

Everyone has their limits: reproductive mode drives amphibian responses to land use in coastal areas

Leonardo F. B. Moreira ^{A,C}, Jéssica B. da Silva^B, Débora S. Knauth^B, Soraya Ribeiro^B and Leonardo Maltchik^B

^ADepartamento de Botânica e Ecologia, Universidade Federal de Mato Grosso, Brazil.

^BLaboratório de Ecologia e Conservação de Ecossistemas Aquáticos, Universidade do Vale do Rio dos Sinos, Brazil.

^CCorresponding author. Email: leonardobm@gmail.com

Abstract. Small wetlands are strongly bound to surrounding terrestrial habitats, so understanding their suitability after conversion to human land uses is critically important to produce an ecologically centred planning for amphibian species. Here, we explored how responses of amphibian assemblage to habitat conversion were influenced by reproductive modes in freshwater coastal wetlands in southern Brazil. We also assessed whether species from different biomes are affected in different ways by land conversion. Using data from tadpole assemblages in a transition zone between Atlantic Forest and Pampa, we tested the hypothesis that aquatic modes would be more affected by habitat conversion than are foam-nest species. Overall, quantitative data were influenced by the percentage of crop area, whereas assemblage structure derived from presence–absence data was associated with biome type. Species with aquatic egg-laying were influenced by the percentage of crop area, and many species were more abundant in ponds surrounded by up to 15% crop area in a 1000-m radius. However, foam-nest species were not influenced by any variable investigated (crops, planted pastures, urban areas and biome). This study has highlighted that agricultural conversion poses environmental filters to amphibian communities, selecting species according to some traits (adult reproductive strategies and tadpole plasticity).

Additional keywords: agriculture, Atlantic Forest, landscape, Pampa, tadpole.

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Introduction

Coastal areas are among the most productive ecosystems, supporting more than one-half of the world's human population (Millennium Ecosystem Assessment 2005; Barbier *et al.* 2011). Historically, humans have been living near coastlines; however, these environments are experiencing substantial urban and agricultural expansion under coastal development. Overall, land-use change is a major cause of biodiversity loss, primarily via loss and fragmentation of habitat (Haddad *et al.* 2015; Newbold *et al.* 2015), but also via the decreased habitat quality and introduction of exotic species (McKinney 2006; Jesse *et al.* 2018). These threats are particularly true for species associated with small or isolated wetlands, which are often being excluded from policy directives (Golden *et al.* 2017).

In coastal wetlands, interaction between human disturbances and climate change affects the water quality and energy flow. For example, decreasing water quality has been linked to variation in composition of microalgal primary producers and the decline of submerged aquatic vegetation (Moorman *et al.* 2017; Ji *et al.* 2018). Vegetation stands serve as an important feeding ground and nursery sites for amphibians, as well as for other organisms such as macroinvertebrates and fishes (Moreira *et al.* 2010; Fuentes-Rodríguez *et al.* 2013; Lanés *et al.* 2018).

Despite there being compelling evidence that habitat conversion plays a fundamental role in species loss and restructuring of amphibian assemblages (Brum *et al.* 2013; Nowakowski *et al.* 2018), to identify winners and losers is still elusive because of the myriad of reproductive modes and differences in life-history strategies.

Over the past two decades, there has been a heightened awareness that life-history traits, such as reproductive mode, are relevant to the amphibian conservation planning and to discriminate community assembly rules (Becker *et al.* 2007; da Silva *et al.* 2012; Crump 2015). Reproductive modes in Atlantic Forest of Brazil encompass almost 70% of the all 39 known modes, with 40% of the amphibian species in the biome having specialised modes dependent on the forest habitats, namely being associated with vegetation, high-gradient stream, or forest floor (Haddad and Prado 2005). Whereas recent studies have reported declines in such specialised species (e.g. Carvalho *et al.* 2017; Becker *et al.* 2019), reproductive modes associated with ponds in open areas (i.e. grasslands, shrub lands, coastal dunes) seem to be favoured by human habitat modification (Haddad and Prado 2005; Dixo and Metzger 2010). However, even generalist species may face a high risk of desiccation in modified landscapes, because both adult and post-metamorphic individuals move to

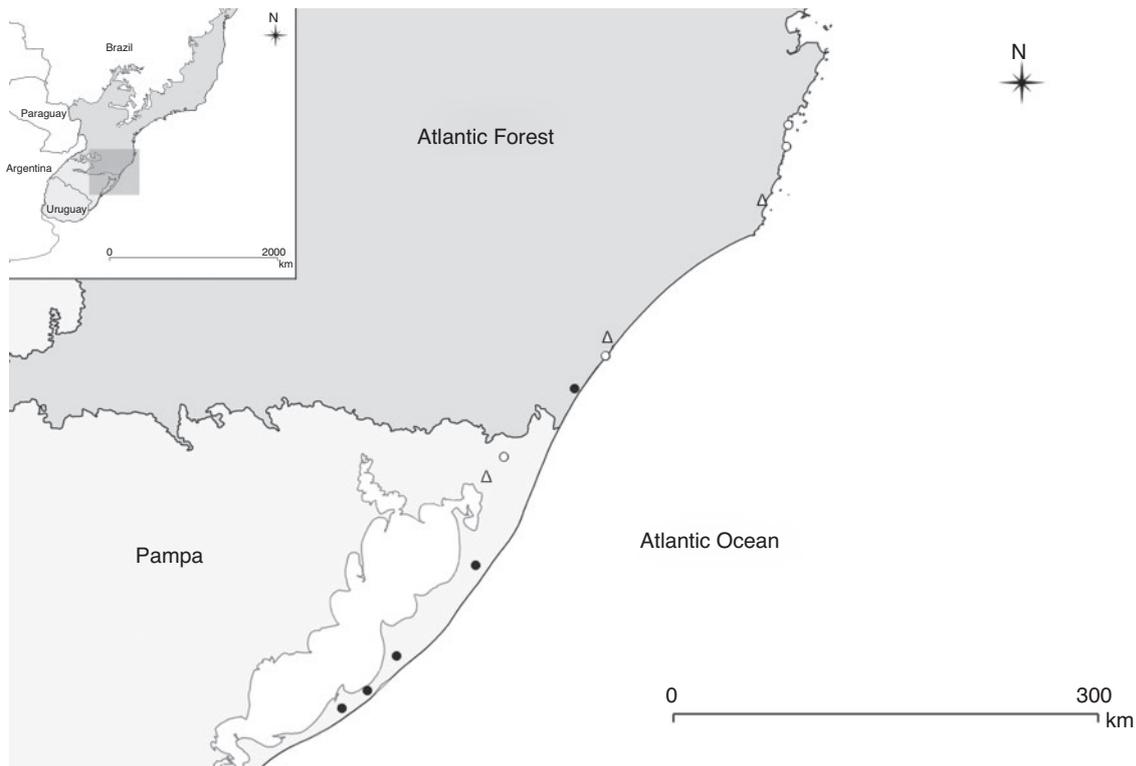


Fig. 1. Location of study region in a transition zone between Atlantic Forest and Pampa biome. Near-pristine ponds (●); semi-degraded ponds (○); and degraded ponds (△).

and from ponds. Furthermore, survival of eggs and tadpoles relies mainly on gradients of aquatic vegetation cover, temperature and pond hydroperiod (Queiroz *et al.* 2015; Moreira *et al.* 2016a; Melo *et al.* 2018). Because small wetlands are strongly bound to surrounding terrestrial habitats, understanding their suitability for different amphibian reproductive modes is critically important so as to produce an ecologically centred planning, including responses to habitat conversion.

It is well known that ecological transitional zones are rich in biodiversity, with both richness and rarity being potentially high (e.g. Kark *et al.* 2007; Maciel *et al.* 2016). In southern Brazil, elements of the Atlantic Forest are gradually replaced by subtropical grasslands of the Pampa, and the boundaries between the biomes are not clearly defined in areas along the coastal stretch (MapBiomias 2019). In such forest–grassland transition, there is evidence that patterns of amphibian β diversity change according to the spatial extent (Knauth *et al.* 2019). Overall, climate and environment jointly affect community composition in the forest regions, whereas environmental features seem to be the major factor in grassland areas. Despite having a lower diversity than in the Atlantic Forest, many amphibian species from the Pampa are endemic and show reproductive modes that minimise the desiccation risk (i.e. foam-nest builders; Maneyro *et al.* 2017). Whether habitat conversion has similar effects on the community in both biomes, and to what extent reproductive modes enable amphibians to persist in such modified landscapes, is a subject open to discussion.

In this study, we investigated how the assemblage structure of pond-breeding amphibians is associated with land use along

500 km in freshwater coastal wetlands in southern Brazil. We also explored (1) whether responses to habitat conversion are influenced by the reproductive modes of species, and (2) whether species from different biomes are affected in different ways by land conversion. Many amphibians from this coastal region are widely distributed and generalist species (Haddad *et al.* 2013; Maneyro *et al.* 2017); however, we expect different responses in relation to human land uses. In both biomes, foam-nest species would be associated with a moderate level of habitat conversion, that is, up to 60%. Species with egg strings or egg masses in water among aquatic vegetation would be negatively affected by agricultural land uses, but patterns will likely be biome dependent. So, species of the Atlantic Forest would be more affected by land-use change than would those of Pampa.

Materials and methods

Study area and data collection

We studied amphibian communities inhabiting small coastal wetlands in a transition zone between the biomes of Atlantic Forest and Pampa, in southern Brazil (Fig. 1). This region is characterised by a mosaic of grasslands, shrubby vegetation, which is also called Restinga, and forests (Marques *et al.* 2015), and encompasses various wetlands, such as marshes, coastal lagoons, inland lagoons and estuaries. As in the most nearshore habitats, expansion of urban development and agro-industrial activities has led to fragmentation and loss of wetlands (Silva and Tagliani 2012). The sampled coastal wetlands (hereafter, ponds) ranged from 0.2 to 0.7 ha, being at least 15 km apart from

each other, and were chosen on the basis of accessibility (i.e. private landowners willing to participate in the study).

In the spring of 2015 and 2016 (September to November), we sampled tadpoles twice in 12 ponds, including six in the Pampa and six in the Atlantic Forest (Fig. 1). Samples were taken by dip-netting (30 cm wide, 250 μ m) and sampling effort was 12 sweeps (\sim 1 m²) per sampling period, haphazardly distributed across the representative microhabitats in the ponds (from the margin up to 4 m). Tadpoles were anaesthetised with clove oil solution and preserved in the field. Species were divided in the following two groups on the basis of the reproductive mode (Haddad and Prado 2005): (1) foam nests: eggs or tadpoles in nests floating on pond or inside subterranean chambers; (2) aquatic: egg-laying directly in water.

We defined circular areas (1000-m radius) and measured land-cover data (Supplementary material Table S1 available at the journal's website) by using Qgis (ver. 2.18.16, <https://qgis.org/en/site/>, accessed 10 December 2019). We based analysis on Google Earth imagery, using a land-cover classification for 2016 produced within the scope of the MapBiomias initiative (MapBiomias 2019).

Statistical analysis

We assessed sampling saturation overall and per biome, with rarefaction and extrapolation curves with Hill numbers (Chao *et al.* 2014). We also estimated species richness per biome with an abundance-based non-parametric richness estimator (Chao 1, Chao *et al.* 2014). Species that could potentially characterise ponds according to the biome type or natural cover class were evaluated using an indicator-species analysis (Indval, Dufrene and Legendre 1997). Thus, ponds were assigned to one of the following three categories on the basis of the percentage of the original cover: (1) near pristine, with natural land cover surrounding pond >70%; (2) semi-degraded, with natural cover between 40 and 70%; and (3) degraded, with less than 40% of natural cover surrounding ponds. The analysis combined species relative abundance with its relative frequency of occurrence in the groups of sites. So, Indval analysis identified indicator species as those that were well distributed among sites within a particular class (i.e. if you were in that type you should find that species). Samples were clustered according to the biome (Pampa or Atlantic Forest) or degradation (described as the categories near pristine, semi-degraded or degraded).

The spatial independence of the sampling ponds was tested using a distance-based Moran's eigenvector-map (dbMEM) analysis (Dray *et al.* 2006). We generated a set of three spatial variables from Cartesian coordinates for the threshold distance of 70 km with dbmem function of adespatial package (Dray *et al.* 2006; ver. 0.3-8, <https://CRAN.R-project.org/package=adespatial>, accessed 11 June 2020) in R (ver. 3.6.1, <https://www.R-project.org/>, accessed 10 December 2019). As the dbMEM analysis did not detect a significant spatial structure in the composition of tadpole assemblage ($F_{3,8} = 0.977$, $P = 0.463$) and land use ($F_{3,8} = 1.001$, $P = 0.442$), spatial autocorrelation was not included in the further analysis.

Although abundance data may be potentially more powerful than are presence-absence data in indicating gradient effects, many tadpoles can come from a few adults, at least for many species of amphibians. In addition, there is a trade-off between

Table 1. Tadpole species richness, abundance, and abundance-based richness estimator across different biomes

Biome	Species registered	Total abundance	Chao 1 (95% CI)
Total	28	1053	30.2 (28–47)
Pampa	20	443	21 (20–31)
Atlantic Forest	18	610	22.5(18.5–53)

presence-absence and quantitative indices related to spatial scales and similar regional species pool (Legendre 2014). So, biotic matrices were constructed considering the structure of the amphibian assemblage, for each sampling pond, in the following ways: (1) three presence-absence data (all species, foam-nest species and aquatic species); (2) three quantitative data (all species, foam-nest species and aquatic species). We used a constrained redundancy analysis (RDA) to evaluate the effects of three landscape variables (proportion of crop areas, planted pastures and urban areas) and the biome type on the assemblage structure. In practice, we did one RDA for each biotic matrix. Before RDA, amphibian data were Hellinger-transformed (Legendre and Gallagher 2001), and redundant variables were excluded from landscape matrix. Significant full models were submitted to a forward selection, on the basis of adjusted R^2 and significance of each explanatory variable (Blanchet *et al.* 2008). A compound graph (Dambros 2014) was used to characterise species distribution across landscape gradients. Sampling curves were generated using the iNext package (Hsieh *et al.* 2016, ver. 2.0.20, <http://chao.stat.nthu.edu.tw/wordpress/software-download>, accessed 10 December 2019) in R. Indicator-species analysis and RDA were computed using the labdsv (Roberts 2016) and vegan (Oksanen *et al.* 2019) package in R.

Results

We collected 1053 tadpoles representing 28 species from four families (Table S2). The most abundant species were *Rhinella icterica* and *Scinax squalirostris*. Overall, many species had a low occurrence (between one and three ponds). Whereas *Boana pulchella* and *Dendropsophus sanborni* were registered in all ponds from Pampa, only *S. squalirostris* was registered in all ponds from Atlantic Forest. Species richness ranged from 3 to 16 species per pond ($\bar{x} = 7 \pm 3.6$), and nine species corresponded to foam-nest builders (Table S2). From the species that deposit eggs directly in water, only *Boana faber* constructs a clay nest, whereas other species lay eggs spread over the water, divided in several portions, or within strings. Species accumulation curves approached, but did not reach, an asymptote for tadpoles overall or in any biome (Supplementary material Fig. S1). Richness registered for Atlantic Forest ponds was lower than estimated richness (Table 1), although confidence interval of richness estimator did not differ significantly between Pampa and Atlantic Forest (Table 1).

Landscape variables explained the variation in total amphibian-assemblage structure and species with aquatic egg-laying (Table 2). Although reduced models accounted for similar variation for both matrices (qualitative and quantitative),

Table 2. Results of redundancy analysis (RDA) describing the relationship between landscape characteristics and whole tadpole assemblage (all species) and for reproductive mode in freshwater coastal wetlands from southern Brazil

Parameter	<i>P</i> (full model)	Adj. <i>R</i> ² (full model)	Landscape variable	<i>P</i>	Adj <i>R</i> ²
All species					
Quantitative data	0.04	0.12	%Crop area	0.03	0.10
Presence-absence	0.03	0.16	Biome	0.004	0.15
Foam nest					
Quantitative data	0.18	0.10			
Presence-absence	0.15	0.13			
Aquatic					
Quantitative data	0.03	0.19	%Crop area	0.012	0.13
Presence-absence	0.08	0.14			

landscape variables were different in each case. Percentage of crop area explained 10% of the variation by using abundance data (Table 2). Overall, many species were more abundant in ponds surrounded by up to 15% crop area in a 1000-m radius (Fig. 2a). By contrast, type of biome explained 15% of variation in assemblage structure derived from presence-absence data. While tadpoles of 10 species were registered only in ponds from the Pampa, eight species were exclusive from Atlantic Forest (Fig. 2b). Landscape was not a significant factor in explaining the variation of the foam-nest species (Table 2). Assemblages of species with aquatic egg-laying were influenced by the percentage of crop area, where many species were more abundant in ponds surrounded by up to 15% crop area (Fig. 3). Considering that our model could be biased, owing to the large abundance of *R. icterica* in only one pond, we excluded this species and re-analysed the data; however, the overall patterns remained (%crop area, $R^2_{adj} = 0.15$, $P = 0.01$). We identified three indicator species associated with Pampa or Atlantic Forest (Table 3), and one additional foam-nest species associated with semi-degraded ponds in both biomes.

Discussion

Our results add to a growing body of literature showing that reproductive modes matter for amphibian responses to land-use change (Becker *et al.* 2010; da Silva *et al.* 2012). Despite being a region with a high density of human population, type of biome explained species composition of pond-breeding assemblages better than did human land uses in coastal areas of southern Brazil. However, quantitative assemblage structure was affected by the percentage of agriculture at a 1000-m radius. Importantly, although we found no relationship between foam-nest builders and landscape variables, species that lay exposed eggs in the water were affected by the agricultural area. Importance of the surrounding matrix, with negative effects of agriculture, is well known for amphibian communities with many forest-specialist species (Dixo and Metzger 2010; Ribeiro *et al.* 2018). However, species from grasslands and shrublands have received little attention across studies. Seventy-one amphibian species have been recorded in coastal areas of southern Brazil, but only 52 species reproduce in freshwater ponds (Haddad *et al.* 2013; Maneyro *et al.* 2017). Thus, ponds sampled in our study harboured more than half of the anuran richness registered in the region. Croplands and pastures may exhibit some similarities

(i.e. vegetation structure) with such pristine open areas, but habitat suitability for amphibians relies on management practices, exposure to contaminants and climate seasonality (Medina *et al.* 2016; Moreira *et al.* 2016a; Pulsford *et al.* 2019).

Many amphibian species that lay eggs directly in water were absent from ponds surrounded by more than 35% agricultural area. Desiccation proneness, a trait often related to mobility, has been suggested as a major trait determining responses to habitat loss or habitat conversion to agricultural lands (Cosentino *et al.* 2011; Watling and Braga 2015). Here, all species with a large size (*Boana faber*, *Leptodactylus latrans*, *Rhinella arenarum*, and *R. icterica*) had low occurrence (one pond each), and most of the 28 registered species were small to medium in size (<5 cm) with a prolonged breeding pattern (up to 6 months). Thus, our results are consistent with those of previous studies (Watling and Braga 2015; Ribeiro *et al.* 2017), showing that agricultural land cover might be more detrimental to larger species. It is hard to identify exactly what is the major factor constraining larger species in agricultural lands (e.g. agrochemicals, crop age or management practices). However, some studies have shown a decline in the resistance to evaporative water loss for large amphibians (Titon and Gomes 2015; Watling and Braga 2015). Given this framework and the potential extreme conditions, that is, many crop fields are bare lands during spring in southern Brazil, we suggest that larger species may face a scarcity of shelters during their breeding migrations.

Contrary to expectations, we found no association between land use and assemblage structure for foam-nest amphibians. The majority of foam-nest species registered here belong to Leptodactylidae. Although leptodactylids are commonly found in human-modified environments, such as pastures and agricultural ecosystems (Machado and Maltchik 2010; Piatti *et al.* 2010; da Silva *et al.* 2011; Moreira and Maltchik 2014; Prado and Rossa-Feres 2014), most of what we know about amphibian declines and responses to land use is related to their adult phase, which is ecologically non-equivalent to their larval stage. Studies evaluating impacts of land conversion on anuran larvae have been scarce (Machado *et al.* 2012; Queiroz *et al.* 2015; Moreira *et al.* 2016b; Schiesari and Corrêa 2016); however, impacts on tadpoles of foam-nest species seem to be more correlated with local pond characteristics (i.e. hydroperiod, water depth, absence of fish) than with particular land covers. Given this apparent absence of univariate effects of land use on

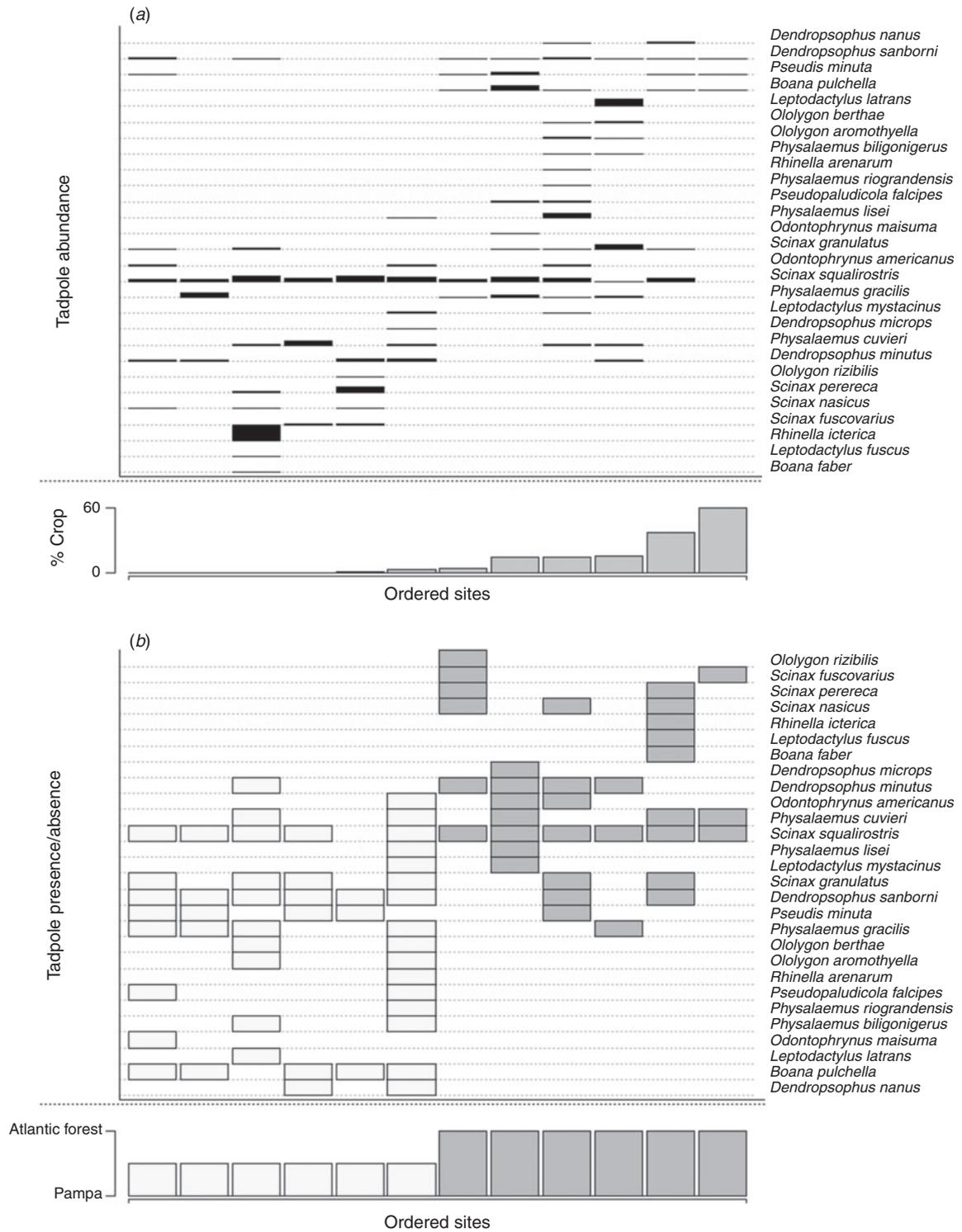


Fig. 2. Distribution of tadpole species in relation to (a) %crop area in a 1000-m radius, bar thickness is proportional to tadpole abundance; (b) biome. Ponds in Pampa biome (light-grey bars); and pond in Atlantic Forest (dark-grey bars).

this group of species, we must keep in mind that human land uses are dynamic and stressors can often interact synergistically, affecting amphibian populations (Mann *et al.* 2009; Schiesari

and Corrêa 2016). So, how different land uses affect the properties of aquatic environment and amphibian predators? With this information available, we can have a better

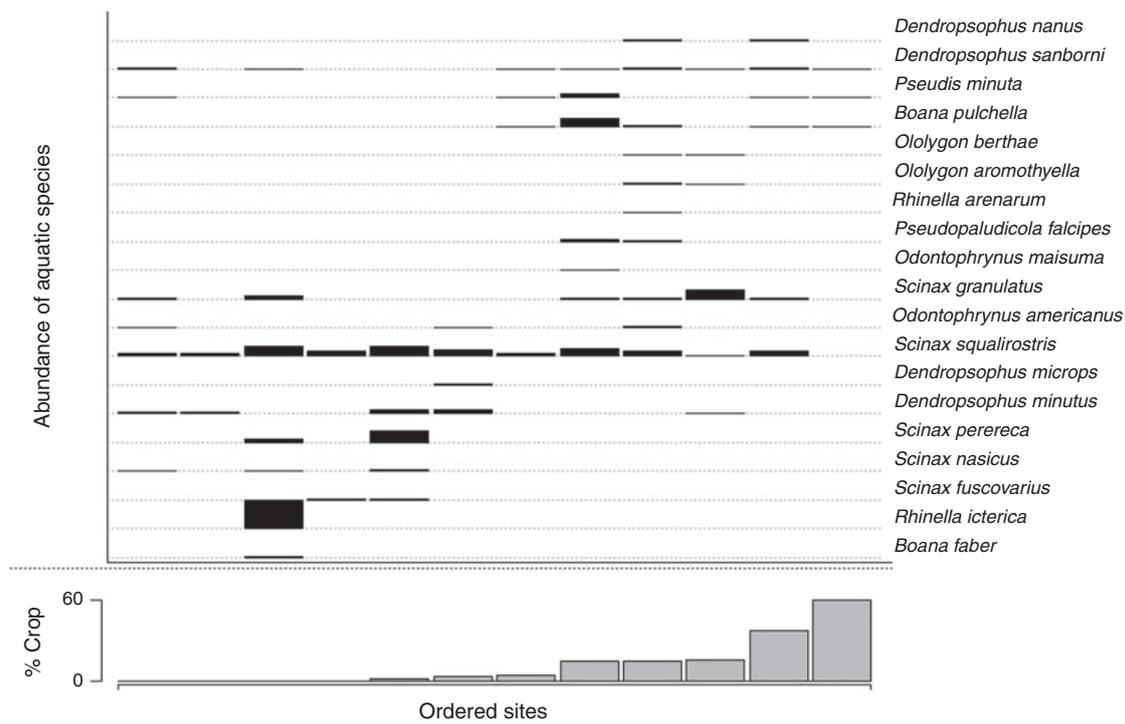


Fig. 3. Distribution of species that lay eggs directly in water in relation to crop area. Bar thickness is proportional to tadpole abundance.

Table 3. Indicator species with the respective indicator value (Indval), probability for the species to be listed as an indicator, category where the species showed the maximum indicator value

Species	Indval	P	Site
<i>Boana pulchella</i>	0.83	0.02	Pampa
<i>Dendropsophus minutus</i>	0.62	0.04	Atlantic Forest
<i>Dendropsophus sanborni</i>	0.77	0.03	Pampa
<i>Physalaemus cuvieri</i>	0.94	0.01	Semi-degraded

understanding of land-use impacts and potential habitat suitability for foam-nest species.

Our results have confirmed early views that agricultural conversion poses environmental filters to amphibian communities, selecting species according to some functional traits (Moreira and Maltchik 2014; Ribeiro *et al.* 2017; Nowakowski *et al.* 2018). However, the above mentioned studies focussed on adult specimens and, generally, discussed responses to habitat modification in terms of habitat suitability for adults and post-metamorphics. Effects of human land uses depend, at least in part, on tadpole development or survival. It is well established that hydroperiod and predation, by fish or invertebrates, jointly affect tadpole distribution (Werner *et al.* 2007; Moreira *et al.* 2016b). Regardless of crop type and management practices, vegetation homogenisation and hydroperiod changes are recurrent impacts on tadpole assemblages from conversion to agricultural lands. The lack of structural diversity of aquatic vegetation, used by tadpoles as shelters from

predators, may decrease tadpole survivorship (Kopp *et al.* 2006; Hartel *et al.* 2007). Moreover, vegetation cover in and around ponds provides temperature attenuation (Carpenter and Lodge 1986; Scrine *et al.* 2017). Elevated water temperature can reshape predator–prey dynamics, decreasing tadpole survival in warmer environments (de Mira-Mendes *et al.* 2019), although tadpole mortality rate is mediated by predator type and species traits (Nomura *et al.* 2011). It is interesting to note that our results for indicator species associated a small-size foam-nest species (*Physalaemus cuvieri*) with ponds surrounded by moderated human land uses. The foam is known to have many ecological properties related to reproduction in dry open areas (Pereira *et al.* 2017), allowing eggs and larvae within foam nests to avoid aquatic predators, buffer from temperature, and protect from solar radiation (Hissa *et al.* 2008; Méndez-Narváez *et al.* 2015). Thus, it is reasonable to assume that traits related to reproduction, which have consequences for both tadpoles and adults, contribute to persistence in human-altered habitats.

In this paper, we showed an important effect of type of biome on species composition of amphibian communities in a transition zone between Atlantic Forest and Pampa. Recently, Vasconcelos *et al.* (2019) found similar results related to patterns of species richness. They showed that, in tropical regions, richness correlated with vegetation structure, whereas temperature and energy–water balance were better predictors in subtropical areas. To conclude, agricultural land use was related to amphibian-assemblage structure in coastal wetlands, with aquatic reproductive modes (eggs deposited directly in water) being the most sensible to habitat modification. We suggest that

future research related to sensitivity to human land uses should also include adult reproductive strategies and tadpole traits (e.g. tadpole feeding, microhabitat use, and predator avoidance).

Conflicts of interest

The authors declare that they have no conflicts of interest.

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