

## Article

## Anuran assemblage changes along small-scale phytophysiognomies in natural Brazilian grasslands

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**ABSTRACT.** We studied the species composition of frogs in two phytophysiognomies within Pampa biome (grassland and forest) of a Ramsar site in southern Brazil to assess the distribution of species and dissimilarities in community composition on a small spatial scale. We tested the hypothesis that the vegetation structure and the types of land cover present in each physiognomy influence species distribution and the compositional dissimilarity patterns between locations. We sampled individuals using pitfall traps and active search in the areas around the traps. We evaluated the existence of these differences by using permutational multivariate analysis of variance and multivariate dispersion. We found that the compositional dissimilarity was higher between the sampling sites from different phytophysiognomies than within the same phytophysiognomy. Also, the difference in anuran species composition between the sampling sites within the forest was considerably high. These differences were mainly due to the type of land cover present in each sampled site. Based on our results, we could assume that the phytophysiognomies evaluated here offer quite different colonization opportunities for anurans, especially those related to microhabitat characteristics, such as microclimate variables. Still, the presence of different types of land cover seems to be a decisive factor for the maintenance of some anuran species, since these can serve as an important source for obtaining food resources, in addition to facilitating the dispersion of individuals within and between locals, serve as sites for the regulation of physiological functions and also refuges against predators.

**KEYWORDS.** Beta diversity; Dissimilarity; forest; south Brazil; Taim.

The composition of species in communities is a result of a complex interaction between organisms and environmental characteristics. In general, the presence of a singular species in an assemblage depends on intrinsic (such as the individual's physiological needs for homeostatic maintenance) and extrinsic processes (such as competition, predation and other biotic interactions). Combined, both of them determine the possibility of a given species to colonize a habitat, as well their long-term maintenance in there (SCHLUTER & RICKLEFS, 1993; XIMENEZ *et al.*, 2014). Abiotic factors, such as climate, the complexity of the vegetation structure, the type of soil, the primary productivity and the physical-chemical composition of the water determine the local characteristics of each community. In terms of community structure patterns, several studies indicate that these factors are mainly responsible for the patterns of dissimilarity in species composition between communities (e.g. IOP *et al.*, 2012; DALMOLIN *et al.*, 2019; CERON *et al.*, 2020). Still, it is assumed that heterogeneous habitats comprise a richer biota (SEMLITSCH *et al.*, 2015) since they offer many different microhabitats, which precisely favors the establishment of species without high niche overlap (BARROWS & ALLEN, 2010; OLIVEIRA *et al.*, 2013).

The process of describing and evaluating the habitat structure is one of the challenges for carrying out ecological studies (STEIN & KREFT, 2015). The concept of habitat heterogeneity is related to much confusion, being frequently used as a synonym of habitat complexity. In structural terms, environments can be described by (i) their complexity - vertical development of vegetation - and (ii) their heterogeneity - horizontal variation in descriptors such as density, dominance and frequency of plant species that compose them (AUGUST, 1983). In a review on the topic, TEWS *et al.* (2004) defend the idea that the concept of habitat heterogeneity includes both vertical and horizontal structure of plant community - a concept adopted in the present study. The possibility of assessing the effect of habitat heterogeneity on the structuring of their communities comes up against the huge number of areas never sampled in the Neotropical region (GARCIA & VINCIPROVA, 2003). This fact also has implications for the establishment of conservation strategies for potentially threatened species - as is the case with many Brazilian anurans (SILVANO & SEGALLA, 2005).

The variety of available habitats and the high levels of species endemism throughout the Brazilian biomes makes it an adequate location to assess the role of environmental

heterogeneity in the activity patterns and community structure of anurans (SILVANO & SEGALLA, 2005). However, most studies on anuran ecology in Brazil are concentrated in forest environments, especially in the Cerrado and the Atlantic Forest biomes (DA SILVA *et al.*, 2011a; IOP *et al.*, 2012; PRADO & ROSSA-FERES, 2014; SACCOL *et al.*, 2017). The Pampa grassland formations and the coastal portion of southern Brazil are home to anuran species that are common in open habitats (NÚÑEZ *et al.*, 2004, VASCONCELOS *et al.*, 2019; DALMOLIN *et al.*, 2019). Although the landscape of these environments consists predominantly of open areas (MACHADO *et al.*, 2012), some forest patches can also be observed (such as swamp forests and dry or sandy forests).

The Brazilian coastal plains are formed by sediments from the Quaternary (MARQUES *et al.*, 2015). It is estimated that these sediments originated from climatic and geological events that occurred in the Upper Pleistocene and the Holocene (more than 120 thousand years ago), although the plains are older and formed even during the Quaternary (in around 2.5 million years; PESSENDA *et al.*, 2012). The vegetation associated with this type of formation is typical of the Edaphic Systems of First Occupation and the Wet Dense Forest of *Várzea*, whose establishment occurs on quaternary sediments (MARQUES *et al.*, 2015). The climatic, geological and oceanographic characteristics of the coastal region differ along its length, so that the topography and composition of soils vary widely on small spatial scales (SILVEIRA, 1964). Consequently, landscapes with unique characteristics are formed in each portion of the Brazilian coast, and this has a direct impact on the type of structure and composition of vegetation, forest formations and associated fauna (MARQUES *et al.*, 2015).

The landscapes of the southern the Brazilian coast differ from the landscapes found in the countryside or mountainous areas of the southern states of Brazil. In general, the coastal plains of the southern Brazil is made up of wide sedimentary and sandy plains associated with lakes of different sizes and small sets of mountains in the Serra Geral (SILVEIRA, 1964; GONÇALVES & DOS SANTOS, 1985). It is estimated that historical and contemporary processes have a direct influence on the climate of this region, which is more humid and hotter; still, the association of these characteristics with the changes in the geomorphology of the region promoted successive historical changes in the vegetation of this region (BARTHOLOMEU *et al.*, 2014; MARQUES *et al.*, 2015). Similarly, these same characteristics are expected to have influenced the selection process of anuran species occurring in the coastal region, since only one third of the more than 100 anuran species known to the state of Rio Grande do Sul occurs in the coastal plains (COLOMBO *et al.*, 2008; DALMOLIN *et al.*, 2019; KNAUTH *et al.*, 2019).

Studies that describe changes in amphibian assemblages over structural changes in vegetation cover can contribute to propose scenarios of landscape changes (DA SILVA *et al.*, 2011b). The process of forests expanding over grasslands under climate change or even converting forested areas into human use would reflect changes in the

amphibian composition (MANENTI *et al.*, 2013; OLIVEIRA & ROCHA, 2015). In this sense, our work aimed to: (i) verify the distribution of anuran species on a small spatial scale; (ii) describe the association between the patterns of dissimilarity in anuran composition between communities of different phytophysiognomies within Pampa biome (forest and grassland) and their environmental descriptors (types of land cover; vegetation cover; vegetation height).

The study design on a small spatial scale is interesting to assess adjacent habitats whose probability of colonization is theoretically the same for all species in the region (XIMENEZ *et al.*, 2014). In addition, the habitat elements linked to the micro-habitat scale are important descriptors of the spatial partition of species (OLIVEIRA & ROCHA, 2015) in particular because they deal with transition zones in a refined way (HOFER *et al.*, 2007). The detection of differences in anuran assemblages between habitats provides a strong indication of the segregation process of these species along a vegetation gradient (DA SILVA *et al.*, 2011a; PRADO & ROSSA-FERES, 2014). We expected to find greater differences in composition in places belonging to different phytophysiognomies than between areas belonging to the same phytophysiognomies, since the environmental and microenvironmental conditions must be similar in these areas, thus reducing their composition dissimilarity (DA SILVA *et al.*, 2011a). In addition, we expect vegetation descriptors to be the main drivers of patterns of dissimilarity in the composition of anurans among the sampled sites, since the structure and complexity of vegetation is important for the most diverse aspects of anuran biology (e.g. physiological controls, sources of food resources and refuge; DALMOLIN *et al.*, 2019, 2020).

## MATERIAL AND METHODS

**Study site.** The study was carried out at the Estação Ecológica do Taim (ESEC Taim; S 32°32'16.6", W 052°32'16.7"), located in the municipality of Rio Grande, Brazil's extreme south (Fig. 1). ESEC Taim encompasses ecosystems of great relevance and, since 2017, was recognized as a Ramsar site (Ramsar Wetland of International Importance; RAMSAR, 2018). The landscape is located on the Pampa biome and consists of wetlands and grasslands in association with remnants of "restinga" and flooded forests, which are dominated by cork trees and fig trees (WAECHTER & JARENKOW, 1998).

The climate of the region is humid sub-temperate, with an annual average temperature of 18.1°C and average temperature of the coldest month of 12.7°C. The annual rainfall is 1162 mm, with periods of drought in the spring and a higher incidence of rain in the winter (MALUF, 2000). The maximum temperature varied between 9.1°C and 39.3°C during the study period (May 2011 to April 2012), with the hottest months being February and March 2012; the minimum temperature varied between 0.9°C and 28.1°C, with the coldest months being July and August 2011. Meteorological data were obtained from the database provided by the Meteorological Station of the Universidade Federal do Rio Grande (FURG), located in the municipality of Rio Grande.

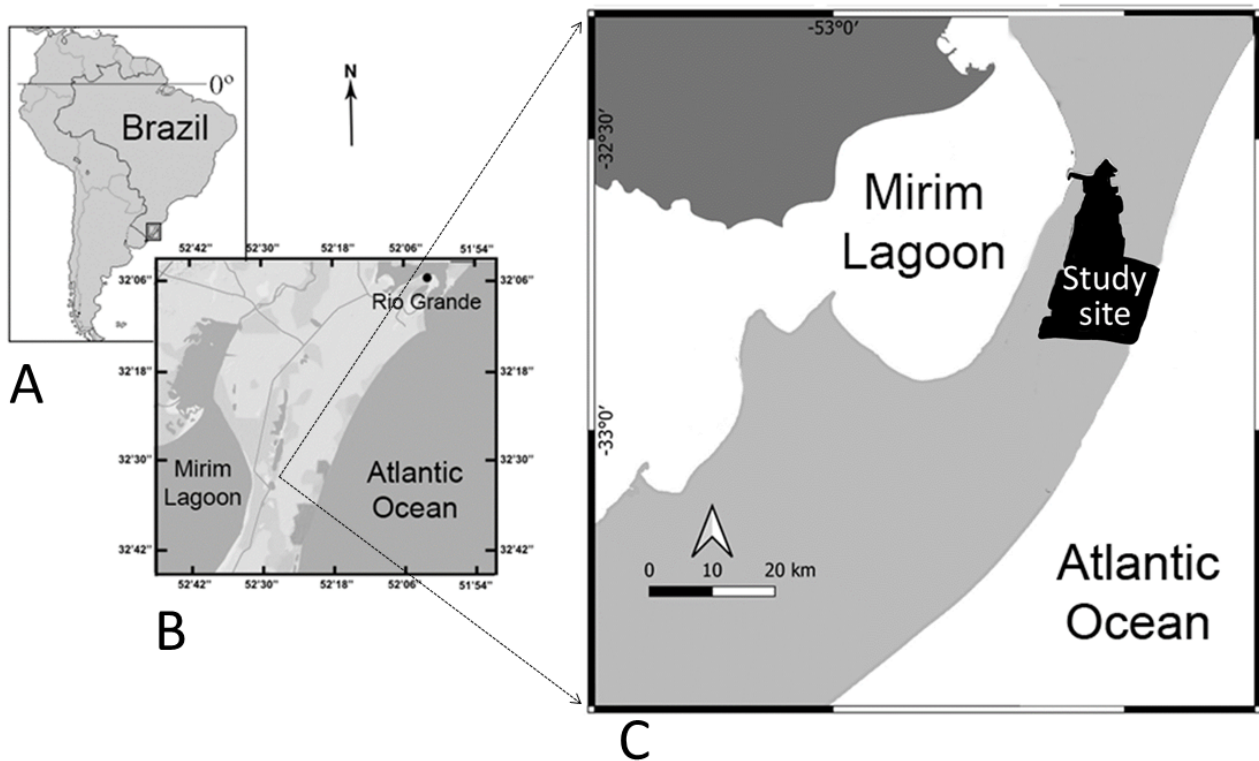


Fig. 1. Geographic location of the study site (C) on the Estação Ecológica do Taim (B) in the state of Rio Grande do Sul (A), Brazil.

**Anuran sampling.** Sampling was carried out in four sampling sites representing the two most remarkable phytophysiognomies of ESEC Taim. The four sampling sites were distributed equally, two in areas of grassland dominance and two in areas of forest dominance (Fig. 2; Supplementary Material Fig. 1). We were able to distinguish the boundary between these two environments precisely even by a visual inspection. This was possible because the forests are distributed in patches merged along the grassland with well-defined boundaries.

Sampling areas were chosen based on vegetation integrity, area with continuous habitat and presence of potential anuran breeding sites. In addition, we considered our accessibility to these areas since many regions of ESEC Taim are permanently flooded, making the displacement of researchers and the installation of pitfall traps not possible. Sampling areas are at least about 800 m from each other. Field campaigns were carried out every two weeks between May 2011 and April 2012. Detailed information about sampling effort was described below. Each campaign comprised four days when all sites were simultaneously sampled. Frogs were sampled by the combination of three methods: (i) pitfall traps with drift fence; (ii) auditory surveys; (iii) visual search.

**Pitfall traps with drift fence (passive sampling).**

We installed sets of buckets arranged in pitfall lines in all the areas of grassland dominance and forest dominance. Grasslands represent the dominant habitat and represents the habitat matrix on entire landscape. Sampled forest are formed by two continuous forest patches with total area of 27 and 22 ha respectively. We installed two lines of buckets

in each both, grassland and forests, resulting in eight lines and 32 buckets (see the Fig. 2 of supplementary material). Pitfalls were arranged following the description of similar studies (e.g. CECHIN & MARTINS, 2000). Each pitfall was formed by four 100-l buckets buried about 13.3 m from each other and connected by a mosquito net (60 cm in height) that served as a guide fence. The guide fence was buried 10 cm into the ground to avoid individuals to transpose the fence (CECHIN & MARTINS, 2000). All buckets had holes at the bottom to prevent them from being flooded by rain.

We maximized the minimum distance of trap lines to reduce the spatial dependence of sampling. None trap line was closer than 0.8 km from other habitat type. Spatial distribution of lines was limited by the low availability of areas free of flooding that could remove the buckets during extensive periods of rain. Considering this the exact point where each pitfall line was installed was defined by a result of a combination between several mandatory criteria that do not permit a random distribution of traps. We grouped the records obtained from each pair of lines of the same sampling point and consider it to be an assemblage of species. Pitfalls remained open during four consecutive days and the process was repeated in intervals of 15 days in a total of 192 hours/open buckets by month. In whole study sampled achieve a total of 2304 hours of open buckets. During the samplings, we carried out daily inspections in the buckets. We identified every captured animal, which was later released about 20 meters from the trap. The collection was carried out with the authorization number 27755-1 from SISBIO.



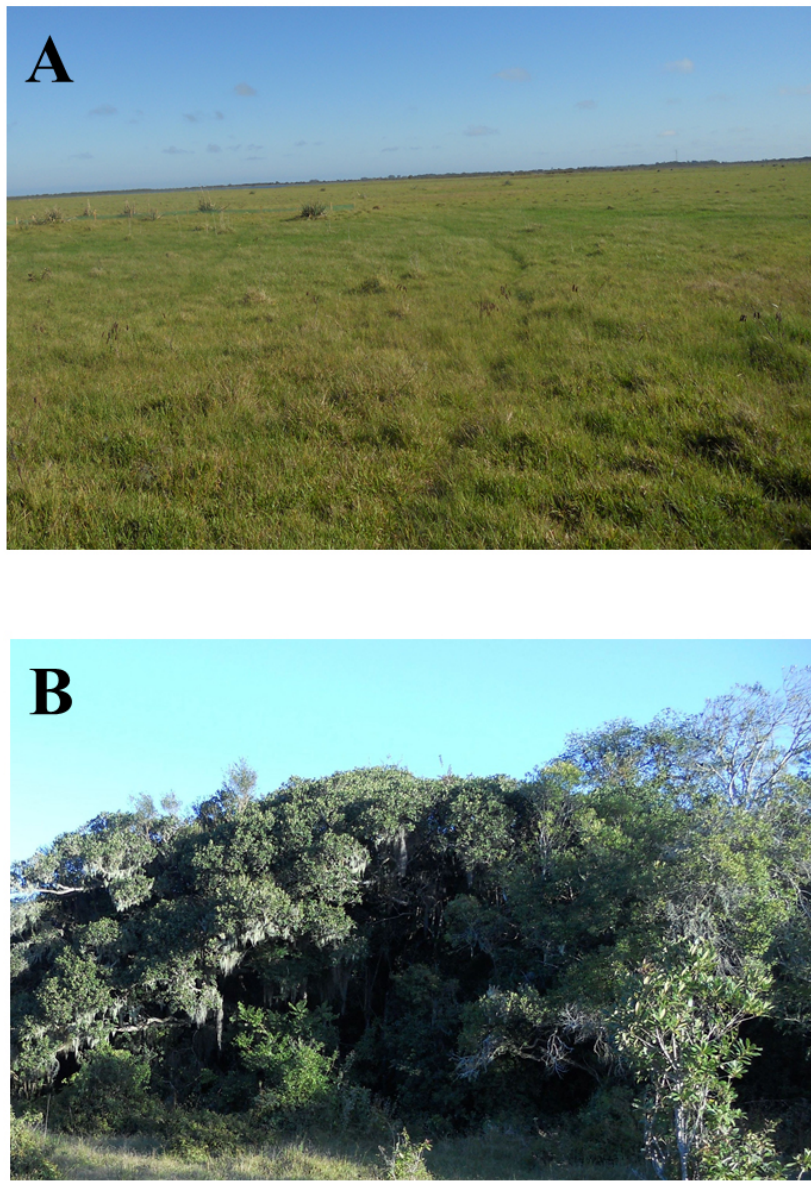


Fig. 2. Phytophysiognomies of ESEC Taim, Rio Grande do Sul, Brazil: (A) sites of grassland dominance and (B) sites of forest dominance.

**Visual search and auditory surveys (active sampling).** Visual search and auditory surveys (HEYER *et al.*, 1994) were performed during the night, starting one hour after sunset. Active sampling was conducted in the vicinity of the pitfall traps. For standardization of sampling effort, we conducted a visual search in an area of about 1 ha around each pitfall line. Based on our previous experience in auditory surveys, we were able to perform a safe species identification of calling males in a maximum area of 5 ha. This was the covered area for calling surveys at each pitfall line. Active sampling was made along four sampling nights and repeated monthly. Sampling started each night in a different environment (grassland or forest), alternately to avoid the same physiognomy to be always sampled at the same time. We applied two hours per person of active sampling. We must highlight that during auditory surveys, we took care to exclude any register that comes from a grassland/forest

interface. By this we avoid to the risks of mismatches in habitat classification of calling males.

**Phytophysiognomy evaluation.** To better characterize the phytophysiognomies of the sampling areas, the vegetation structure was measured through plots (following TOZETTI & MARTINS, 2008). We characterized the vegetation structure in the vicinity of the areas where pitfall traps were installed (see the Fig. 3 of supplementary material). We delimited two plots of 3 m x 10 m, which were distributed perpendicularly in each of the pitfall lines, one of which was placed at the beginning and the other at the end of the line. The following variables of the vegetation were measured in each plot: (i) Types (categories) of land cover - exposed (without any type of cover); cover by grassy vegetation; presence of shrubs; presence of trees; (ii) Vegetation cover (percentual); (iii) Vegetation height (centimeters).

**Statistical analysis.** We evaluated differences in the anuran composition in the areas within and between habitat types by using permutational multivariate analysis of variance (PERMANOVA) and multivariate dispersion (BETADISPER). PERMANOVA is an analysis of variance that accounts for the dissimilarity between different data matrices. This analysis is analogous to MANOVA (multivariate analysis of variance), but is differentiated by the incorporation of permutation algorithms (MCARDLE & ANDERSON, 2001; ANDERSON, 2001). In addition, PERMANOVA is considered a robust alternative for analysis of variance using distance data, since it allows the inclusion of matrices with multiple response variables and predictor variables (which is the case in this study). The composition dissimilarity matrix between communities was obtained through the presence and absence data of each specie in each transect. In PERMANOVA, we used the composition dissimilarity matrix as the response variable, and the environmental descriptors of each sample unit were used as predictor variables. We used the Jaccard index as a dissimilarity measure and performed 9999 permutations.

We use multivariate dispersion (BETADISPER) to visualize the patterns of beta diversity in our dataset. This analysis is commonly incorporated into studies that assess

beta diversity patterns, as its tests the homogeneity of the data distribution (in our case the presence and absence of species in the sample units) in a multivariate space (ANDERSON, 2006). For this, non-Euclidean distances between objects and group centroids are handled by reducing the original distances to principal coordinates. Finally, we used a Similarity Percentages analysis (SIMPER) we used an analysis to discriminate which species were most associated with each type of land cover. PERMANOVA, BETADISPER and SIMPER were run using the “adonis”, “betadisper” and “simper” functions in the R package *vegan* (OKSANEN *et al.*, 2017).

## RESULTS

We recorded 13 species of six families in both phytophysiognomies (Fig. 3; Tab. I). Leptodactylidae and Hylidae were the most representative, with six and four species respectively. The hylid *Boana pulchella* (Duméril & Bibron, 1841) occurred exclusively in grasslands and *Scinax squalirostris* (Lutz, 1925) occurred exclusively in forests. The number of recorded species varied during the sampling period, with the largest number of species recorded in May (12 species), September and November (11 species) in both phytophysiognomies.

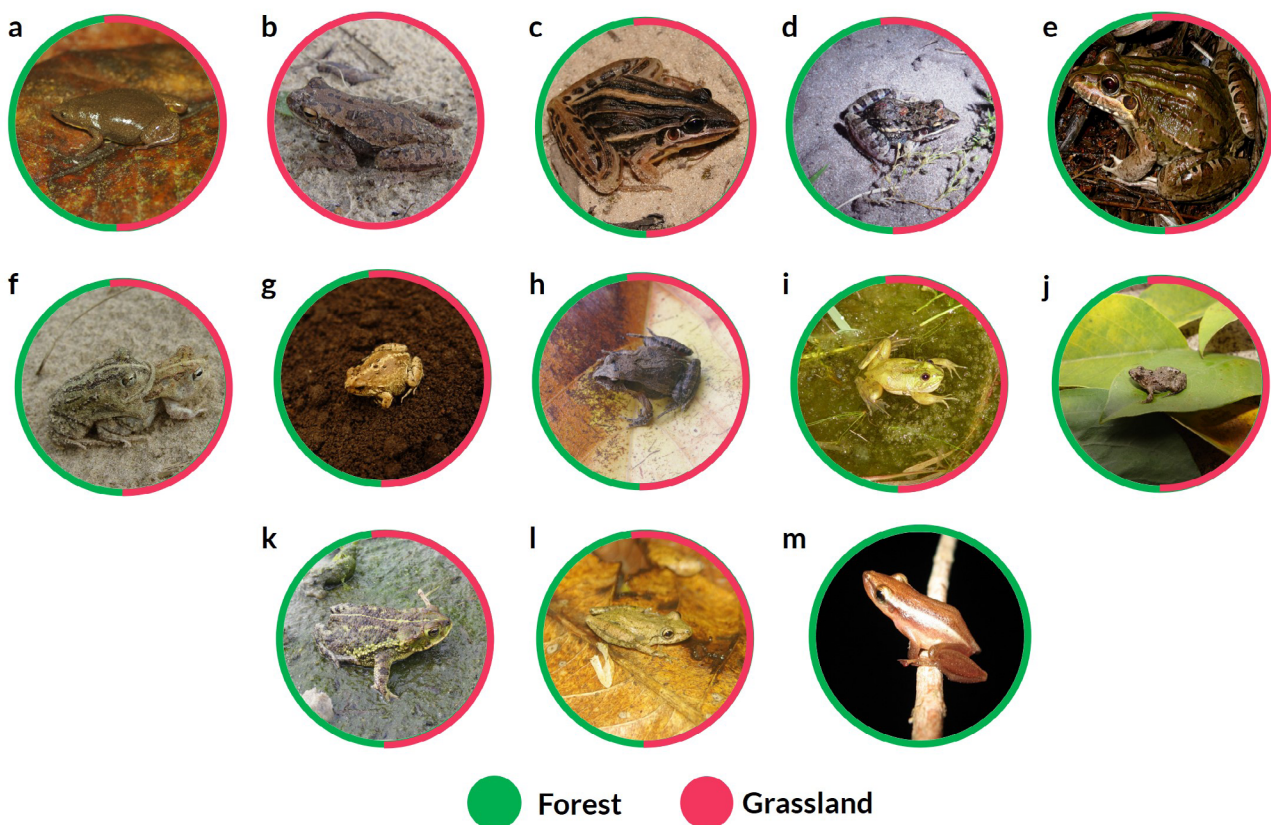


Fig. 3. Anuran species found in two phytophysiognomy types of Estação Ecológica do Taim, southern Brazil, between May 2011 and April 2012. The pink, green and mixed circles (green and pink) indicate the species that were recorded, respectively, in grassland areas, forest areas, and in both areas. (a) *Elachistocleis bicolor* (Guérin-Méneville, 1838); (b) *Boana pulchella* (Duméril & Bibron, 1841); (c) *Leptodactylus gracilis* (Duméril & Bibron, 1840); (d) *Leptodactylus latinasus* (Jiménez de la Espada, 1875); (e) *Leptodactylus luctator* (Hudson, 1892); (f) *Odontophrynus maisuma* (Reinhardt & Lütken, 1862); (g) *Physalaemus biligonigerus* (Cope, 1861); (h) *Physalaemus gracilis* (Boulenger, 1883); (i) *Pseudis minuta* (Günther, 1858); (j) *Pseudopaludicola falcipes* (Hensel, 1867); (k) *Rhinella dorbignyi* (Duméril & Bibron, 1841); (l) *Scinax granulatus* (Peters, 1871); (m) *Scinax squalirostris* (Lutz, 1925).





Tab. III. Effects environmental descriptors on patterns of compositional dissimilarity between phytophysiognomies of Estação Ecológica do Taim, southern Brazil accounted by PerMANOVA. Bold values represent statistically significant effect values.

Environmental descriptors	Sum of squares	R <sup>2</sup>	F	<i>p</i>
Types of land cover	0.27	0.56	2.23	<b>0.04</b>
Vegetation cover	0.06	0.13	1.61	0.24
Vegetation height	0.07	0.14	1.66	0.23

Tab. IV. Cumulative contributions of most influential species in each type of land cover at Estação Ecológica do Taim, southern Brazil accounted by SIMPER.

Types of land cover	Species	Cumulative contributions
Exposed	<i>Physalaemus biligonigerus</i>	0.21
	<i>Rhinella fernandezae</i>	0.42
	<i>Scinax granulatus</i>	0.62
	<i>Pseudopaludicola falcipes</i>	0.81
	<i>Boana pulchella</i>	0.20
Cover by grassy vegetation	<i>Leptodactylus latinasus</i>	0.39
	<i>Pseudis minuta</i>	0.59
	<i>Physalaemus biligonigerus</i>	0.70
	<i>Boana pulchella</i>	0.25
Presence of shrubs	<i>Physalaemus biligonigerus</i>	0.38
	<i>Elachistocleis bicolor</i>	0.51
	<i>Pseudopaludicola falcipes</i>	0.63
	<i>Rhinella fernandezae</i>	0.75
Presence of trees	<i>Leptodactylus latinasus</i>	0.22
	<i>Pseudis minuta</i>	0.43
	<i>Rhinella fernandezae</i>	0.58
	<i>Elachistocleis bicolor</i>	0.73

## DISCUSSION

Our results showed differences in species composition between grassland and forest habitats. They pointed out that differences in the types of land cover are capable to drive significant changes in anuran species composition, which confirms our initial hypothesis. We also highlight that we surveyed adjacent (spatially closely related) sites, which reveals that vegetation has a powerful effect on defining the composition of anuran assemblages. We may assume that the phytophysiognomies evaluated here offer quite different colonization opportunities to anurans, with drastic changes in anuran assemblages across a small geographical area. An obvious relationship between phytophysiognomies and colonization opportunities is related to microhabitat characteristics generated by shading, wind reduction, humidity maintenance, and reduction of dial range of air temperature. Microenvironmental conditions (especially those related to the microclimate) vary substantially between forests and grassland (D'ODORICO *et al.*, 2013) and, in our sampling site, mainly because the transition between them is relatively abrupt. Based on these differences, the

heterogeneity affects a set of microhabitat proprieties, which could enable the maintenance of some species. The effects of substrate characteristics (e.g., litter deep, moisture retention), and dial variation in air temperature are well-known as determining factors for structuring anuran assemblages (DA SILVA *et al.*, 2011b; VAN DYKE *et al.*, 2017). Based on this, we point out that the relatively great difference in anuran species composition between sampling sites in forest is a result of the greater heterogeneity of this habitat in relation to grassland. It makes sense since forest sites would vary in both vertical and horizontal components of vegetation cover whereas grasslands vary mostly across the horizontal component (DALMOLIN *et al.*, 2019, 2020).

Differences in land cover were recognized as the main drivers of patterns of compositional dissimilarity in communities of different taxa, including birds (LEE & MARTIN, 2017), amphibians (IOP *et al.*, 2020; MOREIRA *et al.*, 2020) and reptiles (WANGER *et al.*, 2010). In general, the presence of soils with some type of vegetation cover is an essential condition for the maintenance of species, especially in the southern region of Brazil, where the conversion of natural habitats to human activities is intense (IOP *et al.*, 2020; MOREIRA *et al.*, 2020). More precisely, habitats composed of different types of vegetation are structurally more complex and, a priori, add a greater set of ecological niches that can be occupied by species with different ecological requirements (VALÉRIO *et al.*, 2016; DALMOLIN *et al.*, 2020). Thus, it is expected that habitats with greater complexity in the vertical and horizontal structure of the vegetation will be able to provide more diversified resources for the species, which leads to a considerable increase in the local diversity of species (TEWS *et al.* 2004; VALÉRIO *et al.*, 2016). For anuran communities, these findings are totally plausible, since heterogeneous habitats are essential to shelter the great diversity of reproductive modes and foraging strategies presented by this group (HADDAD & PRADO, 2005). For example, males of the species of the Hylidae family use vegetation as perches to vocalize; species of the Leptodactylidae family, on the other hand, vocalize on the soil and use vegetation as a substrate or as a way to camouflage themselves, thus, reduce the risk of predation (SANTOS *et al.*, 2008; DALMOLIN *et al.*, 2020).

Land cover also influences other important aspects of amphibian biology. Soils provided with vegetation cover should facilitate the process of dispersion of frogs, since they offer both food and local resources that can be used as refuges. For communities present in environments subject to flooding (which is the case of Estação Ecológica

do Taim), these resources provided by soils covered by vegetation seem to determine the local species richness, as was observed for the Brazilian Pantanal (MOREIRA *et al.*, 2017). In addition, soils covered by vegetation have a greater capacity to retain humidity, which is essential for individuals to maximize their thermoregulation and internal water balance processes (RITTENHOUSE *et al.*, 2009; NOWAKOWSKI *et al.*, 2018; MORLEY *et al.*, 2019; RUBALCABA *et al.*, 2019). For species that have limited dispersion capacities and move preferentially through the terrestrial habitat (which is the case of *Odontophrynus maisuma* and *Rhinella dorbignyi*), the presence of soils covered by vegetation can be a decisive factor.

In general, it is expected that forest environments will have a greater variety of microhabitats (AFONSO & ETEROVICK, 2007; PRADO & ROSSA-FERES, 2014; VAN DYKE *et al.*, 2017). As a result, the occurrence of a greater number of species with different functional traits and evolutionary histories is enhanced (DALMOLIN *et al.*, 2019). This possibility opens a precedent for new studies with the specific objective of evaluating the way species use these habitats, as well as their preferences in terms of microhabitats.

We must highlight the fact that *Scinax squalirostris* was recorded only in forests. This result is different from what was expected since this species is associated with low vegetation such as grass and shrubs (XIMENEZ *et al.*, 2014; MANEYRO *et al.*, 2017; DIAS *et al.*, 2019). Another aspect to be taken into account is that hylids are less likely to be caught in pitfall traps because of their climbing habits (OLIVEIRA *et al.*, 2013; DOSSO *et al.*, 2019). This could have caused some sampling bias and, consequently, affected the observed patterns (which was not our case, since we used different, complementary sampling methods). In addition, some studies indicate that even specific sampling methods such as calling surveys are prone to the observer's effect on the pattern of results (DOSSO *et al.*, 2019).

The fact that we have associated different sampling methods favored the record of species that make wide use of each habitat. Estimations based exclusively on auditory surveys, for example, prioritize the record of habitat use related to reproductive activity (SANTOS *et al.*, 2016; MOSER *et al.*, 2019) limiting the projections regarding habitat requirements (OLIVEIRA *et al.*, 2016; SANTOS *et al.*, 2016). This is not the case in our study, as previous work carried out in the same region reported the occurrence of nine to fifteen species (XIMENEZ *et al.*, 2014; XIMENEZ & TOZETTI, 2014; DALMOLIN *et al.*, 2019, 2020). Thus, our samplings can be considered effective for the representativeness of anuran species in Brazil's extreme south.

The richness and diversity of anurans recorded in our study is relatively less than those recorded in other studies conducted on the coast of Rio Grande do Sul (e.g. COLOMBO *et al.*, 2008; KNAUTH *et al.*, 2019). In general terms, these differentiations may be the result of the strength of species selection based on different historical and contemporary processes. The southern end of the Brazilian coast is

surrounded by mountain ranges, such as the Escudo Sul-Rio-Grandense, which is located in the southeastern region of Rio Grande do Sul (GONÇALVES & DOS SANTOS, 1985). It is assumed that the mountainous areas of the Atlantic Forest and Campos Sulinos biomes have contributed to the speciation processes and in the modulation of the patterns of richness and diversity of anurans in the region (VASCONCELOS *et al.*, 2019); this, therefore, these mountainous areas serve as barriers for the dispersion of species and individuals, contributing to the processes of allopatric, parapatric and sympatric speciation (VENCES & WAKE, 2007; ANTONELLI *et al.*, 2009; FIELD *et al.*, 2009), as well as for the evolution of the considerable diversity of reproductive modes in anurans (HADDAD & PRADO, 2005).

The mountainous areas of Rio Grande do Sul also directly influence the climate of the most diverse regions of the state, as well as the primary productivity of the associated ecosystems (HAWKINS *et al.*, 2003). These set of factors seems to be more pronounced for anurans in the extreme south of the Brazilian coast, since recent analyzes of the patterns of richness and distribution of subtropical species are in line with the expected pattern for the hypothesis of climatic variability (STEVENS, 1989; VASCONCELOS *et al.*, 2019). According to this hypothesis, environments with a wide range of climatic variation select from the regional pool only those species that throughout their evolutionary history have developed physiological, morphological and behavioral characteristics that give them wide ranges of physiological tolerances to support such variations (STEVENS, 1989; VASCONCELOS *et al.*, 2019). Consequently, these regions will be composed of species with broader ecological niches and, at the same time, with greater ranges of geographic distribution (STEVENS, 1989; VASCONCELOS *et al.*, 2019). This is precisely the case for most representatives of the families Hylidae, Leptodactylidae and Microhylidae registered in our study areas. Finally, temperature is also considered the limiting factor for the distribution and occurrence of anurans in the southern portion of the Brazilian coast (VASCONCELOS *et al.*, 2019). It is worth mentioning that these regions suffer from constant anthropogenic changes, which can have direct effects on the microclimate conditions of the environments, so that the modification of the habitats and vegetation associated with them can cause the loss of species and ecological functions which are important for the maintenance of coastal ecosystems (DALMOLIN *et al.*, 2020).

The results herein obtained draw attention to the role of heterogeneity and environmental complexity on anuran composition. They also warn about the imminent risk of changing landscapes due to the invasion of forest species such as *Eucalyptus* and *Pinus* species. Although the sampled communities do not include any endangered species, it is worth mentioning that the study area is a Ramsar site, which is of particular concern when dealing with an area of enormous ecological relevance and importance for the maintenance of many ecosystem functions.



**Supplementary material.** The following online material is available for this article: Fig. 1. Spatial distribution of traps in habitats. Each asterisk represents the position of a line of traps (set of four buckets). Red asterisks are traps in forest areas and yellow ones in grassland areas. The grassland are the matrix of the habitat, while the forests are distributed in patches. The two samples sampled are delimited by the red line, being spot A (27 hectares) and spot B (22 hectares). On the right, images with details of the landscape and the line of traps indicated by the arrows. Fig. 2. Detail of the inside of a bucket, showing the Styrofoam plate used as protection for the captured animals. The guide fence was buried 10 cm into the ground to avoid individuals to transpose the fence. All buckets had holes at the bottom to prevent them from being flooded by rain.

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