High species turnover shapes anuran community composition in ponds along an urban-rural gradient

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Abstract

The rapid expansion of urban areas in which natural and semi-natural areas are replaced by human infrastructure, such as buildings and streets, is a major threat to biodiversity worldwide. However, little is known about how the structure of biotic communities is affected by urbanization in the tropics. Here, we tested the effect of land use types in urban and peri-urban areas on frog species richness and community composition in central Brazil. We selected 20 ponds differing in size and surrounding levels of urbanization as well as natural forest cover. We then used a Poisson GLM and a distance-based Redundancy Analysis (db-RDA) to relate species richness and community composition, respectively, to environmental variables. Variation in species richness was best explained by pond size (positive effect) and amount of urbanization (negative effect) in the surrounding 500 m. Community composition was mainly driven by species turnover than by nestedness, with db-RDA showing that turnover was explained primarily by urban infrastructure and forest cover. Our results indicate that urbanization negatively influences species richness. Moreover, as the amount of urbanization increased, several species were replaced by others taxa that appear better adapted to urban environments. Our results indicate that maintaining large ponds with surrounding native vegetation in urban environments might be an effective strategy for conserving frog communities.

Keywords: beta diversity, biotic homogenization, urbanization, tropical anurans.

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49 **Author contribution**

50 CCG and MAG conceived the idea, designed the study and collect field data. CCG, MAG,
51 and DBP performed the data analyses. All authors commented on drafts and gave final
52 approval for publication.

1. Introduction

Urbanization is a key threat to biodiversity, causing extirpation of populations and species worldwide (Miller and Hobbs 2002, McKinney 2008, Batáry et al. 2018). Currently, more than 50% of the world's human population lives in urban areas and it is estimated that this number will increase to approximately 65% by 2030 (Grimm et al. 2008, United Nations 2018). Urbanization can drastically alter the chemical, physical, and ecological condition of ecosystems, with several studies highlighting the negative effects of urbanization on species dispersal (Findlay et al. 2001, Rubbo and Kiesecker 2005), ecological interactions (Fischer et al. 2012), and community structure (Christie et al. 2010, Zhang et al. 2016, Gagné and Fahrig 2007, McDonnell et al. 1997, Kinzig and Grove 2001, Johnson et al. 2013). For example, in an investigation of bird communities along a gradient of urban influence, Dale (2018) found that urbanization led to a predominance of species with generalist diets and nesting habits.

Differences in composition among communities (beta-diversity, Whittaker 1960) may reflect two distinct ecological processes: species loss (nestedness), in which the composition of species-poor assemblages represents a subset of richer sites (Bender et al. 2017), or replacement (turnover) of species, in which sets of species are replaced by others (Baselga 2010, Anderson et al. 2011, Leibold and Chase 2018). Urbanization has been shown to affect species richness leading to nested communities in cities compared to less urbanized areas (González-Oreja et al. 2012, Ficetola and De Bernardi 2004). For example, Fernández-Juricic (2002) showed that bird species exhibited a nested pattern in areas subject to high levels of human influence. Similarly, taxonomic composition of ant communities in most urbanized locations were a subset of the least disturbed locations (Slipinski et al. 2012), and dragonfly beta diversity in urban stormwater ponds was explained mostly by differences in richness rather than by turnover (Johansson et al. 2019).

Amphibians are the most threatened group of vertebrates globally, with approximately 40% of its species classified in at least one threat category of the IUCN (IUCN 2020). Nearly 1,000 amphibian species are classified as threatened with extinction because of land use changes for urban development (Maxwell et al. 2016), likely due to the fact that most amphibian species exhibit complex life cycles (Wells 2007), and urbanization can seriously affect both aquatic and terrestrial environments (Zhang et al. 2016). For example, Knutson et al. (1999) showed that urban development affected both tadpole and adult stages, by modifying terrestrial environments as well contaminating water bodies. Similarly, major changes in landscape composition through urbanization severely impacted anuran populations, affecting richness, abundance, and occurrence of several species (Ficetola et al. 2011, Youngquist et al. 2017). In the few studies investigating specific components of urban landscapes, pond size has generally proved to be a strong predictor of species richness and abundance (Dickman 1987, Parris 2006, Gagné and Fahrig 2007), although its effect on community composition is unclear.

Despite of anuran diversity being strongly affected by urbanization, amphibians are among the least studied vertebrate groups in urban landscapes worldwide (McDonnell and Hahs 2008). Although the number of studies on amphibians in urban areas has grown, information is still lacking to effectively guide amphibian conservation in most of the world's urbanized landscapes (but see Parris et al. 2018), especially in the highly diverse tropics. Here, we tested the effect of landscape composition on anuran communities in ponds along an urban-rural gradient. We hypothesized that anuran species richness in cities is positively related to habitat area and negatively related to urbanization. We also investigated which process (nestedness or turnover) was responsible for differences in anuran community composition along an urban-rural gradient. We hypothesized that decreasing habitat area and increasing urbanization would lead to the local extinction of sensitive species without

replacement of species. To the best of our knowledge, this is the first study testing the contribution of separate components of beta diversity on changes in anuran community composition across an urban-rural gradient.

2. Methods

2.1 Study site

We conducted this study in Campo Grande city (20° 28' 13"S, 54° 37' 25"W), Mato Grosso do Sul state, central Brazil. This region was originally covered by savanna vegetation, with scattered trees and shrubs mixed with forest formations (known as Cerrado; Ribeiro and Walter, 1998). Currently only ~ 21% of the original native cover persists, while the remaining 79% of the municipality consists primarily of pastures, agricultural fields, and urban areas (PLANURB 2019). The climate is characterized by a dry season (between April to September) and a rainy season (October to March), with an annual average rainfall of 1,530 mm, and an average annual temperature ranging from 18 °C to 29 °C (Ferreira et al. 2017). The urban area of Campo Grande covers 154.4 km², with ~ 900,000 inhabitants, and a mean population density of 104 inhabitants/km² (Ferreira et al. 2017).

2.2 Sampling design

We georeferenced and visited 156 ponds in urban and peri-urban areas, and selected 20 ponds for survey (Fig 1). We based pond selection on a careful systematic procedure. First, we included only ponds that were a minimum distance of 1 km apart (1.1 to 26.7 km), to maximize independence of sampling units (Semlisch and Bodie 2003). We tested for independence by completing a Mantel correlogram and found no evidence of spatial autocorrelation in our data (Fig. S1). Second, we selected ponds that maximized variation of explanatory variables (i.e. amount of surrounding native forest cover, degree of urbanization,

127 and pond size; Table S1). Third, we selected ponds to encompass a broad range of pond sizes
128 (109 to 3,080 m²; Table S1).

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130 **Fig. 1** Study area showing the location of the 20 ponds sampled in urban and peri-urban areas in Campo Grande, Mato Grosso do Sul, central

131 Brazil. Land use classification was extracted from the MapBiomas database for 2018.

2.3 Frog sampling

We estimated the abundance of frogs through visual encounter surveys (Crump and Scott Jr 1994) at night (19:00 h to 00:00 h), using headlamps. This is considered the most efficient method to detect anurans (Doan 2003, Flint and Harris 2005, Grover 2006). We also used acoustic identification because some anuran species have low detectability due to their small body size, rarity, or their ability to camouflage among the leaf litter or underground (Sá et al. 2018, Lima et al. 2019). However, while this alternative method allowed for the detection of species with predominantly subterranean habits (which otherwise would have been overlooked), only the abundances of two comparatively rare species (*Elachistocleis helianneae* and *Elachistocleis bicolor*) were estimated by acoustic identification. We therefore assumed there was low impact of the two different methods on abundance estimates.

We visited each pond three times on different days between October of 2018 and December 2018, with each visit lasting 30 minutes and performed by three people. This gave a sampling effort of 4.5 h per pond and 90 h in total. During the surveys, researchers walked the entire perimeter of the pond more than once, looking for individuals at the edge of, and inside, ponds. We identified each individual to species level and then marked it with Visible Implant Elastomer (VIE) Tags (Northwest Marine Technology, Inc.), to avoid recounting the same individual. This is an alternative to the traditional toe-clipping method, but does not harm animals (Davis and Ovaska 2001). Mean sampling coverage (proportion of observed richness relative to richness estimated by Chao 1) for all ponds was 0.9 (range: 0.41 to 1), indicating that sampling effort was sufficient to estimate species presence in most local communities (Table S2).

2.4 Landscape metrics

We obtained information on land use types based on intermediate resolution images (30 m) provided by the MapBiomass platform (<http://mapbiomas.org>; collection 4.0), for 2018. We calculated the percentages of land use classes around ponds using ARCGIS 10.6.1. For each pond, we measured pond size (m²; through polygon tool, available in Google Earth), and the percentage of native forest as well as urban infrastructure in buffer sizes of 500 and 1,000 m radius. We defined native forest using the classification “Natural Forest” provided by MapBiomass, including forest and savanna formations. Urban infrastructure included all non-native land uses, like roads and buildings. We selected the two buffer sizes based on previous studies (Semlitsch and Bodie 2003, Almeida-Gomes et al. 2016). We did not add smaller scales due to very low variation in land use coverage (Table S1), thereby precluding analyses. Likewise, we excluded buffers at larger scales (> 1,000 m) due to high levels of overlap with nearby buffers, thereby potentially leading to pseudoreplication. The percentage of native forest cover varied from 0.3 to 36.1% in a 500 m buffer and 1.8 to 47.3% in a 1,000 m buffer. Urban infrastructure varied from 0 to 89.4% in a 500 m buffer and 0 to 84.5% in a 1,000 m buffer (Table S1).

2.5 Data analysis

We standardized all five predictor variables to zero mean and unit variation prior to analysis. We used the variance inflation factor (VIF) in the usdm package (Naimi et al. 2014) to check for multicollinearity. Our final dataset only included uncorrelated variables (VIF < 10): pond size, native forest in 500 m and 1,000 m buffer, and urban infrastructure in 500 m buffer.

2.5.1 Species richness

To test the effects of forest cover (native forest), urbanization (urban infrastructure), and pond size on amphibian richness, we used generalized linear models (GLMs) with Poisson

distributed residuals. We used the sjstats package (Lüdtke 2019) to check for overdispersion and conduct residual diagnosis. All models had normally and homogeneously distributed residuals. We found no evidence of overdispersion.

We built and fit 12 candidate models to test alternative hypotheses about the importance of groups of variables in explaining amphibian species richness: three models to test the effect of forest cover, urbanization, and pond size at two spatial scales, one model for each spatial scale to test the effect of urbanization and forest cover, and one model for each spatial scale to test the combined effect of pond size, urbanization, and forest cover. We used Akaike Information Criterion corrected for small samples (AICc) and Akaike weights to rank models, considering as plausible all models with $\Delta AICc \leq 2$. We conducted analyses in the MuMIn package (Barton 2018).

2.5.2 Beta diversity partitioning

We decomposed total beta diversity into two components: turnover and nestedness, following Baselga (2010). We used presence-absence and abundance data to calculate dissimilarity and its two components using Jaccard and Bray-Curtis indices, respectively. We conducted our analyses in the betapart R package (Baselga et al. 2018) and the three dissimilarity matrices were summarized using Principal Coordinates Analysis. After these analyses, we performed a distance-based Redundancy Analysis (db-RDA) to test which landscape variables best explained the nestedness or turnover distance matrices. We conducted the analysis in the vegan package (Oksanen et al. 2019). db-RDA exhibited a high level of performance, with a negligible false-negative rate (Jupke and Schäfer 2020), and was an adequate constrained ordination method to relate distance matrices to predictor variables. As we did not detect a high degree of spatial autocorrelation in the community composition

(Fig. S1), we did not include any spatial predictors (e.g., Moran Eigenvector Maps) in our model. We completed all analyses in R v. 3.6.0 (R Core Team 2019).

3. Results

We found 835 individuals of 20 anuran species from five families (Table S3). The most speciose families were Hylidae and Leptodactylidae (nine and seven species, respectively). The most abundant species were *Dendropsophus nanus*, with 266 individuals, which represented 31.8% of the total sampled individuals and *Scinax fuscomarginatus* (87; 10.4%). Frog richness in ponds ranged from one to 13 species and abundance from six to 139 individuals.

We found a single best-fit model to explain frog species richness ($w_i = 0.608$; $R^2 = 0.804$), which contained pond size and percentage of urban infrastructure in a 500 m buffer (Table 1). Our analyses revealed that pond size (Coefficient $\pm$ SE: 0.22 ± 0.07) and urban infrastructure (-0.31 ± 0.11) had a positive and negative effect on species richness, respectively (Fig. 2).

220 **Table 1** Results of model selection based on Akaike Information Criterion (AICc) explaining
 221 anuran richness. We highlight the best model and the null model in bold and italics,
 222 respectively. Area – pond size in m²; For_500 – percentage of native forest in a buffer of 500
 223 m; For_1000 – percentage of native forest in a buffer of 1000 m; Urb_500 – percentage of
 224 urban infrastructure in a buffer of 500 m; LL – model log likelihood; w_i - Akaike weights; R²
 225 - Nagelkerke's R² (1991).

Models	K	LL	AICc	ΔAICc	w _i	R ²
Area + Urb_500	3	-41288	90.1	0.00	0.608	0.804
Area + For_500 + Urb_500	4	-41192	93.1	2.97	0.137	
Area + For_1000 + Urb_500	4	-41284	93.2	3.16	0.125	
Urb_500	2	-45461	95.6	5.55	0.038	
Area	2	-45760	96.2	6.15	0.028	
Area + For_1000	3	-44668	96.8	6.76	0.021	
Area + For_500	3	-44808	97.1	7.04	0.018	
For_500 + Urb_500	3	-45163	97.8	7.75	0.013	
For_1000 + Urb_500	3	-45253	98.0	7.93	0.012	
<i>Null</i>	<i>1</i>	<i>-51086</i>	<i>104.4</i>	<i>14.32</i>	<i>0.000</i>	
For_1000	2	-50319	105.3	15.27	0.000	
For_500	2	-51043	106.8	16.72	0.000	

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Fig. 2 Effects of landscape metrics on anuran species richness. A) Positive relationship between pond size (m²) and species richness, after controlling for urban infrastructure in a 500-m buffer. B) Negative effect of percentage of urban infrastructure in a 500-m buffer (%) on species richness, after controlling for pond size. Solid lines represent the estimated relationship among variables, and dotted lines are 95% confident intervals.

233 The composition of amphibian communities in ponds differed considerably, ponds
 234 with high urban infrastructure were distinguished from those in less urbanized areas in the
 235 ordination diagram (Fig. 3). This separation was mostly explained by turnover (92.7%) rather
 236 than nestedness (7.3%). Notably, ponds with similar percentage of urbanization were more
 237 similar in composition indicating biotic homogenization along the gradient (Fig. 3). The
 238 overall results did not change if we used data on species abundance (Fig. S2).

Fig. 3 Ordination diagram showing the Principal Coordinate Analysis for the total (A), nestedness (B), and turnover (C) pair-wise dissimilarity matrix between sites, considering presence-absence data. Symbols are shaded according to the amount of urban infrastructure in a buffer of 500 m surrounding each pond (Urb_500).

Our application of db-RDA showed ($r^2 = 0.34$, $P = 0.02$) that the variables that best explained turnover were the percentage of urban infrastructure in a 500 m buffer ($F_{3,16} = 4.32$, $P = 0.002$) and native forest in a buffer of 500 m ($F_{3,16} = 2.47$, $P = 0.035$; Fig. S3). The nestedness component ($r^2 = 0.72$, $P = 0.03$) was best explained by pond size ($F_{3,16} = 2.91$, $P = 0.036$; Fig. S4), and the total beta diversity ($r^2 = 0.23$, $P = 0.02$) was best explained by pond size ($F_{3,16} = 2.26$, $P = 0.021$; Fig. S4), percentage of native forest in a 500 m buffer ($F_{3,16} = 2.20$, $P = 0.031$; Fig. S4) and, percentage of urbanization in a 500 m buffer ($F_{3,16} = 4.32$, $P = 0.001$; Fig. S4).

The proportion of black (presence) and gray (absence) blocks in the diagram ordered by the urbanization gradient (Fig. 4) added to the evidence that the community was structured by turnover. When the percentage of urbanization increased, some species were replaced by others. For example, in a comparison of pond 12 (0% urbanization) and pond 2 (35% urbanization), we found that both supported the same number of species ($n = 10$), but the composition was different, with *Leptodactylus fuscus*, *Physalaemus nattereri*, and *Elachistocleis helianneae* absent from pond 2, but present in pond 12, and the addition of *Boana punctata*, *Leptodactylus labyrinthicus*, and *Dendropsophus minutus* to pond 2.

Fig. 4 Incidence of all species ordered by the urbanization gradient (ranging from 0% to 89.4%, in a 500 m buffer). Black and gray blocks indicate the presence or absence of the species, respectively.

4. Discussion

Consistent with our predictions at the onset of this study, we found that anuran species richness was positively related to pond size and negatively associated with the degree of urbanization. In contrast to our initial predictions, total dissimilarity was mostly explained by turnover rather than nestedness, and turnover was best explained by the amount of urban infrastructure surrounding ponds.

The effect of pond size on species richness represents a positive species-area relationship (SARs), which is one of the most pervasive and robust patterns in ecology (Arrhenius 1921, Preston 1960, Connor and McCoy 2001), and has been described in urban context for a variety of organisms such as plants (Bräuniger et al. 2010), birds (Aida et al. 2016, Callaghan et al. 2018), and mammals (Matthies et al. 2017). Positive SARs are most commonly assumed to be caused by greater habitat heterogeneity in larger ponds supporting a larger number of species in larger areas (Williams 1943), as well as increased availability of resources allowing larger populations, which have low extinction probabilities (Hanski 1994). While these processes are likely to operate here, pond size might additionally be important in mitigating edge effects, with larger areas are relatively less affected by edge effects compared to smaller areas (given a similar shape) (Connor and McCoy 2001). Thereby, within an urban context, local disturbances at edges of ponds (Egger 2006, Du et al. 2010, Hu et al. 2018) might be less likely to affect the entire pond in large ponds, thereby decreasing the impacts of disturbance. In addition, a greater amount of water in larger ponds, may dilute the effects of pollution in larger ponds (Abel 1996).

We found evidence of a negative association between species richness and urban infrastructure. This result may be related to inhospitable characteristics of the urban environment for amphibians, such as artificial light (Baker and Richardson 2006), noise (Leon et al. 2019, Yi and Sheridan 2019), roads (Carr and Fahrig 2001, Pillsbury and Miller 2008),

and possible contaminants (Knutson et al. 1999). Such drivers may influence the anuran life cycle in several ways. Noise pollution and artificial light can directly affect amphibian calling behavior, potentially leading to changes in survival and reproduction rates (Sun and Narins 2005, Baker and Richardson 2006). In addition, roads can increase mortality during dispersal and thereby increase probability of local extinction (Ashley and Robinson 1996, Findlay et al. 2001, Rubbo and Kiesecker 2005). Furthermore, since anurans feed on invertebrates, and several studies have found a decrease in invertebrate diversity as well as abundance in urban environments (e.g., Beavan et al. 2001, Moore and Palmer 2005, Jones and Leather 2013), urbanizations may reduce the availability of resources for anurans. A combination of these factors may negatively influence the ability of species to maintain viable populations in ponds in areas with a high degree of urbanization.

Contrary our predictions at the outset of this study, and the results from other studies (e.g., González-Oreja et al. 2012, Ficetola and De Bernardi 2004), we found that differences in community composition among ponds were caused primarily by turnover. However, similar results were found by Rádková et al. (2014) and Specziár et al. (2018) among invertebrate communities in aquatic environments in non-urban context. Our results suggest that urbanization is acting as an environmental filter (Piano et al. 2019), leading to the replacement of species not adapted to urban conditions by species that are more efficient in exploiting urban resources (McKinney 2006, Menke et al. 2011). As a result of such turnover of species, communities in ponds in highly urbanized areas are similar to each other, a process known as biotic homogenization (McKinney and Lockwood 1999, Olden and Rooney 2006). Biotic homogenization is a likely common consequence of anthropogenic disturbance (McKinney 2006, Olden 2006, Schwartz et al. 2006), and can have potential consequences for a variety of ecosystem services (Schwartz et al. 2006). Thereby, our results show that in more urbanized areas anuran communities are not only losing species, but also are becoming more

homogeneous, which highlights a need for strengthened conservation efforts in the face of increasing replacement of natural habitat by urban areas (Grimm et al. 2008, Seto et al. 2011, 2012).

We found that the importance of different explanatory variables differed between species richness and community composition. For example, pond size was more important for the number rather than the identity of species. Similarly, forest cover was not important in models of species richness, but was a key predictor of the turnover component of beta diversity. This result highlights the need to protect forest habitat when the goal is to conserve habitat specialist species in peri-urban environments.

Management implications

Our results provide valuable information for effective conservation of anurans in urban environments. While it is not feasible to reduce the percentage of urbanized areas to increase anuran richness, focusing conservation efforts on large ponds in highly urbanized environments might be an effective strategy to maintain a maximum number of species. Therefore, the negative effect of urbanization on amphibians could be reduced by increasing pond size. Although relationships among anuran communities and urbanization areas is far from being completely understood, and more studies focusing on anuran in urban context are necessary, our results may provide useful information for on-the-ground conservation actions.

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