of anuran activity may be regulated by distinct strategies in response to resource availability and competition (Humfeld, 2013; McCauley et al., 2000). 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. Furthermore, 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 (Llusia et al., 2013; Saenz et al., 2006), 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 (Mason et al., 2008; Schoener, 1974).

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 here 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 favours 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 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 et al., 2007; Werner et al., 2007), and our findings suggest that increasing landscape heterogeneity may indirectly increase the effects of spatial-related stochastic processes on signalling anuran assemblages.

The nightly compositional similarity was relatively high ( $\bar{x} = 0.64$  between early-late period, 1-hr 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 signalling individual whose calling activity induces competing conspecific males to start advertising, initiating a chain reaction that may last for hours (Brooke et al., 2000; Llusia et al., 2013; Prado et al., 2005; Wells & Schwartz, 2007). Chorusing formation may benefit calling energetic costs by increasing attractiveness for mates to a common breeding site and minimizing predation risk (Schwartz & Bee, 2013). Although chorusing attendance and diel activity patterns are widely described in species-specific studies (Bertoluci & Rodrigues, 2002; Gottsberger & Gruber, 2004; Heinemann et al., 2015; Lopez et al., 2011; Schalk & Saenz, 2016), community-wide approaches remained elusive (Dubos et al., 2020; Guerra et al., 2020; Ulloa et al., 2019). 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 behaviour have mainly been investigated in light of acoustic communication, with species eventually altering signalling parameters or behaviour when exposed to heterospecific calls (Both & Grant, 2012; Phelps et al., 2006), 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, that is, 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., 2019) 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 et al., 2013; McCann et al., 2017), disregarding diel differences in animal activity within communities leads to a poorer

representation of co-occurring species. Consequently, temporal resolution may yield 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 (Brumm, 2006; Humfeld, 2013; Schwartz, 1987). Importantly, we found that even a small change in temporal resolution (from 1- to 3-hr 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.

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### AUTHORS' CONTRIBUTIONS

L.S.M.S. and T.S. conceived the presented idea; L.S.M.S., T.S.F.S. and D.L. contributed to design the study; L.S.M.S. and T.S.F.S. collected the data; L.S.M.S. performed the analysis and took the lead in writing the manuscript; all authors revised the manuscript critically; D.L. and T.S. 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).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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