
ASSOCIATION BETWEEN LAND USE AND COMPOSITION OF AMPHIBIAN SPECIES IN TEMPERATE BRAZILIAN FOREST HABITATS

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Abstract.—We evaluated the influence of landscape composition on the diversity of anurans in an Atlantic Forest habitat in southern Brazil. As natural habitat provides better conditions for the survival of amphibians, we expected to find more diverse communities in areas with greater forest cover. We sampled tadpoles in 25 waterbodies distributed in seven forest areas. We recorded 22 anuran species and richness varied from six to 12 species per area. Most of the recorded species were not forest specialists, except for Forest Treefrog (*Boana curupi*) and Schmidt's Spinythumb Frog (*Crossodactylus schmidtii*). There was a significant overlap in the species composition among all waterbodies, and the Generalized Linear Mixed Model indicated that landscape configuration did not strongly affect species richness; however, land use drives the dissimilarity in the composition of the communities among waterbodies. Our main results show that forests and livestock farming influence changes in species assemblages among habitats. We reinforce the need for future studies incorporating temporal scale and a variety of spatial scales to assess landscape effects on species composition.

Key Words.—conservation; frog communities; landscape; tadpoles

INTRODUCTION

The increase of the human population generates demands to use larger areas for agriculture and livestock farming, as well as construct more roads and buildings, which leads to increased consumption of natural resources. Consequently, humans promote a variety of landscape modifications (Gururaja et al. 2008; Zhou et al. 2017). When roads, buildings or other urban facilities replace natural habitat, many ecological interactions can change, such as predation, competition, and host/parasite relationships (Nomura et al. 2011; Laufer et al. 2015; Preuss et al. 2020; Santos et al. 2020a). These changes can vary according to the intensity in which habitat is lost and air, soil, and water are polluted (Riley et al. 2005; Brand et al. 2010). One of the most studied negative effects of agriculture on wildlife is its role as a source of contamination by pesticides and herbicides (Koumaris and Fahrig 2016). When a forest is replaced by agriculture or cattle pasture, in addition to the aforementioned issues, habitat complexity and

landscape heterogeneity decline (Machado et al. 2012; Saccol et al. 2017), which leads to a gradual reduction in species diversity (McKinney 2008; Barrows and Allen 2010). The intensification of human activity leads to the expansion of the urban areas, which become closer to natural habitats, causing a series of indirect (and less studied) impacts on fauna, such as light pollution (Dias et al. 2019), noise pollution (Pellet et al. 2004), and road kills (Diniz and Brito 2015). In sum, the consequences of human occupation listed above highlight the relevance of continued monitoring of biodiversity.

Landscape evaluation is a powerful tool to assess the risks of land use on biodiversity, and, consequently, supports environmental management. At the species level, landscape configuration affects fauna persistence (Fahrig and Nuttle 2005), which is a baseline for testing models of metapopulation and metacommunities. In general, species with low dispersal ability, such as amphibians, are more responsive to landscape changes (Schmutzer et al. 2008; Dixo and Metzger 2010; Diniz and Brito 2013; Cayuela et al. 2015). Most amphibians

breed in aquatic sites, and changes in landscapes can restrain access to ponds or streams (Becker et al. 2007, 2010; Machado et al. 2012; Cayuela et al. 2015; Saccol et al. 2017; Dalmolin et al. 2019). This can promote morphological and physiological changes in tadpoles and adults (Costa et al. 2017). In addition, reduced reproductive potential can cause changes in community structure and composition (Berriozabal-Islas et al. 2018; Dalmolin et al. 2020), as well as population declines or local extinctions (Marsh and Trenham 2001; Rothermel 2004; Goutte et al. 2013). Therefore, amphibians are good model organisms for understanding the impact of landscape changes on physiology, morphology (Costa et al. 2017; Berriozabal-Islas et al. 2018), and species diversity (Becker et al. 2007; Pillsbury and Miller 2008; Nomura et al. 2011; Collins and Fahrig 2017).

The Brazilian Atlantic Forest, a biodiversity hotspot (Myers 2000; Mittermeier et al. 2005), is highly fragmented. More than 97% of its fragments are < 250 ha (Ribeiro et al. 2009; Zanella et al. 2012). Nonetheless, the Atlantic Forest harbors high anuran richness and endemism (Haddad et al. 2013). In the southern Atlantic Forest, most of the original forest areas have been replaced by agriculture, pasture, silviculture, and urban areas (Ribeiro et al. 2011). Studies on amphibians in this region have found positive associations between species diversity and characteristics of habitat heterogeneity (Gonçalves et al. 2015; Knauth et al. 2018; Figueiredo et al. 2019), but few analyses encompass sufficiently wide

spatial scales to consider the effects of the landscape on species composition. Landscape analyses allow the detection of changes in land use and human occupation at scales compatible with the distribution of species or groups in question (Hamer and Parris 2011), and thus can help define local and regional conservation strategies.

Many studies have focused on the role of size and connectivity of forest fragments on species diversity; however, less attention is given to the role of surrounding environments generated by human occupation. Despite the negative effect of habitat modification, mosaic-like habitats often exhibit high environmental complexity, offering a variety of resources and physical conditions that may favor increased species richness (Connell, 1978; Shea et al. 2004). We evaluated the influence of the composition of the surrounding landscape on the diversity of waterbodies used by anurans as breeding sites in forest habitat of southern Brazil.

MATERIALS AND METHODS

Study area.—We conducted this study in an Atlantic Forest habitat in southern Brazil (Fig. 1; Supplemental Information Table S1). The sampled area consisted of mixed ombrophilous forest and seasonal forest with a variety of surrounding matrices including livestock pastures, agriculture, silviculture, and urban areas (Ribeiro et al. 2009; Pillar and Vélez 2010;

FIGURE 1. Study sites in southern Brazil. Satellite images (from <https://earthexplorer.usgs.gov>) 1–7 show details of the sampled areas in scale of 1:30,000 m: 1 = Parque Estadual de Vila Velha, Ponta Grossa/PR; 2 = Parque Estadual Rio Guarani, Três Barras/PR; 3 = Reserva Privada Enele, São Lourenço do Oeste/SC; 4 = Parque Estadual das Araucárias, São Domingos/SC; 5 = Reserva Privada Quebra-Queixo, São Domingos/SC; 6 = Parque Estadual Fritz Plaumann, Concórdia/SC; 7 = Parque Estadual do Turvo, Derrubadas/RS.

sosmatatlantica.org.br). The climate is subtropical, with annual air temperatures varying from 16° C to 24° C and rainfall varies from 1,600–2,200 mm annually (Alvares et al. 2013). We selected forested areas for anuran sampling based on the following criteria: (1) presence of well-preserved forest (areas protected by law); (2) similar climatic conditions; (3) elevation between 300 m and 900 m above sea level; (4) similar topography; and (5) presence of lentic and lotic waterbodies used as breeding sites by anurans. We selected seven forest areas between the coordinates 22°30' to 33°45' S (latitude) and 48°02' to 57°40' W (longitude), where we sampled tadpoles in the waterbodies. We sampled at least one lentic and one lotic waterbody in each one of the seven areas to assess a wide variety of habitats and tadpole communities (Melo et al. 2017). We caught tadpoles in one to six waterbodies per area (total n = 25: 11 lentic, 14 lotic waterbodies; Supplemental Information Table S1). In lentic waterbodies, we performed time-limited sampling (1 h) that allowed us to cover a mean area of 386.45 ± 307.39 (standard deviation) m². In lotic waterbodies, we sampled 100-m-long sections for 1 h and the mean stream width was $1.76 \text{ m} \pm 0.79$ (range, 0.60–3.50 m). The mean depth of the lentic waterbodies was $0.8 \text{ m} \pm 0.40$ (range, 0.30–1.50 m) and of lotic waterbodies was 0.45 ± 0.12 (range, 0.15–0.70 m; Supplemental Information Table S1).

Tadpole sampling.—We sampled tadpoles from October 2018 to March 2019, which corresponds to the peak of the anuran breeding season in southern Brazil and is the most favorable period for detection of tadpoles (Both et al. 2008; Santos et al. 2008). The whole region presents a subtropical climate regime with a relatively cold and harsh winter for tropical anurans, which dramatically reduces their activity. For this reason, most species reproduce during summer when almost all species can be detected, both for adults and tadpoles (Preuss et al. 2020; Santos et al. 2020b). As the waterbodies have a wide range of geographical distribution, covering an area of about 10,500,000 ha, we were able to sample each one just once. We performed tadpole sampling from 0800–1800 using a 3-mm²-mesh dip-net (Heyer 1976). We systematized sweepings that consisted of scouring the margins of the pond (Vasconcelos and Rossa-Feres 2005; Santos et al. 2007; Both et al. 2009; Bolzan et al. 2016). In the lotic waterbodies, we also used small dip nets to sample narrow spaces between rocks (adapted from Jordani et al. 2017). Each sample consisted of 1 h of sweeping efforts through the greatest possible variety of microhabitats.

Immediately after capture, we euthanized tadpoles by immersion in a solution of 2% lidocaine, following Brazilian Regulations (Conselho Nacional para o

Controle de Experimentação Animal 2018), and subsequently transferred tadpoles to absolute ethanol. In the laboratory, we identified tadpole species with the aid of a stereomicroscope and identification keys (Machado and Maltchik 2007; Gonçalves 2014). We classified species as habitat specialists or generalists according to the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN; 2021). We considered habitat specialists as those species that are more dependent on forest habitats and have a smaller distribution area than generalists and generalists as those that are less dependent on forest habitats and have a larger geographical distribution area than specialists.

Landscape assessment.—We assessed land use based on the analysis of satellite images (Landsat 8 multispectral images, sensor Operational Land Imager from the U.S. Geological Survey; <https://earthexplorer.usgs.gov>). We classified the images from their vectorization in the software ArcGIS version 10.3 (Esri, Redlands, California, USA), considering a 500-m-radius buffer for each sampled waterbody. We defined buffer size by the estimated size of habitats used by anurans (Semlitsch and Bodie 2003; Smith and Green 2005; Tozetti and Toledo 2005; Canessa and Parris 2013; Marques et al. 2018). We used images captured in the year of sampling (2019) and which had minimal cloud cover without significant radiometric noise. We performed the following stages of image preprocessing: (1) geometric corrections due to the inherent geometric distortions in images collected in distinct moments, by georeferencing these images; (2) atmospheric corrections aiming to reduce the interference of atmospheric scattering on the images (Soares et al. 2015); and (3) mosaicking (converting overlapping images into a single one) and contrast stretching of the different images obtained on different dates, aiming to reduce seasonal effects on the visual aspect of the image. We used the software ENVI, version 5.51 (L3Harris Geospatial, Boulder, Colorado, USA) for pre-processing. After the pre-processing stages, we defined the categories of land use and occupation with adjustments based on field observations. We identified the following categories (landscape variables) of land use: (1) Agriculture (cultivated areas, with soybean, corn, or wheat); (2) Aquatic environments (streams, artificial and natural ponds); (3) Forest (native forest formations in intermittent and advanced successional process); (4) Livestock pastures (extensive livestock farming); and (5) Urban area (buildings). We projected the polygons of each cover type with the reference system SIRGAS 2000, Universal Transverse Mercator (UTM) projection, zone 22S, and calculated areas in square kilometers (km²).

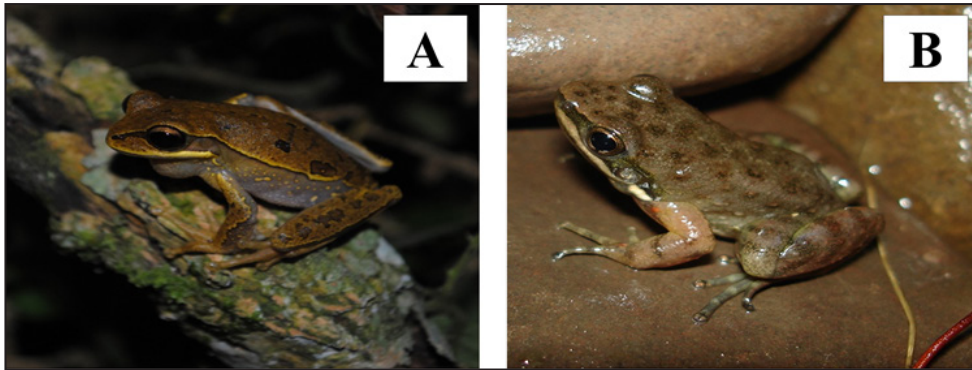


FIGURE 2. Two species found only in forest habitat waterbodies (breeding sites) of Atlantic Forest in southern Brazil. (A) Forest Treefrog (*Boana curupi*) and (B) Schmidt's Spinythumb Frog (*Crossodactylus schmidti*). (Photographed by Elaine Maria Lucas).

Data analysis.—We compared species richness based on rarefaction curves (interpolation and extrapolation method) representing standardized measures of individual abundance (Chao and Jost 2012). We calculated confidence intervals (95%) associated with the curves using the Bootstrap method (50 randomizations). For this analysis, we used the iNEXT program (iNterpolation and Extrapolation; http://chao.stat.nthu.edu.tw/wordpress/software_download/ 2016).

We tested the influence of landscape variables (Supplemental Information Table S3) on species richness using Generalized Linear Mixed-effects Models (GLMMs). We made the rarefaction and extrapolation analysis of species richness using the iNEXT program (iNterpolation and Extrapolation; http://chao.stat.nthu.edu.tw/wordpress/software_download/ 2016). We included waterbodies as a random variable. We evaluated the significance of each explanatory variable for species richness using the ANOVA function. We analyzed all the full models using the glm function of the lme4 package (Bates et al. 2015), in R v.3.6.0 (R Core Team 2019). We assessed the differences in species composition between the 25 waterbodies (β -diversity) and the relationship with landscape variables by using Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations (Borcard et al. 2011; Magurran and McGill 2011). PERMANOVA (which is widely used in studies focused on the beta diversity patterns) is a geometric partitioning of multivariate variation in the space of a chosen dissimilarity measure according to a given ANOVA design, this procedure uses free permutation techniques with appropriate distribution to obtain *P*-values (Anderson 2017). We measured the beta diversity by using the Bray-Curtis dissimilarity, which is appropriate for abundance data. In the PERMANOVA, we used the β diversity value as a response variable and the landscape descriptors as predictor variables. Additionally, we used a Non-Metric Multidimensional Scaling (NMDS)

to visualize and interpret the differences in species composition between waterbodies. We performed the PERMANOVA and NMDS, respectively, by using the adonis and metaMDS functions of the vegan package in R v.3.6.0 (R Core Team 2019). For analysis using landscape variables on abundance data, we used 25 waterbodies to avoid overlapping buffers used to assess land use (see Supplemental Information Table S3). We used as exclusion criterion the maximum overlap of up to 40% between two buffers (see Supplemental Information Table S4).

RESULTS

We recorded 22 anuran species belonging to eight families: Bufonidae (two species; 9.1% of the total), Hylidae (12; 54.5%), Hylodidae (one; 4.5%), Leptodactylidae (three; 13.6%), Microhylidae (one; 4.5%), Odontophrynidae (one; 4.5%), Phyllomedusidae (one; 4.5%) and Ranidae (one; 4.5%), which was the non-native American Bullfrog, *Lithobates catesbeianus* (Table 1). Generalist species were numerically dominant in terms of habitat use, showing wide geographic distribution, except the Forest Treefrog (*Boana curupi*) and Schmidt's Spinythumb Frog (*Crossodactylus schmidti*), which are forest-related species (IUCN 2021; Fig. 2). We recorded that species

TABLE 1. Results of the Generalized Linear Mixed-Effect Models (GLMM), with the function glm for amphibian richness and 500-m-buffer landscape variables in 25 waterbodies (breeding sites) of Atlantic Forest habitats in southern Brazil, recorded from October 2018 to March 2019.

Variable	df	<i>F</i>	<i>P</i> -value
Forest	1, 19	0.14	0.704
Agriculture	1, 19	0.17	0.677
Livestock farming	1, 19	0.22	0.640
Urban area	1, 19	0.04	0.841
Aquatic environment	1, 19	1.15	0.296

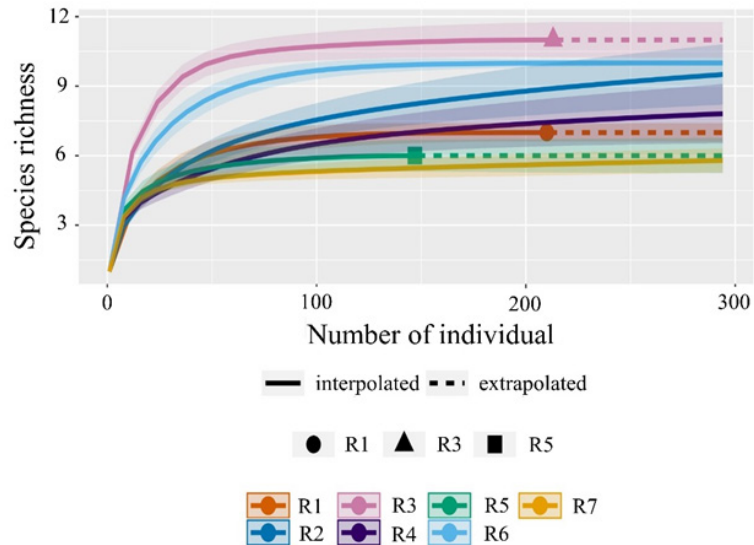


FIGURE 3. Comparison of the richness of anuran species in seven Atlantic Forest sites in southern Brazil through rarefaction (interpolation, solid lines, and extrapolation, dotted lines for ● R1, ▲ R3, and ■ R5) based on the number of individuals of tadpoles in waterbodies. The acronym R1 (orange) = Parque Estadual de Vila Velha; R2 (navy blue) = Parque Estadual Rio Guarani; R3 (lilac) = Reserva Privada Enele; R4 (purple) = Parque Estadual das Araucárias; R5 (green) = Reserva Privada Quebra-Queixo; R6 (sky blue) = Parque Estadual Fritz Plaumann; R7 (yellow) = Parque Estadual do Turvo.

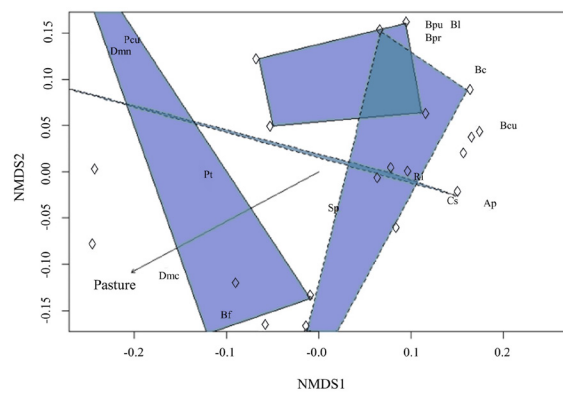


FIGURE 4. Non-metric Multidimensional Scaling (NMDS) based on Bray-Curtis distances showing the association between landscapes classes and composition dissimilarity (beta diversity) in 25 waterbodies. The shapes shown in blue connect the points representing different landscapes classes. The symbols (◇) represent the sampled waterbodies. The amphibian species are: Ap = Green Treefrog (*Aplastodiscus perviridis*); Bc = Forest Treefrog (*Boana curupi*); Bcu = *Boana* cf. *curupi*; Bf = Gladiator Treefrog (*Boana faber*); Bl = Striped Treefrog (*Boana leptolineata*); Bpr = Burnmeister’s Treefrog (*Boana prasina*); Bpu = Montevideo Treefrog (*Boana pulchella*); Cs = Schmidt’s Spinythumb Frog (*Crossodactylus schmidti*); Dmc = Nova Friburgo Treefrog (*Dendropsophus microps*); Dmn = Swamp Treefrog (*Dendropsophus minutus*); Eb = Two-colored Oval Frog (*Elachistocleis bicolor*); Lc = American Bullfrog (*Lithobates catesbeianus*); Li = Criolla Frog (*Leptodactylus latrans*); Pa = Avelino’s Smooth Horned Frog (*Proceratophrys avelinoi*); Pca = *Physalaemus* cf. *carrizorum*; Pcu = Barker Frog (*Physalaemus cuvieri*); Pt = Monkey Treefrog (*Phyllomedusa tetraploidea*); Rh = Striped Toad (*Rhinella henseli*); Ri = Cururu Toad (*Rhinella icterica*); Sf = Snouted Treefrog (*Scinax fuscovarius*); Sg = Granulated Snouted Treefrog (*Scinax granulatus*); Sp = Perereca Snouted Treefrog (*Scinax perereca*).

composition was dominated by habitat generalists, including Gladiator Treefrog (*Boana faber*), Swamp Treefrog (*Dendropsophus minutus*), American Bullfrog (*Lithobates catesbeianus*), *Physalaemus* cf. *carrizorum*, Barker Frog (*Physalaemus cuvieri*), and Snouted Treefrog (*Scinax fuscovarius*). Interpolation and extrapolation curves showed that species richness ranged from six to 12 among sites (Fig. 3). Landscape use did not affect species richness (Table S2), with the largest amount of richness (88%) explained by a random effect ($R^2_m = 0.06$; $R^2_c = 0.88$).

The dominant classes of land use were forests and livestock farming (Supplemental Information Table S2). Forests and livestock farming were the main landscape components that explained the patterns of compositional dissimilarity (beta diversity) among waterbodies (forest, $r^2 = 0.07$, $F_{1,24} = 1.77$, $P = 0.032$ livestock farming, $r^2 = 0.07$, $F_{1,24} = 2.01$, $P = 0.010$; see Table 2, Fig. 4).

DISCUSSION

We recorded 22 anuran species, which correspond to approximately two-thirds of the richness found in similar forest remnants in southern Brazil (Lucas and Fortes 2008; Iop et al. 2012; Bastiani and Lucas 2013). Hylidae comprised over half of species, most of which are considered generalists and found in both forest environments and grasslands or forest edges (Lucas and Fortes 2008; Almeida-Gomes and Rocha 2014; Barbosa et al. 2014; Oliveira et al. 2017). The lack of any strong association between tadpole species richness and land use suggests that frogs are not sensitive to the

TABLE 2. Results of PERMANOVA showing the contribution of landscape variables to the dissimilarity patterns in amphibian composition in the set of waterbodies (breeding sites) of Atlantic Forest habitats in southern Brazil. Asterisks (*) indicate significant *P* values. The abbreviation SS = sum of squares.

Variable	df	SS	<i>F</i>	<i>P</i> -value	<i>r</i> ²
Forest	1	0.72	1.76	0.032*	0.07
Agriculture	1	0.48	1.18	0.281	0.04
Livestock farming	1	0.81	2.01	0.010*	0.07
Urban area	1	0.49	1.21	0.182	0.04
Aquatic environment	1	0.30	0.74	0.868	0.03
Residuals	19	7.73			0.73
Total	24	10.54			1.00

habitat components we measured. This result must be viewed with caution, however, because breeding site configuration, such as pond characteristics (e.g., depth, substrate, and aquatic vegetation), may play a bigger role than land use in determining tadpole species diversity (Dalmolin et al. 2020). We also must consider the differences among species regarding their breeding season. Species with a shorter reproductive season will be more difficult to detect, and thus demand high sampling effort. We assume that under-detection of such species did not influence our results, but we encourage future studies with a higher number of samples per site or an all-year sampling protocol to test the assumption.

Several studies have shown that microhabitat characteristics affect amphibian richness (D’Anunção et al. 2013; Knauth et al. 2018; Figueiredo et al. 2019; Almeida et al. 2020). Forest heterogeneity, leaf litter depth, canopy cover and presence of clearings are examples of local features that are not detectable at a landscape level but affect anuran species composition (Provete et al. 2014; Ferrante et al. 2017; Howell et al. 2019). Most local elements of the habitats support species persistence by providing fundamental resources as well as shelter (Erős et al. 2014; Landeiro et al. 2014; Datry et al. 2016; Collins and Fahrig 2017). This idea is reinforced by the fact that we found Forest Treefrog (*B. curupi*) and Schmidt’s Spinythumb Frog (*C. schmidti*) only where local characteristics, such as lotic waterbodies with a rocky bottom, were present (Bastiani et al. 2012; Bastiani and Lucas 2013; Caldart et al. 2013).

The importance of fine-scale habitat features does not minimize the relevance of landscape properties, such as the amount of available habitat, for the colonization and persistence of species (Faggioni et al. 2021). Seasonal movements by frogs (e.g., to mate and lay eggs) involve many risks, and landscape changes could negatively affect them, causing a strong impact on reproductive cycles (Becker et al. 2010). Thus, we

strongly recommend new landscape studies at multiple scales that consider different levels of environmental integrity.

The predominance of habitat generalists and widely distributed species (IUCN 2021) has already been documented in other forest habitats in this portion of the Atlantic Forest (Lucas and Fortes 2008; Lucas and Marocco 2011; Bastiani and Lucas 2013). Deforestation of the Atlantic Forest may favor generalist species that are adapted to open conditions, and they may replace specialized species adapted to the forest (Haddad and Prado 2005). Homogenization of biota (Ferrante et al. 2017; Nowakowski et al. 2018) could explain the lack of relationship between species composition and landscape properties that we recorded.

We highlight the fact that, in the whole sampled area, we found only two forest specialist species. We have no information about the species composition in the forest habitat we studied in past decades. Thus, we cannot determine whether we are showing a recent or a well-established scenario about the regional anuran species composition. Forest-related species tend to be more prone to population decline due to their low ability to migrate across areas where the canopy cover is absent (Howell et al. 2019). The conversion of forest to pasture, which occurred decades ago, could have contributed to the local extinction of other forest-related anuran species. These habitat changes also favor the colonization by species such as the Gladiator Treefrog (*B. faber*) and Swamp Treefrog (*D. minutus*; Aquino et al. 2004, 2010; Scott et al. 2004; Lavilla et al. 2010; Silvano et al. 2010). These species are often found in fragmented landscapes and expanding open areas (Preuss 2018; Figueiredo et al. 2019; Menin et al. 2019). We also recorded the non-native American Bullfrog (*L. catesbeianus*) in four of the seven forested areas. This species is widely distributed and well established in altered environments of the south region of Brazil (Both et al. 2011; Madalozzo et al. 2016). The process of dispersion and colonization of new localities is possibly expanding (Santos-Pereira and Rocha 2015) together with anthropogenic changes. Little is known about the persistence of populations of *L. catesbeianus* in altered environments, so this is an important subject for future studies.

The presence of livestock pasture (farming) and forests were the landscape components that best explained the dissimilarity in species composition. The role of forests and pastures in shaping amphibian species composition is relatively well understood (Haddad et al. 2013; Howell et al. 2019). At the same time, the conversion of forests into areas of pasture, agriculture, or urbanization, may limit or prevent the permanence of forest-associated species. In this sense, the composition of amphibian communities in remaining natural areas

may change over time as a result of the colonization or permanence of generalist species (Ferrante et al. 2017). Future studies that examine past and present species composition and the role of changes in landscape and surrounding matrices in past decades in shaping current species assemblages would be beneficial.

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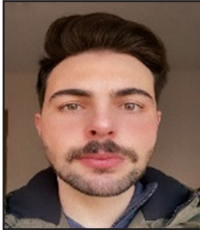
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