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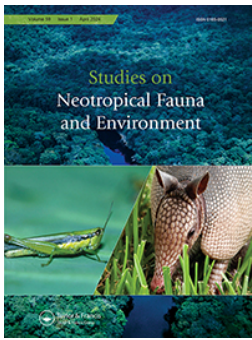


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The role of artificial ponds for anuran diversity in managed areas of the Atlantic Forest

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ABSTRACT

Artificial ponds can be important reproductive sites for anurans in human-disturbed habitats. However, this capacity depends on the configuration of the habitat where they are inserted. We evaluated how anuran beta diversity was influenced by the configuration of the surrounding habitat and water parameters in artificial ponds in southern Brazil. Physicochemical parameters of water and the configuration of the surrounding habitat were the elements that best explained the variation in beta diversity. However, the surrounding habitat had a predominant role in the differences between communities. The level of exposed soil was the component that best acted on the turnover component of beta diversity followed by urbanization, which highlights the impact of human presence on anuran diversity. In other words, we observed that anthropogenic changes caused changes in species composition in the evaluated ponds. Among water parameters, only phosphate was relevant for the configuration of communities. Phosphate peaks may result from sewage or fertilizer contamination, not infrequent in the region despite the low human density and the small-scale agriculture economy. Even though they are anthropogenic environments, artificial ponds can help maintain the anuran communities, but their effectiveness will depend on the presence of forest remnants and water quality.

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Introduction


Habitat conversion in anthropogenic landscapes changes the physical, chemical, and biological properties of the environment, compromising ecosystem functions and resulting in biodiversity loss (Fracetto et al. 2013; Neves et al. 2014). Despite being a phenomenon that can be seen with the naked eye, such as the suppression of vegetation cover, the effects of habitat loss can be studied at different levels using several parameters (Porter et al. 2000; Becker et al. 2007, 2017). On a smaller scale, when changes are assessed over a few square meters, the impact of habitat loss on populations can be seen at the local level (Woolbright 1985; Knutson et al. 1999; Porter et al. 2000). The conversion of natural habitats into agricultural landscapes is certainly one of the greatest threats to biodiversity worldwide, and South America is no

exception (Díaz et al. 2005; Leal et al. 2012; Wang et al. 2015; Zee & Fukami 2015; Morante-Filho et al. 2016; Almeida-Gomes et al. 2019). Therefore, understanding the relationship between landscape and biodiversity in these places is an urgent concern for nature conservation (Benton et al. 2003; Fahrig et al. 2011). In Brazil, the conversion of natural habitats to agriculture and livestock is a common practice and one of the major conservation challenges (Browder et al. 2008; Fracetto et al. 2013) as more and more new cropland is needed, while water and soils are contaminated by agricultural residues (Rubbo & Kiesecker 2005). These agricultural activities are strongly present in the Atlantic Forest, making it a critical biome for conservation actions (Laurance 2009; Zachos & Habel 2011).

In general, landscape changes affect more intensely those taxa with specificity to certain habitats and that

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have low dispersal capacity, such as many amphibians (Storfer 2003; Stuart et al. 2004; Cushman 2006). Amphibians have been intensely threatened due to the loss and fragmentation of natural habitats, in addition to pathogen-related population declines (Becker et al. 2007; Hayes et al. 2010). Some amphibian species are especially vulnerable to environmental changes (Stoate et al. 2009; Becker et al. 2010; Arntzen et al. 2017). The transformation process of the Atlantic Forest has been occurring for centuries and has a homogenizing effect on its landscape (Santos et al. 2021), reducing habitat complexity and, in turn, species richness (Hazell et al. 2001; Olden et al. 2004; Vasconcelos and Rossa-Feres 2005; Bitar et al. 2015). Differences in habitat configuration (Von May et al. 2010) or disturbance degree (Bitar et al. 2015) can induce changes in the beta diversity (species composition) of a community through either species loss (nestedness) or species replacement (turnover). For example, Knauth et al. (2019) observed that the beta diversity of a tadpole community was mainly structured by species exchange (turnover) and that landscape characteristics played a fundamental role in promoting anuran turnover in the community. Therefore, understanding how habitat configuration influences beta diversity and its components (nestedness and turnover) can provide us with information about the processes of community formation (Leprieur et al. 2011), which can serve as a tool for biodiversity conservation planning (Angeler and Kühn 2013; Socolar et al. 2016).

Anurans depend on these habitats not only for shelter and foraging but also for reproduction. For many species, the presence of water bodies, such as ponds and streams, is essential for the completion of the reproductive cycle or aquatic larval development (Wells 2019). Therefore, the absence of water bodies is a limiting factor for the survival of their populations in human-modified environments (Becker et al. 2007). Studies have shown that artificial ponds are important components in the process of maintaining and conserving anuran species in forest habitats (Knutson et al. 2004; Prado and Rossa-Feres 2014; Smalling et al. 2015). In southern Brazil, the Atlantic Forest is mostly constituted by remnants embedded in an anthropogenic matrix (Viana et al. 1997; MapBiomias 2022). Here, the establishment of ecological corridors would not significantly increase the permeability of the matrix due to their low displacement capacity (Moser et al. 2019). Thus, in the deeply fragmented southern Atlantic Forest, the landscape presents a high level of isolation for amphibian species. This isolation can occur, in functional terms, when amphibians do not

have access to reproductive sites (Becker et al. 2010). In the context of this discussion, the presence of artificial ponds appears to be a way to provide access for individuals to reproductive sites within their areas of occurrence. It should also be remembered that the presence of water alone is not sufficient to become a reproductive site. Therefore, several studies have attempted to understand the processes involved in selecting sites for reproduction, vocalization, and oviposition (Zina and Haddad 2005; Carvalho et al. 2015; Santos et al. 2016; Cassiano-Lima et al. 2020; Farina et al. 2021).

Agricultural areas have omnipresent aquatic habitats that are potentially valuable for wildlife. For example, Machado and Maltchik (2010) indicate that rice paddies can help to maintain an important part of amphibian abundance in wetlands of southern Brazil, by serving as refuges for biodiversity. Furthermore, Magnus and Rannap (2019) observed that amphibian diversity was greater in artificial ponds than in natural ponds, with the two threatened species evaluated (*Pelobates fuscus* and *Triturus cristatus*) preferring artificial ponds over natural ponds for breeding. In this sense, the review by Chester and Robson (2013) indicates that anthropogenic waters need to be recognized for their potential to conserve biodiversity. The negative effects of pollution at these sites are exacerbated when animals do not recognize them as low-quality habitat, making those aquatic habitats ecological traps (Sievers et al. 2018). An ecological trap occurs when an environment has characteristics that cause animals to preferentially inhabit it but actually have long-term negative effects on the populations of those animals (Robertson and Hutto 2006). For example, Sievers et al. (2018) confirm the potential for urban stormwater wetlands to function as ecological traps; in fact, tadpoles show lower survival and are less responsive to predator olfactory cues when raised in more polluted stormwater wetlands, but also reach metamorphosis earlier and at a larger size.

Habitat scarcity may be one of the reasons that relatively complex communities are found even within plantations (Cunha et al. 2021). This leads to the assumption that the mere presence of water bodies accessible to anurans would be sufficient for them to use as breeding sites. However, the configuration of habitats associated with breeding sites is critical to population viability (Laan and Verboom 1990; Marsh et al. 2000; Marsh and Trenham 2001; Gibbons 2003; Vasconcelos et al. 2009). In addition to the habitat surrounding water bodies, water quality is one of the most important factors for amphibian populations (Dayton and Fitzgerald 2005; Lima and Peixoto 2007)

because most species are aquatic in the larval stage and the availability of dissolved oxygen, temperature, pH, and the presence of pollutants and contaminants are important for the survival of even terrestrial species (Piano et al. 2020; Ganci et al. 2022).

However, there is no consensus on how the environmental components occur together and influence the structuring of anuran communities (Vasconcelos et al. 2009; Silva et al. 2012). For example, Wanger et al. (2010) evaluated the amphibian community in natural and disturbed areas and observed a high beta diversity, where a few species dominated disturbed habitats. In contrast, Dehling and Dehling (2023) observed that amphibian communities in agricultural areas showed higher local alpha diversity than amphibian communities in natural habitats. These discordant results, as well as the knowledge gaps on this subject, represent an opportunity for studies in human-altered areas (Vellend et al. 2007). Therefore, areas with a mosaic of different land uses are considered good opportunities to assess the relationship between habitat changes and amphibian diversity.

In southern Brazil, there are small agricultural plots (e.g. cattle pasture, soybean, and corn plantation) where this mosaic occurs under intensive use, providing an excellent opportunity for a fine-scale assessment of landscape impacts on amphibian diversity. Such agricultural plots present different levels of environmental pollution and anthropogenic landscape changes, harboring an extremely favorable scenario for the study between occupation and soil use, water quality in reproductive sites, and amphibian diversity (Preuss et al. 2020). Here, we designed a study to explore the role of artificial ponds in supporting anuran diversity. We expected community composition to be influenced by habitat configuration and water quality of those artificial ponds, which will result in changes in beta diversity, with greater species richness in more heterogeneous ponds and a greater abundance of generalist species in more homogeneous ponds.

Material and methods

Study area

The study was conducted in ten permanent artificial ponds located in different agricultural properties in the west of the state of Santa Catarina, southern Brazil (Figure 1). The ponds are located in private properties (usually <10 ha) in which family farming is developed. Five of the sampled ponds have pig farms around them, with the presence of pig waste in the water.

Exotic fish (*Cyprinus carpio* and *Oreochromis niloticus*) are kept in all ponds and eventually used for local consumption. The surrounding habitat of the ponds consists of a mosaic of native and human-disturbed habitats. The climate is mesothermal subtropical humid, Cfa type of Köppen (Alvares et al. 2013) in the Atlantic Forest and, thus, several amphibian species use these water bodies as reproductive sites. The relief is characterized by steep valleys, a mean altitude is 630 m above sea level, and is occupied by fragments of Seasonal Forest remnants (Klein 1978; Vibrans et al. 2010).

Sampling design

We sampled 10 permanent artificial ponds measuring on average 1954 m² (minimum = 530 m²; maximum = 3979 m²) with an average depth of 2 m (1.20 to 3.60 m), (Figure 1), with a minimum distance of 0.66 km and a maximum distance of 28.08 km between the ponds. Before the selection of the ponds, they were inspected to determine their use as sites for vocalization and oviposition.

Anuran sampling

Samplings were conducted through the recording of vocalizing males around each pond (Dias et al. 2019). Between September and December of 2020, each pond was sampled one night per month. Due to the direct relationship between temperature, humidity, and the vocalization activity of amphibians (Ximenes and Tozetti 2015), three ponds were monitored simultaneously every night. This allowed all ten ponds to be sampled in four days and reduced climatic variations between the ponds. We register each species using an automated recording system of anuran vocalizations (Bridges and Dorcas 2000). The system was equipped with a digital voice recorder (model Sony ICD-PX312/PX312F) installed one meter above the soil at each pond (Dias et al. 2019). We programmed the equipment to record the environmental sound between 19:00 h and 07:00 h of the following day (13 hours of continuous recording). This period corresponds to the peak of the activity of anuran species (Santos et al. 2016). The audio evaluation followed the protocol used by Dias et al. (2019). Thus, one audio file was generated for each night sampled at each pond. From each audio file, we extracted 13 audio subsamples with a duration of three minutes, counting from the start of the records and with an interval of one hour (example: sample 1: from 19:00 h to 19:03; sample 2: from 20:00 h to 20:03; sample 3: from 21:00 h to 21:03; sample 13:

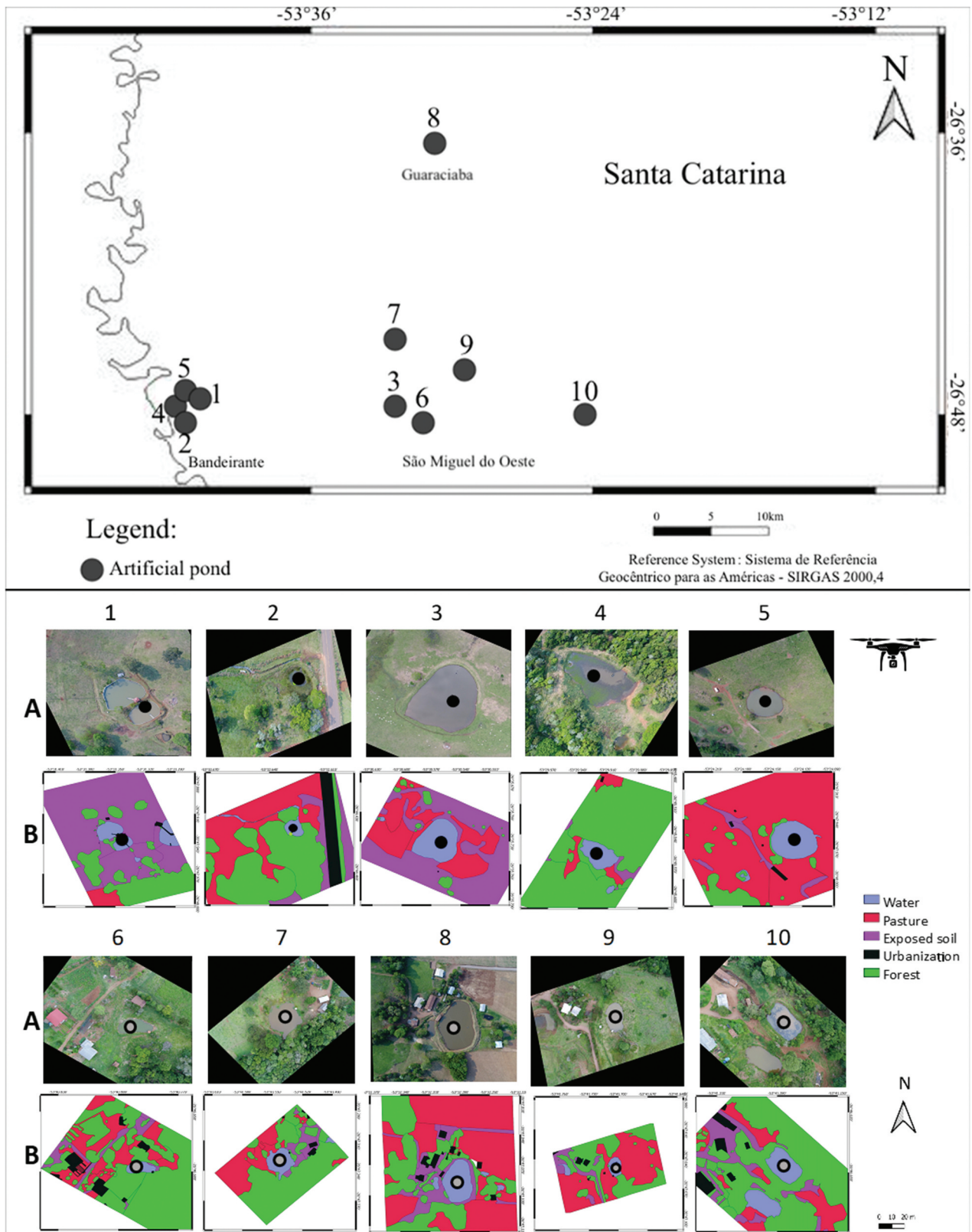


Figure 1. Geographic distribution, aerial drone images (A) and georeferenced orthomosaic (B) of the 10 artificial ponds sampled in the west of the state of Santa Catarina, Brazil. Black dots = presence of pig raising; Gray dots = no pig raising.

from 07:00 h to 07:03). The recorded species were identified using an audio database constructed from audio recorded at the study area, as well as from sound guides of the species (Haddad et al. 2005; Kwet and Márquez 2010). We estimated the abundance of individuals through the number of vocalizing males considering four categories: A) 1–4 vocalizing individuals; B) 5–9 vocalizing individuals; C) 10–20 vocalizing individuals; D) > 20 vocalizing individuals (Table S3) (Bertoluci and Rodrigues 2002; Ximenez and Tozetti 2015). For the analyses of abundance, we used the minimum number of vocalizing males (Ximenez and Tozetti 2015; Dias et al. 2019).

Evaluation of the water characteristics of the ponds

In October 2018, we manually collected 0.5 L of surface water in each pond using sterile polyethylene flasks for chemical and microbiological analyses. Surface water was collected 10 cm from the edge of the ponds at randomly selected points, and the samples were kept refrigerated (2–8 °C) and were analyzed up to 48 hours after the sampling in the Laboratory of Microbiology of the Universidade do Oeste de Santa Catarina (UNOESC), campus São Miguel do Oeste. Microbiological analysis of the most likely number of thermotolerant coliforms (MLN/100 mL) was conducted using the multiple-tube fermentation technique according to the standard method for testing water and effluents (APHA, 2005). To evaluate the water-quality parameters associated with nutrient enrichment, we conducted the following chemical analyses using a spectrophotometer (Spectroquant pharo 100) with Merck Ready Kits: total phosphorus (Merck Colorimetric analogous to APHA 4500), ammonium nitrogen (Merck Colorimetric analogous to APHA 4500), nitrate (Merck Colorimetric), and chemical oxygen demand (COD; Merck Colorimetric analogous to APHA 5220). In the laboratory, pH was also measured by the electrometric method with a multiparameter (Akso). The physicochemical and microbiological conditions of the ponds are shown in Table S1.

Evaluation of the habitat surrounding the ponds

We consider as surrounding habitat a mean area of 36,000 m² around each pond. The evaluation occurred through images captured with a drone at a height of 120 m and aligned with the central point of each pond. To account for the surrounding area of the ponds, we standardized a radius of 200 m² around the ponds. This extension of the analyzed area was

chosen due to the low dispersal capacity of individuals (Tozetti and Toledo 2005; Moser et al. 2019). The photointerpretation and vectorization of the features of interest in this study were conducted in the free software QGIS, version 3.14. Image capture occurred in October 2020 using the application DJIGO 4 on a smartphone iPhone 11 Pro connected to the radio control of a drone model Phantom 4 advanced, which includes GPS/GLONASS and a camera with 20 megapixels of resolution attached to the remotely piloted device. The georeferenced orthomosaic of the aerial images was the basis for the photointerpretation and studies that supported this monitoring. After conducting the georeferencing of the mosaics, the features of interest were vectorized using the free software QGIS, version 3.14. We created five classes according to the photointerpretation conducted in the orthomosaic obtained with the aerial mapping, viz. water bodies, exotic pasture, soil, urbanization, and native forest (Figure 1 and Table S2).

Data analysis

Analysis of abundance of vocalization activity

Based on Ximenez and Tozetti (2015), the data on the abundance of each species in each month were transformed into a mean. By listening to the 13 three-minute audio samples of each sampled night, we built a table with the data of species abundance (in the abundance classes) per day and per hour sampled. We conducted this evaluation with the twelve species shared between both types of sampling units.

Spatial predictors

We used Moran's eigenvector maps based on distance (dbMEMs, Legendre and Legendre 2012; Dray et al. 2012) to create spatial variables (eigenvectors) based on the Euclidean distance matrix of the geographic coordinates of the ponds. First, we defined the neighborhood matrix, which describes the spatial relationships between the objects (Dray et al. 2012). In other words, we defined which ponds are neighbors and which are not. We used as graphs of spatial neighborhood 'Delaunay triangulation,' 'Gabriel graph' and 'minimum spanning tree,' and, as a measurement of weight, we used the linear distances between ponds. We selected the best neighborhood matrix based on the AICc (Akaike Information Criterion corrected). The most parsimonious model was the one based on the 'Gabriel graph' and the truncation distance was 18.54 km (AIC = 84.82 against 85.91 for the null model). This model also generated nine spatial variables (eigenvectors), two of which with positive autocorrelation.

Evaluation of the components of anuran beta diversity

Before the analyses, we transformed the abundance data using the Hellinger distance to homogenize the variation in abundance of the species (Legendre and Legendre 2012). We divided beta diversity into general components of beta diversity, turnover, and nestedness following the methods proposed by Baselga (2010). This procedure was conducted using the function 'beta.pair' in the R package betapart (Baselga and Orme 2012). We used the Bray-Curtis dissimilarity for the abundance data. This procedure produced three dissimilarity matrices: total beta diversity (general spatial turnover, β_{Bray}); turnover component (turnover that is immune to the variation in species richness, β_{Bal}); nestedness component (nestedness that results from the differences in species richness between locations, β_{Gra}). We considered the dissimilarity values high when they were above 70%.

Community-environment relationships

We used the distance-based redundancy analysis (dbRDA) in each matrix of biological dissimilarity to examine in more detail the community-environment relationships (Legendre and Anderson 1999). This method is similar to the redundancy analysis but can be based on any dissimilarity or distance matrix (in our case, Bray-Curtis dissimilarity) (Legendre and Legendre 2012). Initially, we selected only predictors of environmental variation that are significant to beta diversity and its components, which were then used for the environmental model (Legendre and Anderson 1999). We used direct selection with 9999 permutations to select the environmental variables to execute the environmental model. For this, we used the matrices containing each component of beta diversity and the environmental predictors. For subsequent analyses, we used only variables retained in the last selection step (Blanchet et al. 2008). The procedure of direct selection was executed with the function 'ordistep' of the R vegan package (Blanchet et al. 2008). The ordistep function returns the selected model by applying an ANOVA, followed by brief information on steps taken. The summarized results of the procedure of direct selection are presented in Tables S4 and S5.

Variation partitioning for anuran taxonomic and beta diversity

The relative contributions of the environmental descriptors and spatial variables for the patterns of beta diversity were evaluated using partial redundancy analysis (pRDA) with variation partitioning (Dray et al. 2012). This analysis divides the variation in the community composition

resulting from (1) each explanatory variable ($[E]$ = environment and $[S]$ = spatial), (2) the unique contribution of each explanatory variable ($[E/S]$ = environment – purely environmental variables – or $[S/E]$ = spatial – purely spatial variables) and (3) the total variance explained by the environmental and spatial variables together (spatially structured environmental variables). The variance explained by each fraction was based on the adjusted R^2 (Peres-Neto et al. 2006). The environmental variables used in the environmental model and the spatial variables that make up the spatial model were those previously selected in db-RDA and direct selection as described above.

The significance of the dbRDA axes and pRDA fractions were tested through an ANOVA-type permutation test to evaluate the significance of the restrictions using 9999 permutations. The dbRDA and pRDA analyses were conducted using the functions 'capscale' and 'var.part,' and the permutations using the function 'anova.cca' of the R package vegan (Oksanen et al. 2019).

Results

We recorded 12 anuran species distributed into five families: Bufonidae (1), Hylidae (5), Leptodactylidae (4), Odontophrynidae (1), and Ranidae (1). The most abundant recorded species were *Physalaemus cuvieri* (Fitzinger, 1826), *Dendropsophus minutus* (Peters, 1872), and *Aquarana catesbeiana* (Shaw, 1802), with a mean of 9.32 (± 11.25), 8.56 (± 10.86), and 5.08 (± 4.08), respectively, of the total of individuals recorded in the 10 ponds (Table S3).

Partition variation of beta diversity and its components

The total observed beta diversity for the set of communities was 75%. Of this total, 71.2% concerned the turnover component, while nestedness was responsible for only 3.8% of the variation. The analyses of variance partitioning (pRDA) of beta diversity and its components identified significant effects of the aquatic, surrounding, and spatial components on the patterns of anuran beta diversity in artificial ponds. We observed that the total beta diversity was the diversity component whose variation had the highest percentage of explanation by the set of predictors ($\beta_{\text{Bray}} = 33\%$; Figure 2). Of the total explained variation, the fractions that were unique to the surrounding habitat and spatial predictors were the ones that generated more contributions (15% and 10%, respectively). However, we also observed a substantial amount of explained variation by the fractions shared by water and spatial predictors (9%) and, to a lesser extent, by spatial and surrounding habitat

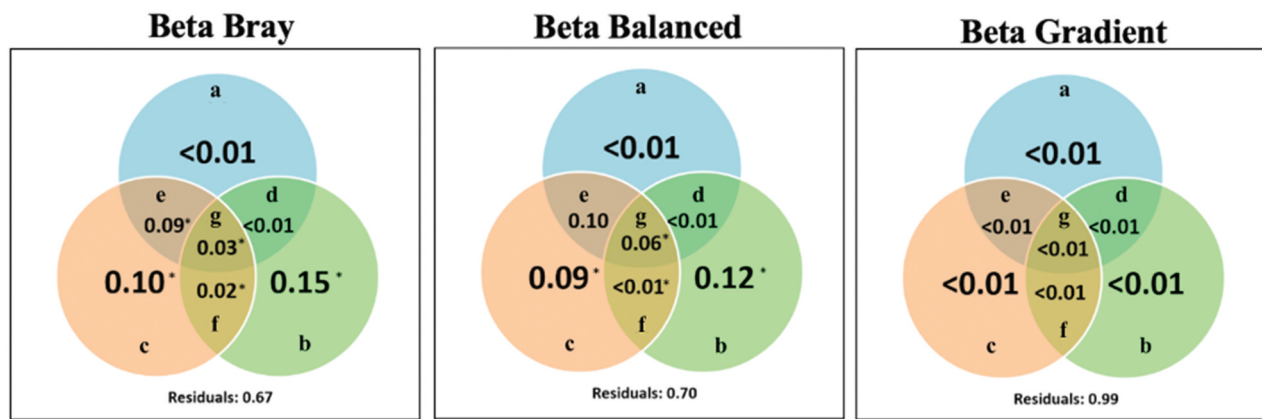


Figure 2. Partition variation for total beta diversity (Beta Bray) and its components (turnover = Beta Balanced; nestedness = Beta Gradient) of anuran communities. (a) water variables; (b) surrounding habitat variables; (c) spatial variables; (d) fraction shared between water and surrounding habitat; (e) fraction shared by water and spatial; (f) fraction shared between spatial and surrounding habitat; (g) fraction shared by all; (*) $p < 0.05$.

predictors (2%), and by the shared fraction of all three sets of predictors (3%). Similarly, our sets of predictors were able to explain 30% of the total variation attributed to the turnover component. For this component, the unique fractions of the surrounding habitat (12%) and spatial (9%) predictors were the most significant, besides the fraction shared by the three sets of predictors (6%). On the other hand, our sets of predictors explained, in total, less than 1% of the variation attributed to the nestedness component. We did not find any significant relationship between the three sets of predictors and this component of beta diversity.

Environmental and spatial predictors and beta diversity

The set of aquatic, surrounding and spatial predictors retained in the direct selection analysis was similar between beta diversity and its components. Similarity was higher between the total beta diversity and the turnover component (Table S2 and S4). The

selected water predictors were phosphate, COD, total coliforms, and total N (Table S5). Phosphate was selected for all components of beta diversity. Similar to the set of water predictors, the set of selected environmental predictors was similar for all components of beta diversity. The surrounding predictors that had the greatest influence on beta diversity were exposed soil (shared by all beta diversity components) and urbanization (which only affected beta nesting; Table S5).

DbRDA analyses relating water and spatial predictors to patterns of dissimilarities among communities revealed consistent patterns between beta diversity and its components (Tables 1 and 2). We did not detect any significant relationship between water predictors and beta diversity and its components (Table 1). On the other hand, we found significant relationships regarding the characteristics of the surrounding habitat, such as exposed soil and total beta diversity and the turnover component, although the fraction of explained variation was relatively low (β Bray: $R^2_{adj} = 0.14$,

Table 1. Results of dbRdas based on the distance for the data of the estimation of abundance of vocalizing males. The analyses were conducted based on total beta diversity, turnover, and nestedness dissimilarities. Complete models and marginal significance tests for unique aquatic variables are shown (i.e. a separate significance test for each variable in a model when all the other terms are in the model).

TOTAL (β Bray)			TURNOVER (β Bal)			NESTEDNESS (β Gra)		
General test			General test			General test		
R^2_{adj} : 0.05;			R^2_{adj} : 0.08;			R^2_{adj} : 0.13;		
F : 1.52;			F : 1.26;			F : 1.32;		
p : 0.16			p : 0.23			p : 0.15		
Predictor Variable	F	p	Predictor Variable	F	p	Predictor Variable	F	p
Phosphate	1.52	0.16	COD	0.97	0.42	COD	2.3	0.01
			Phosphate	1.62	0.14	Coliforms	0.76	0.69
			Total N	1.2	0.3	Phosphate	0.82	0.59
						Total N	1.41	0.15

Table 2. Results of dbRdas based on the abundance data. The analyses were conducted based on total beta diversity, turnover, and nestedness dissimilarities. Complete models and marginal significance tests for unique variables of the surroundings are shown.

TOTAL (β Bray)			TURNOVER (β Bal)			NESTEDNESS (β Gra)		
General test			General test			General test		
R^2_{adj} : 0.14;			R^2_{adj} : 0.11;			R^2_{adj} : 0.09;		
F : 2.48;			F : 2.06;			F : 1.43;		
p : 0.04			p : 0.04			p : 0.11		
Predictor Variable	F	p	Predictor Variable	F	p	Predictor Variable	F	p
Exposed soil	2.48	0.04	Exposed soil	2.06	0.04	Exposed soil	1.7	0.07
						c	1.16	0.26

$F = 2.48$, $p = 0.04$; β Bal: $R^2_{adj} = 0.11$, $F = 2.06$, $p = 0.04$; Table 2). The nestedness component did not show a significant relationship with any predictor of the surrounding habitat.

Relationship of the environmental variables with species abundance

DbRDA analyses relating water and spatial predictors to patterns of dissimilarities among communities revealed consistent patterns between beta diversity and its components (Tables 1 and 2). We did not detect any significant relationship between water predictors and beta diversity and its components (Table 1). On the other hand, we found significant relationships regarding the characteristics of the surrounding habitat, such as exposed soil and total beta diversity and the turnover component, although the fraction of explained variation was relatively low (β Bray: $R^2_{adj} = 0.14$, $F = 2.48$, $p = 0.04$; β Bal: $R^2_{adj} = 0.11$, $F = 2.06$, $p = 0.04$; Table 2). The nestedness component did not show a significant relationship with any predictor of the surrounding habitat.

Discussion

Our results showed that most of the variation in beta diversity was due to species turnover rather than nestedness. However, only 25% of the total beta diversity and 30% of the turnover fraction were explained by environmental predictors, such as surrounding habitat characteristics and spatial components. Among the latter, exposed soil and urbanization were the most important, both reflecting anthropogenic impacts on the landscape. Water characteristics did not seem to have a strong influence on the structure of the metacommunity.

The three most abundant species were *Physalaemus cuvieri*, *Dendropsophus minutus* and *Aquarana catesbeiana*. They present different habitats, biology and ecological preferences, but all of them are often

abundant in altered areas. In a brief comparison based on their natural history aspects, we see that: *Physalaemus cuvieri* is a generalist species that can become dominant in altered areas, and appears to be expanding its geographical distribution due to deforestation and changes in the natural landscape (Haddad and Prado 2005; Moraes et al. 2007; Haddad et al. 2013); *Dendropsophus minutus*, is found in a wide range of microhabitats as grasses, aquatic and herbaceous-shrubby vegetation surrounding ponds (Oliveira et al. 2007; Ferreira-Silva et al. 2016); and *Aquarana catesbeiana* is an invasive and exotic species that benefits from open and/or human-disturbed habitats (Both et al. 2014; Preuss 2017).

Influence of the turnover component on the composition of communities

A species' life history plays a relevant role in the pattern of beta diversity (Soininen et al. 2007), in particular its ability to disperse (Dobrovolski et al. 2012), and colonize a variety of different phytophysiognomies (Da Silva et al. 2017; Dalmolin et al. 2021). Most of the partitioning of beta diversity concerned the turnover component (71.2%), while nesting accounted for only 3.8% of the variation. In other words, the sampled ponds presented a pattern of species replacement, where anuran species from 'species-poor ponds' are not subsets of anuran species from 'species-rich ponds' (Tavares and da Silva 2019). Our results are consistent with those of Melchior et al. (2017) and Knauth et al. (2019), where beta diversity was mainly driven by species turnover rather than species gain or loss in Atlantic Forest ponds at both large and small scales. Tavares and da Silva (2019) also observed that the turnover component best explained the variation in beta diversity in amphibians from agricultural ponds. The role of turnover in shaping community dynamics suggests that species composition in each pond is influenced by stochastic factors, such as recruitment or random colonization (Melchior et al. 2017). Furthermore, given the number of amphibian species

recorded for the sampled site ($n = 12$), which consists of a highly human-modified landscape, it is plausible that these artificial ponds are important for the regional diversity of anurans. In fact, Magnus and Rannap (2019) observed that amphibian diversity was greater in artificial ponds than in natural ponds and, besides that, the results of this study also demonstrated that two threatened species (*Pelobates fuscus* and *Triturus cristatus*) preferred artificial ponds over natural ponds for breeding. These results indicate that artificial ponds can be an important tool for maintaining amphibian diversity in a scenario of loss and alteration of natural habitats (Magnus and Rannap 2019). Furthermore, although artificial ponds may not be suitable for the reproduction of amphibians that are more sensitive to environmental changes, these ponds can serve as ecological corridors, facilitating the movement of amphibians to other environments (Becker et al. 2007).

Habitat availability is crucial for the presence and persistence of the populations of the recorded species and ensures their access to the sampled ponds. However, the maintenance of these populations would depend on the existence of remaining habitats adjacent to the ponds (Vasconcelos et al. 2009; Silva and Rossa-Feres 2011; Silva et al. 2011). For example, from our data, we observed that *Phyllomedusa tetraploidea* was only present in ponds with greater amounts of native forest and less exposed soils. Similarly, *Aplastodiscus perviridis* and *Boana faber* were more abundant in ponds with these characteristics. These are all species that need a certain degree of environmental complexity in terms of vegetation cover and pond configuration for reproduction (Haddad et al. 2005). As our sampling method was based on calling surveys, we assumed that all sampling sites were reproductive sites offering minimal conditions for reproduction (humidity, shelter, microhabitat) including sites for oviposition (Parris and McCarthy 1999; Afonso and Eterovic 2007; Vasconcelos et al. 2009) and larval development (thermoregulation and food acquisition) (Wells 2019). Furthermore, ponds located near or at the edge of forest fragments supported higher anuran abundance and species richness than those far from forest fragments or in open environments (Silva et al. 2012), which reinforces the importance of the presence of remnant habitats. Dalmolin et al. (2019) observed that the presence of ponds distributed along gradients facilitated by substrate type and edge vegetation is paramount for the maintenance of anuran populations and communities, and changes in these landscapes can drastically alter metacommunity organization patterns.

It is worth highlighting that the current habitat structure reflects a long process of suppression of the original forests of this region, leading to a lower vertical stratification (Silva et al. 2012; Pirani et al. 2013), lower structural complexity, and lower microhabitat diversity (Silva and Rossa-Feres 2007; Vasconcelos et al. 2009; Silva et al. 2012; Oda et al. 2016, 2017; Figueiredo et al. 2019). This reduced habitat heterogeneity directly influences the composition and abundance of species in the community (Vasconcelos et al. 2009). The landscape change would have resulted in the replacement of the original community by a new one with a predominance of species more tolerant to the matrix (Olden et al. 2004; Bengtsson 2010). For example, the most frequently encountered species, *D. minutus*, *A. catesbeiana* and *P. cuvieri*, are considered generalist and resistant to habitat disturbance (Haddad & Prado 2005; Moraes et al. 2007; Oliveira et al. 2007; Haddad et al. 2013; Both et al. 2014; Ferreira-Silva et al. 2016). Given the generalist nature of most species recorded in the ponds studied and the influence of the turnover component, stochastic processes (e.g. recruitment or random colonization) may be driving the structure of the assemblages in the ponds (Melchior et al. 2017).

Effects of environmental variables on communities

We found that aquatic and spatial variables explained about 40% and 25%, of the variation in species abundance, respectively, and these values are similar to those found in other studies carried out in forest regions of Brazil (Prado and Rossa-Feres 2014; Provete et al. 2014). In our study, among the elements of the surrounding habitat, the percentage of exposed soil and the urbanization rate stood out. Both are landscape elements directly related to the suppression of the Atlantic Forest by agriculture, cattle ranching, or the expansion of urban areas, for example. However, only the variable of exposed soil had a significant effect on the variation in species richness. In this sense, the lack of influence of environmental variables on species abundance may be due to the homogenization of the ponds as a result of the agricultural impact in the region studied, similarly to what was reported by Santos et al. (2007).

Ponds without vegetation on the banks are expected to host a lower diversity of anurans since there are no microhabitats available for some species to establish their vocalization and oviposition sites (Vasconcelos et al. 2009). Indeed, sampled ponds with a greater amount of exposed soil had lower abundances of most species, while the most abundant were

Leptodactylus plaumanni, *Scinax* sp. and *Physalaemus cuvieri*, all generalists (Kwet et al. 2010).

We predicted that water quality should act as a limiting factor for the maintenance of anuran communities, even when habitat is available. Phosphate was the water element with the greatest effect on community structure. Considering that the contamination of water bodies with organic matter leads to phosphate peaks (Cordell et al. 2009; Petzet and Cornel 2013), it is reasonable to assume that the increasing contamination of these ponds has a selective effect on the species of the anuran community. Experiments investigating the effect of phosphate on tadpoles found that the effects are widely idiosyncratic, with some species showing increased survival, others showing decreased survival (Hamer et al. 2004), and others being unaffected (Hamer et al. 2004; Smith 2007; Earl and Whiteman 2010). However, this result must be treated with caution as phosphate is correlated with other spatial factors, making it difficult to attribute a causal effect of water parameters in community structure. Ponds with the highest phosphate levels (ponds 1, 2, 3, 4 and 5) were also the ponds with the highest levels of COD and total coliforms. This is because these five ponds receive the largest amount of organic matter (effluent from livestock) (Preuss et al. 2020). Artificial ponds are known to be an important element in increasing anuran diversity in degraded landscapes (Caballero-Díaz et al. 2020; Valdez et al. 2021). Therefore, our results highlight that the contamination of water bodies by wastewater can be a threat to anuran communities.

Conclusion

Our results indicate that turnover was the component explaining most of the variation in beta diversity in our sample, suggesting that while some species disappear in some conditions, others seem to thrive. Therefore, while the viability of some anuran populations in agricultural mosaics may be threatened, others do not seem to be affected. Nonetheless, amphibians are known to be sensitive to habitat changes and pollution (Blaustein et al. 1994; Sievers et al. 2018, b), and the presence of phosphate in the aquatic environment may further reduce survival when it occurs in combination with other pollutants (Relyea 2009). Furthermore, a subsequent study carried out in the same ponds as the present study showed that amphibians in ponds with swine slurry have higher infection loads by the pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*) and more bacteria that facilitate chytrid infection when compared to amphibians in ponds without swine slurry (Preuss et al. 2020). So, our results should

be interpreted with caution as they may not tell the whole story; sub-lethal effects may be at play, and these may only be detected with increased and long-term monitoring. Despite that, we emphasize that artificial ponds with adequate management (i.e. presence of low vegetation around the ponds, absence of fish, and no dumping of large amounts of organic matter) can be a refuge for amphibians in a scenario of loss of natural reproductive sites.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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