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Something is not quite right: Effects of two land uses on anuran diversity in subtropical grasslands

Leonardo Felipe Bairos Moreira[1] | Henrique Zanette de Castilhos[2] | Santiago Castroviejo-Fisher[2]

[1]Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Instituto de Biociências, UFMT—Universidade Federal de Mato Grosso, Cuiabá, Brazil

[2]PUCRS—Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil

Correspondence
Leonardo Felipe Bairos Moreira, Instituto de Biociências, Universidade Federal de Mato Grosso, Cuiabá CEP-78060-900, Brazil.
Email: leonardobm@gmail.com

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Abstract

Although habitat modification is considered one of the main causes of biodiversity loss, the relative contribution of different rural land uses to biodiversity conservation is far less known. Additionally, the realization of the multidimensionality of biodiversity demands studies integrating variation of functional traits and phylogenetic information as complements to address the effects of land use on the structure of animal communities. Herein, we investigated the effects of land use (i.e., intensive agricultural and extensive livestock rearing) on functional and phylogenetic diversity of anuran communities in farmland ponds from the Uruguayan savanna ecoregion, while considering the effects of local factors (i.e., water depth) on species composition. We surveyed adults and tadpoles in 22 ponds and quantified five traits related to tadpole feeding, habitat use, and predator avoidance. Tadpole identification was corroborated by DNA barcoding based on a fragment of the mitochondrial 16S rRNA gene. We observed a decline in phylogenetic mean nearest taxon distance associated with increase of surrounding agricultural land use. While land use intensification did not affect richness (functional or phylogenetic), ponds in livestock ranches hosted about four times more tadpoles than agricultural ponds. Functional evenness decreased with water depth, although such relationship disappeared when considering phylogenetic non-independence. Our results indicated that specific anuran clades were more sensitive to intensification in land use, reinforcing a recent view of phylogenetic homogenization following habitat conversion. Additionally, our study suggests that extensive cattle grazing over wide native pastures may provide an alternative more compatible with conservation than short-term crops in subtropical grasslands.

Abstract in Portuguese is available with online material.

KEYWORDS

agriculture, community phylogenetic, livestock, Pampa, tadpoles

1 | INTRODUCTION

Habitat modification is the primary driver of population declines and species extinctions (Kehoe et al., 2015), with food production—through agriculture and cattle ranching—as one of the main causes of habitat change (Veach, Moilanen, & Di Minin, 2017). In landscapes where the conversion has already taken place, agricultural intensification may enhance biodiversity loss through increased mechanization, decreased crop diversity, input of hazardous pesticides, and grassland conversion to arable fields (Schiesari & Corrêa, 2016; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). After conversion to croplands, vegetation homogenization and a

lterations in the hydrological regimes are the immediate impacts on freshwater communities. Thus, across a wide range of animal and plant taxa, it is unsurprising that pristine areas support greater levels of biodiversity than agricultural or pastoral lands (Flynn et al., 2009; Tscharntke et al., 2005).

When compared to intensively used agroecosystems, the relative contribution of non-intensively exploited areas to conservation is well acknowledged (Phillips, Newbold, & Purvis, 2017). Planted pastures may support moderate levels of biodiversity in relation to intensive crops, although pastures are often far less suitable than forested areas (Schiesari & Corrêa, 2016). However, exotic planted pastures occur by removing the original vegetation—often transforming forest and woodland ecosystems—and establishing exotic species (Moreira, Solino-Carvalho, Strüssmann, & Silveira, 2016). This is contrastingly different to using natural grasslands for moderate or extensive domestic animal grazing. Despite the importance of natural grasslands as ecosystems and their role in human economic activities, their relevance as economically productive systems that allow for the conservation of a more diverse biota, depending on management practices, has received little attention in the literature (Dotta, Phalan, Silva, Green, & Balmford, 2016; Isacch, Maceira, Bo, Demaría, & Peluc, 2005). Negative effects of grazing on freshwater communities result from direct nitrogenous waste input into ecosystems and changes in vegetation structure (Jansen & Healey, 2003; Schmutzer, Gray, Burton, & Miller, 2008). Recent reviews show no clear consensus about responses to livestock use of wetlands, although potential negative (even mixed or positive) effects seem dependent on grazing regimes and stocking densities (Howell et al., 2019; Schieltz & Rubenstein, 2016). Therefore, we identify a need for more integrative studies based on empirical data to understand how the biodiversity of open areas, in its different dimensions (e.g., functional and phylogenetic), copes with a changing habitat. More importantly, we should understand how different land uses modify natural grasslands—which uses have more pervasive impacts and which uses help to supplement the biodiversity conserved in protected areas.

The recognition that species trait diversity may contribute disproportionately to ecosystem functioning has led to new insights about ecological patterns and ecosystem health (Cadotte, Carscadden, & Mirotchnick, 2011). Organism's traits have direct and indirect consequences for its fitness, making functional traits a proxy for understanding the environmental tolerances and habitat requirements (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). Levels of trait variation (i.e., functional richness) are expected to decrease with high disturbance levels, while functional evenness—which incorporates both species traits and abundance—decreases even under moderate levels of disturbance (Mouillot et al., 2013; Villéger, Miranda, Hernández, & Mouillot, 2010). This happens because functional evenness reflects the balance between competitive interactions (at low disturbance levels) and trait filtering associated with the increase of disturbance intensity, while functional richness decreases with species extinctions with extreme traits (Mouillot et al., 2013).

Animal functional traits that describe food acquisition and habitat use may influence species composition in modified landscapes (Flynn et al., 2009; Trimble & van Aarde, 2014). Although trait-based approaches might be a valuable tool, trait data are not readily available or the investigated traits are hard to quantify. Methodological issues remain to establish the underlying mechanisms driving community assembly, including trait selection and types of functional diversity measures (Schmera, Heino, Podani, Erös, & Dolédec, 2017; Tsianou & Kallimanis, 2016). As an alternative, phylogenetic diversity metrics have been used as a surrogate for functional diversity (Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015), based on the general assumption that proximity of common ancestry correlates with niche similarity. However, the generality of this assumption is contentious and commonly found processes in empirical studies, such as evolutionary convergence, ecological speciation, and phenotypic plasticity, will distort such associations (Cadotte, Davies, & Peres-Neto, 2017; Stroud & Losos, 2016).

While several studies have addressed the effects of land use intensification on functional and phylogenetic diversity (Lee & Martin, 2017; Ribeiro et al., 2017; Trimble & van Aarde, 2014), there are important knowledge gaps on the impacts of land use in grasslands and freshwater ecosystems. In particular for amphibians, phylogenetic homogenization following habitat conversion seems to be a global pattern (Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018), although local responses to conversion can vary widely in the functional context. Function-related responses to land use seems to be complex; modified habitats often show less functional groups, yet not all human land uses affect functional richness (Díaz-García, Pineda, López-Barrera, & Moreno, 2017; Riemann, Ndriantsoa, Rödel, & Glos, 2017; Trimble & van Aarde, 2014). In subtropical grasslands, biodiversity erosion has been documented under moderate levels of habitat loss. Such agricultural landscapes had fewer number of species, lower phylogenetic diversity, and higher nestedness (Saccol, Bolzan, & Santos, 2017; Staude et al., 2018), in which disturbance-tolerant species are favoured and non-random local extinctions occur in some evolutionary lineages.

Here, we investigated the relationship between anuran diversity and land use (intensive agricultural areas versus extensive livestock rearing) in farmland ponds from the Uruguayan savanna ecoregion. We considered two aspects of functional diversity (richness and evenness) and two aspects of phylogenetic diversity (richness and divergence). Explicitly, we explored whether: (a) there are different amounts of evolutionary history represented by the anuran communities at each land use; (b) in a phylogenetic context, species within ponds surrounded by cultivated land would be more related than expected in a random assemblage, reflecting the role of environmental filters in selecting disturbance-tolerant species; (c) functional diversity patterns, based on tadpole traits related to food acquisition, habitat use, and predator avoidance would be linked to different land uses. We posit that functional evenness would decline with land use intensity, but without significant change in functional richness. Intensive agricultural areas are subject to physical (native vegetation removal and crop harvest) and chemical (pesticides and fertilizers) disturbances, whereas extensive cattle grazing leads to a change in grassland structure (Moreira, Solino-Carvalho, et al., 2016; Schiesari & Corrêa, 2016). In this way, extensive livestock ranches would support moderately higher levels of biodiversity in relation to more impoverish agricultural areas.

2 | METHODS

2.1 | Study area and data collection

We selected 22 ponds in southern Brazil (29.64°–30.10°S, 54.05°–57.33°W), each with adjacent areas of intensive cultivated land (*N* = 11) or land used for extensive rearing livestock through grazing (*N* = 11). The Brazilian Pampa corresponds to the northern portion of the Uruguayan savanna ecoregion (Figure 1), which includes a mosaic of grasslands, scrub savannas, and gallery forests. Cattle grazing and fire have shaped this landscape for over 300 years (Bernardi, Holmgren, Arim, & Scheffer, 2016; Overbeck et al., 2007). But since the second half of the twentieth century, conversion of native grasslands to more profitable agricultural activities, mainly rice and soybean, have greatly expanded (Oliveira et al., 2017). Nowadays, livestock farming (65%) and intensive crop-based agriculture (20%) dominate the land use patterns (Modernel et al., 2016).

In the spring of 2015 (10–16 October), we sampled tadpoles in ponds located 5.5–316 km apart (Figure 1). Most anuran species in the Uruguayan savanna were spring breeders or overwinter as tadpoles (Maneyro & Carreira, 2012). We selected small ponds surrounded by similar land use up to 500 m (crop or livestock). Ponds were close to 0.15 ha (range 0.01–0.35), although one large pond was included in the sampling (0.76 ha). Sampled ranches raise cattle and sheep in natural grasslands (i.e., area for livestock grazing mostly formed by non-planted pastures with negligible amounts of external inputs). Stocking rates estimates range from 0.68 to 1.0 animal units/ha, although ranchers could adjust it according to the winter conditions and overgrazing may occur (Modernel et al., 2016). Intensive agricultural areas were used for short-term crops (soybean or rice). Application of agrochemical, inorganic fertilizers, and glyphosate-based herbicides is concentrated in the initial growth stage (October–November). In order to ensure that the landscape composition surrounding each pond did not change over different scales, we also defined circular areas (1,000 m radius) and measured land-cover data (Table S1), using Qgis 2.18.16 (QGIS Development Team, 2018). We based analysis on Google Earth imagery, using a land-cover classification for 2015 produced within the scope of the MapBiomas initiative (Project MapBiomas, 2019). Other land uses (natural forests, forest plantation, and mosaics) showed small areas within buffers (Table S1), and there was a strong negative correlation between natural grasslands used for cattle ranching and intensive agricultural area (*r* = −.972). Thus, we used agricultural area as predictor variable inversely expressing livestock farming.

At each pond, we performed eight dip-net sweeps (30 cm diameter, 2 mm mesh), each covering approximately 1 m^2 and distributed at different pond depths (i.e., four sweeps near the edge of the pond

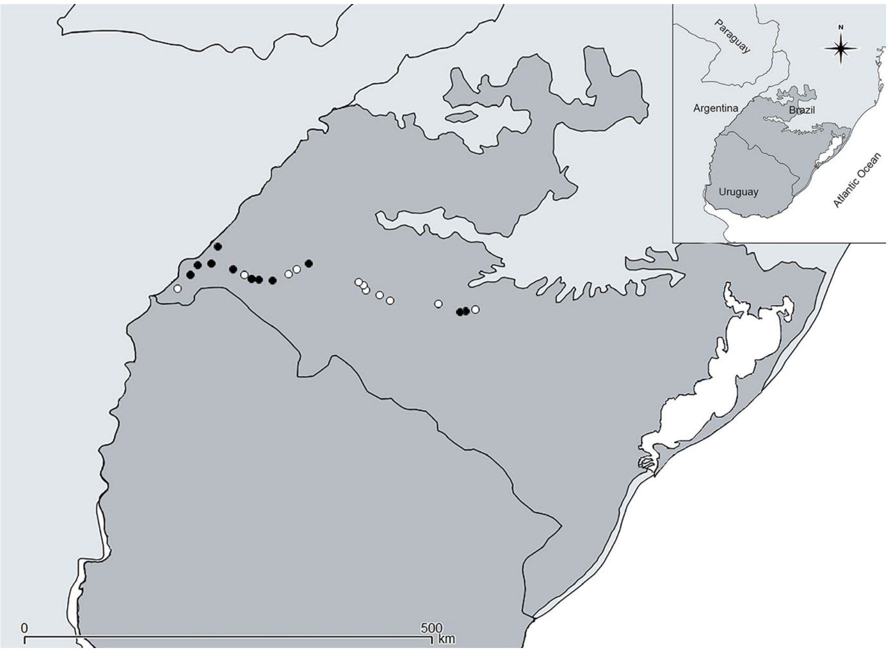

FIGURE 1 Location of Uruguayan savanna (dark gray) and the study sites in southern Brazil. Solid circles represent agricultural ponds and open circles livestock ranch ponds

and four sweeps in deep water near the center of the pond). Sweeps were pooled into one sample per pond (3.5 L plastic bucket), where the collected tadpoles were euthanized with a benzocaine solution and sorted into series based on their morphology (i.e., coloration, body shape, eyes position, tail fin proportion, and mouth position). From each series, tail samples were taken from three specimens to corroborate tadpole identification by DNA barcoding based on a fragment of the mitochondrial 16S rRNA gene (Grosjean, Ohler, Chuaynkern, Cruaud, & Hassanin, 2015). We also registered the presence of all observed adults, visually or acoustically, during tadpole sampling. Voucher specimens were deposited at the Amphibian Collection of the Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCT-PUCRS), Brazil.

Five functional traits were selected to reflect tadpole feeding, habitat use, and predator avoidance (Azizi, Landberg, & Wassersug, 2007; Strauss, Reeve, Randrianiaina, Vences, & Glos, 2010; Venesky, Wassersug, & Parris, 2010). To accommodate differences across tadpole developmental stages, all traits were ratios between morphological measures (Table 1). Each specimen was rinsed in distilled water and then measured for a set of eight morphological traits on an automated stereomicroscope—Leica M205A (Figure S1). Morphological terminology followed that of Altig and McDiarmid (1999), and only specimens without tail injuries between Gosner' stages 29 and 39 were measured. Phylogenetic relationships among species were obtained from a time-calibrated phylogenetic tree generated by Pyron (2014). We pruned the phylogeny to match the species pool of both land uses. When resolution for our taxa was not present in the phylogeny, we manually incorporated our species following a range of published sources for between-species relationships (Figure S2). Mean path length calibration was used to adjust branch lengths (Britton, Oxelman, Vinnersten, & Bremer, 2002).

2.2 | Diversity measures and phylogenetic signal

Some degree of phylogenetic signal in functional traits is common for taxa that share a common ancestor, so we quantified the phylogenetic signal in the traits using Blomberg's K statistic implemented in the phytools package (Revell, 2012) in R. To summarize anuran phylogenetic variation, we chose metrics related to richness and divergence: (a) Faith's phylogenetic diversity (PD) to represent the sum of accumulated phylogenetic differences (i.e., sum for a total branch lengths for the species occurring in each pond); (b) mean nearest taxon distance (MNTD) to represent the mean phylogenetic relatedness within an assemblage (i.e., mean of the branch lengths separating each species from its closest relative in each pond).

To quantify changes in functional trait variation across livestock ponds and crop ponds, we calculated two functional metrics: functional richness (FRic) and functional evenness (FEve) (Villéger, Mason, & Mouillot, 2008). The former describes a multidimensional trait space filled by the species assemblage, while the latter reflects the regularity of abundance distribution in the functional trait space. Functional richness is independent of species abundance, while FEve value is proportional to species relative abundance. Both functional metrics were calculated for all ponds with a minimum of three recorded species. To facilitate comparison between the different metrics (functional and phylogenetic), the magnitude of the differences was calculated based on standardized effect size (SES; Gotelli & McCabe, 2002). Standardized effects were derived from a null model that preserves regional species occurrence frequency and pond species richness (independent swap algorithm; Gotelli, 2000). Positive or negative SES. PD/FRic values indicate, respectively, phylogenetic/functional richness higher or lower than expected by the null model. For

TABLE 1 Traits and measurements used to calculate functional diversity indices

Trait	Measure	Relevance
Body form	BL/TL	Swimming type and endurance. High values entail lateral bending during swimming, evading attacking predators. Low values entail little lateral flexion, enabling more endurance in higher flow velocity
Tail shape	(DTH + VTH)/TMH	Position in the water column. Deep tail fins may distract the predator, deflecting deadly strikes to the body wall
Tail position	TAL/BL	Acceleration and maneuverability. Larger tails enhance sprint swimming speed of tadpoles
Oral disk position	OD/BL	Food acquisition. Low values entail feeding mainly on midwater or surface, while high values entail feeding on pond bottom
Number of tooth rows	TR/OD	Food acquisition and substrate anchorage. Low values entail suspension feeders and midwater macrophagous tadpoles. More labial tooth rows enable tadpoles to feed on other resources by scraping or biting off material from substrate (macrophytes and carrion)

Abbreviations: BL, body length; DTH, dorsal tail fin height; OD, oral disk width; TAL, tail length; TL, total length; TMH, tail muscle height; TR, tooth rows number; VTH, ventral tail fin height.

TABLE 2 Species occurrence and tadpole abundance registered in 22 ponds distributed in different land uses (crop $N = 11$, livestock $N = 11$) of the Uruguayan savanna

Species	Crop		Livestock ranch	
	Occurrence	Abundance	Occurrence	Abundance
Bufonidae				
Melanophryniscus atroluteus	1^{a}	7	1^{a}	
Rhinella diptycha			5^{a}	
Rhinella dorbignyi	3^{a}	1	3^{a}	1
Hylidae				
Boana pulchella	4	22	7^{a}	35
Dendropsophus minutus	1	3	4^{a}	27
Dendropsophus sanborni	1^{a}	1	3^{a}	4
Ololygon aromothyella			3^{a}	
Pseudis minuta	1^{a}	6	7^{a}	5
Scinax fuscovarius			3^{a}	
Scinax nasicus	1	9		
Scinax squalirostris	5^{a}	21	9^{a}	128
Leptodactylidae				
Leptodactylus gracilis	4^{a}	14	5^{a}	41
Leptodactylus latinasus	2^{a}	2	4^{a}	
Leptodactylus latrans			5^{a}	432
Physalaemus biligonigerus	4^{a}	15	1	6
Physalaemus cuvieri	3^{a}		2^{a}	
Physalaemus gracilis	4	4	2^{a}	1
Physalaemus henselii			2^{a}	
Physalaemus riograndensis	5^{a}	42	6^{a}	8
Pseudopaludicola falcipes	7^{a}	25	11^{a}	19
Microhylidae				
Elachistocleis bicolor	2^{a}	2	5^{a}	8
Odontophrynidae				
Odontophrynus americanus			2	14

[a] Species also registered by calling activity of adults.

SES.MPD/FEve, positive significant values indicate clustering, and negative values indicate phylogenetic/functional overdispersion. Phylogenetic and functional diversity measures were computed using the picante (Kembel et al., 2010) and FD (Laliberté, Legendre, & Shipley, 2014) packages in R.

2.3 | Statistical analysis

We assessed sampling saturation overall and per land use with rarefaction and extrapolation curves with Hill numbers (Chao et al., 2014). We also estimated species richness per land use with two non-parametric richness estimators: one abundance-based (Chao 1) for tadpole data and one incidence-based (Chao 2) that include also anuran species identified from vocalizations. Sampling curves were generated using the iNext package (Hsieh, Ma, & Chao, 2016) in R.

Linear models with forward selection (Blanchet, Legendre, & Borcard, 2008) were used to evaluate the effect of pond characteristic (water depth) and the landscape effect (agricultural area) on SES.PD/MNTD or SES.FRic/FEve. Phylogenetic signal in traits may inflate type I error in the functional metrics used here (Diniz-filho, Cianciaruso, Rangel, & Bini, 2011; Duarte, Debastiani, Carlucci, & Diniz-Filho, 2018). So, we performed a phylogenetic correction for functional traits in two steps: (a) performing phylogenetic generalized least squares (PGLS) on each trait modeled only by its mean and variance; (b) taking the model normalized residuals as phylogeny-free estimates of trait variation (so-called S-component). These residuals were used to calculate phylogeny-free SES.FRic/FEve that was regressed on agricultural area and water depth. Finally, we performed a test for spatial autocorrelation in the residuals from all linear models, using Moran's I statistic implemented in the spdep package (Bivand & Piras, 2015) in R.

3 | RESULTS

Summarizing data over all sampled ponds, we found tadpoles of a total of 17 anuran species, representing 11 genera from five families (Table 2). Five additional anuran species were registered visually or acoustically as adults only (*Ololygon aromothyella*, *Physalaemus cuvieri*, *P. henselii*, *Rhinella diptycha*, and *Scinax fuscovarius*), bringing the total number of observed species to 22. Functional diversity indices were calculated from 294 individual measurements of five traits of the 17 species from the 22 ponds—note that many specimens had tail injuries and could not be included. We produced 67 barcodes (GenBank codes: MT460167–MT460233), corresponding to specimens of all species and tadpoles' series (MCP 13526–13602), that were used to confirm morphological identifications by comparing them with homologous fragments available in GenBank. Ponds in livestock ranches hosted about four times more tadpoles than agricultural ponds (Table 3). Across all study ponds, the most abundant species was *Leptodactylus latrans*, corresponding to 48% of all the collected individuals (Table 2). Even after the exclusion of *L. latrans*, livestock ranches hosted around two times more tadpoles than agricultural ponds. Species accumulation curves approached but did not reach an asymptote for anurans overall or any land use (Figure S3). Confidence interval of both indicators did not differ significantly between land uses (Table 3).

We observed a considerable degree of phylogenetic signal for most measured traits, indicating conserved evolution for three traits (Table S2). Overall, diversity metrics exhibited random distributions, with few values being significantly less than expected from the null model (Table S3). Only one cattle pond showed a significant low value of SES.FRic. Many crop ponds exhibited low values of SES.MNTD ($N = 7$), but only two ponds had significant low values, indicating environmental filtering. Regarding SES.FEve, one cattle pond showed functional clustering and one crop pond showed overdispersion (Table S3). Effect size of PD was not related to water depth or landscape, while MNTD was significantly related to land use intensification (Table 4). Average distances between each species and its nearest phylogenetic neighbor in the community decreased with agricultural area (Figure 2a). Variation in FRic was not explained by any of the measured variables while functional evenness was related to water depth (Figure 2b). However, when corrected by phylogenetic proximity, we found no significant relationship (Table 4). Considering that our estimate of FEve could be biased, due to the large abundance of *L. latrans*, we excluded this species and reanalyzed the data, but the overall patterns remained (Figure S4). None of the model residuals showed evidence of spatial autocorrelation (Table 4).

4 | DISCUSSION

In line with accumulating evidence of ongoing biodiversity erosion in subtropical grasslands (Egorov et al., 2014; Saccol et al., 2017; Staude et al., 2018), our results showed that anuran communities respond negatively to land use intensification (i.e., conversion from native grasslands to intensive croplands). Although we found no relationship between richness (functional or phylogenetic) and land use, our results show that ponds surrounded by intensive crops contain species that are closely related to one another. This can be linked to phylogenetic homogenization, in which specific anuran clades were more sensitive to disturbances associated with agriculture. Functional evenness decreased with water depth, although this was probably a statistical artifact generated by phylogenetic non-independency among species.

In our study, ponds in the sampled properties harbored half of the anuran species richness normally found in conservation areas of the Brazilian Pampa (André, Cechin, & Santos, 2019; Bolzan, Saccol, & Santos, 2016) and about 30% of the species registered at the Uruguayan savanna ecoregion (Canavero et al., 2010; Maneyro, 2008). Such impoverishment could be due to a sampling effect, because of low detection probabilities of many anuran species in the region (Moreira, Moura, & Maltchik, 2016). However, our results agree with other estimates of total richness at Pampa farmlands that were not based on a single sampling period (Bolzan, Hartmann, & Hartmann, 2014; Machado & Maltchik, 2010; Moreira & Maltchik, 2015; Saccol et al., 2017). Together, these studies revealed a complementary pattern in relation to the composition of anuran assemblages in the Pampa biome. Many species that could be considered as generalists have unexpected gaps in their distribution. Such idiosyncrasies are commonly attributed to local vegetation variations associated with soil heterogeneity, topography, and land use (Bolzan et al., 2014; Lipinski & Santos, 2014). In spite of the extensive geographic extension of the Uruguayan savanna ecoregion, few areas within it are protected by conservation units. It is interesting to note that the species registered as adults only have the southern limit of their geographical distribution in the border between Brazil and Uruguay (*P. cuvieri* and *S. fuscovarius*; Maneyro, 2008; Maneyro & Carreira, 2012) or have low frequency of occurrence in the region (*O. aromothyella*, *P. henselii*, and *R. diptycha*; Bolzan et al., 2014; Bolzan et al., 2016; Santos, Kopp, Spies,

TABLE 3 Amphibian species richness (number in parentheses include audio surveys), tadpole abundance, and abundance/incidence-based richness estimators across different land uses

	Species registered	Total abundance	Chao 1 (95% CI)	Chao2 (95% CI)
Total	17 (22)	903	17 (17–18.3)	22.1 (22–25.4)
Crop	15 (16)	174	16 (15.1–26)	21.7 (16.9–42)
Livestock	14 (21)	729	15 (14.1–28.1)	21.4 (21–26.8)

TABLE 4 Linear models relating phylogenetic and functional diversity to agricultural area and pond depth in the Uruguayan savanna, Brazil

Variable	Adj. R^2	$F_{(df)}$	Coefficients		Moran's *I*
			Area	Depth	(*p*-values)
Phylogenetic diversity					
SES.PD	≈0	$0.512_{(2,19)}$			0.93 (.16)
SES.MNTD	0.20^{*}	$6.811_{(2,19)}$	−1.44		0.67 (.25)
Functional diversity					
SES.FRic	0.07	$1.674_{(2,17)}$			−0.57 (.72)
SES.FRic (S-component)	≈0	$0.593_{(2,17)}$			0.7 (.24)
SES.FEve	0.17^{*}	$4.890_{(2,17)}$		−0.03	0.26 (.39)
SES.FEve (S-component)	≈0	$0.302_{(2,17)}$			−0.44 (.67)

Note: S-components control for phylogeny non-independency.
$^{*}p < .05$.

Trevisan, & Cechin, 2008). Moreover, they display an explosive reproduction strategy and are usually recorded after heavy rainfall events (>50 mm/day).

The decline in MNTD associated with ponds inside a large matrix of croplands indicates that they tend to harbor a greater number of recently divergent species. This result reflects the greater occurrence of foam nest species (family Leptodactylidae). Indeed, it seems that leptodactylids are more tolerant to habitat conversion (Machado & Maltchik, 2010; Nowakowski et al., 2018). Reproductive modes associated with foam nests, floating on pond or inside subterranean constructed nests, enable adults and tadpoles to overcome several drawbacks that are common in open environments: desiccation risk, thermal damage, difficulty in oxygen exchange, and microbial colonization (Fleming, Mackenzie, Cooper, & Kennedy, 2009; Hissa et al., 2008; Zina, 2006). Moreover, foam nest has been pointed at as a key innovation in Leptodactylidae, increasing diversification rates in lineages with it (Pereira et al., 2017). Yet, not all leptodactylids respond similarly to land use constraints, and foam nest is only one of the various potentially relevant life history traits involved (Medina, Ponssa, & Aráoz, 2016). For example, the most abundant species in our sampled ponds (*L. latrans*) appears to be well adapted to habitat modification (Heyer et al., 2010). However, recent studies have also reported low occurrence of *L. latrans* in areas surrounded by agricultural fields (Moreira & Maltchik, 2015; Prado & Rossa-Feres, 2014). Tadpoles of this species have schooling behavior, and relative levels of water availability seems to be an important factor affecting tadpole survival—*L. latrans* tadpoles select deeper microhabitats covered by clay substrate (Melo, Garey, & Rossa-Feres, 2018). Agricultural runoff and changes in the water availability associated with crop cycle can be particularly challenging for this species and others with similar behavior. To elucidate why clades other than Leptodactylidae are less frequent in agricultural ponds is a tricky task, because of synergetic effects among various co-occurring stressors affecting amphibians. Toxic stress has consequences on amphibian survival and susceptibility to parasites (Hua et al., 2017; Peltzer et al., 2013), but there is no consensus about the existence of phylogenetic signal in the impact of agrochemicals (Egea-Serrano, Relyea, Tejedo, & Torralva, 2012; Guenard, Carsten von der Ohe, Carlisle Walker, Lek, & Legendre, 2014).

Several studies have stressed the role of depth gradients enabling different guilds of anuran larvae to co-occur in the same habitat (Both, Cechin, Melo, & Hartz, 2011; Melo et al., 2018). Such link between tadpole guild and water depth is commonly invoked to explain responses to habitat alteration. For instance, Queiroz, da Silva, and Rossa-Feres (2015) suggested that some traits (triangular bodies, high dorsal and ventral fins, and the presence of flagella) enhanced tadpole performance in medium depth ponds (40–70 cm deep) in agricultural landscapes of the Cerrado ecoregion. Thus, nektonic species with such traits would be poorly adapted to shallow or deep waters in ponds. Although human induced changes are often correlated with amphibian functional diversity, decoupling observed patterns from phylogenetic autocorrelation is not a common practice. While other studies found anatomical modifications associated with some strata in the water column, we did not find a signal of changes in functional evenness when controlled for phylogenetic relatedness among species. In this sense, our results reinforce the idea that phylogenetic relationships have to be considered in analyses trying to correlate functional diversity with environmental variation or land use changes.

An important point here is that the presence of tadpoles depends on breeding-site preferences of adults (Both, Melo, Cechin, & Hartz, 2011). However, amphibian adults and tadpoles live in different contexts and land use may have distinct effects for each stage. Extensive cattle production of Uruguayan savanna is associated with native grasslands (Oliveira et al., 2017) and despite unsuitable management problems (i.e., overgrazing and erosion), traditional extensive livestock rearing have maintained many areas of Uruguayan savanna as grasslands with low level of disturbance (Oliveira et al., 2017; Overbeck et al., 2007). On the other hand, conversion to intensive agricultural lands is followed by a homogenization of plant communities and water physicochemical properties (Schiesari & Corrêa, 2016; Staude et al., 2018). Relative benefits and drawbacks of agroecosystems to amphibians are often crop dependent (Cosentino, Schooley, & Phillips, 2011), but common negative

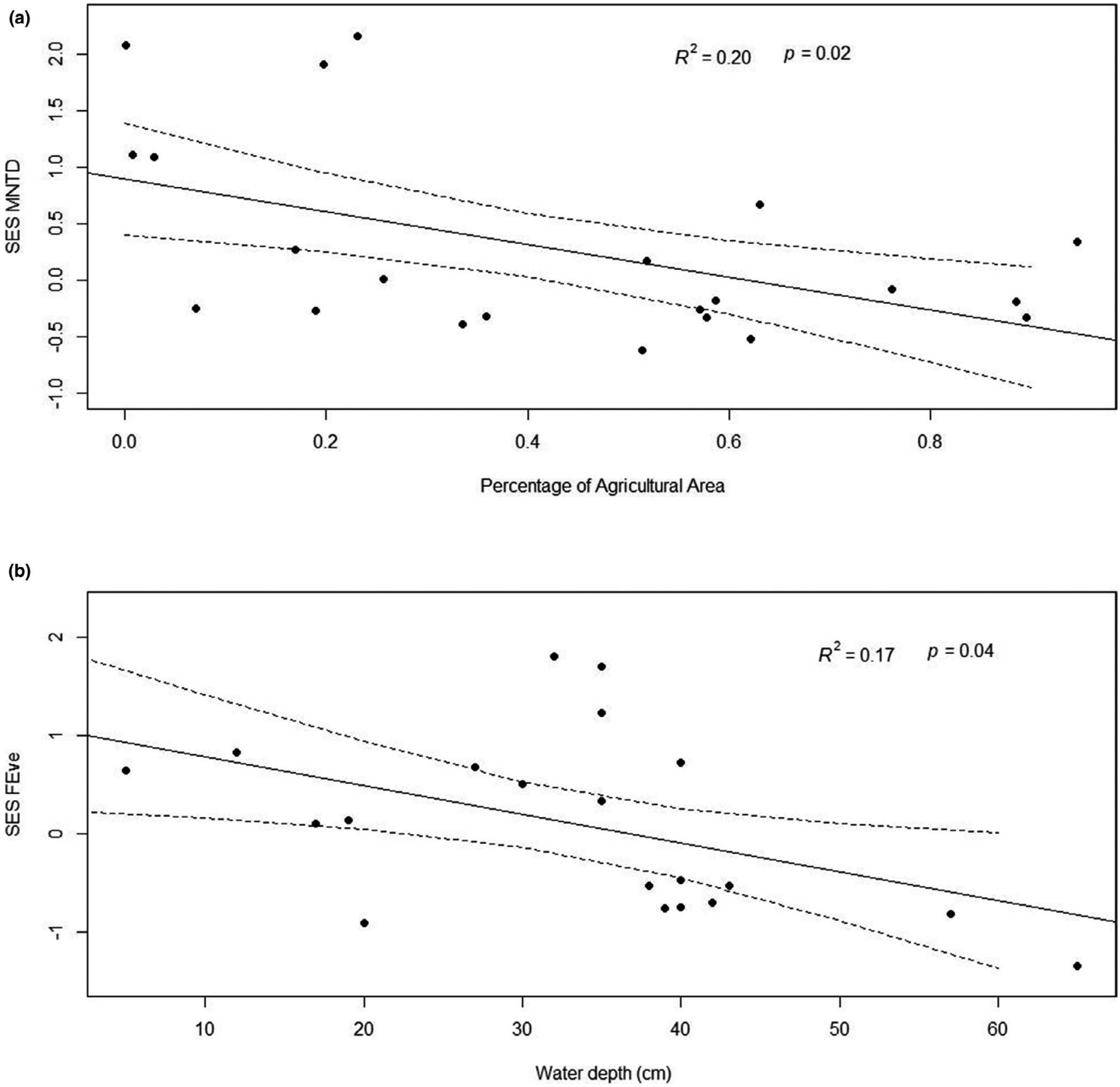

FIGURE 2 Relationship between phylogenetic/functional measures and environmental descriptors. (a) Mean phylogenetic relatedness (SES MNTD: standard effect size for mean nearest taxon distance) and landscape agricultural area; (b) functional evenness (SES FEve: standard effect size for functional evenness) and pond water depth. Hatched lines represent the 95% confidence boundaries

impacts result from the input of agrochemicals, periodic land preparation, and pond water consumption (Mann, Hyne, Choung, & Wilson, 2009; Schiesari & Corrêa, 2016). Thus, part of the lack of an influence of the land use on the tadpole functional metrics might be derived from constraints influencing juveniles and adults, because tadpoles do not choose the pond where they will live—only the microhabitat they use within a pond.

Studies that investigate community assembly in amphibians have observed divergent results according to the used null model (Both, Melo, et al., 2011; Moreira & Maltchik, 2012; Tsianou & Kallimanis, 2019). Our choice of null model was based on a specific biological hypothesis (i.e., habitat filtering) and statistical properties (i.e., low type I error rates). However, the performance of null models against different assembly processes is an ongoing debate and may depend on the choice of the metric (Miller, Farine, & Trisos, 2017). In this sense, we highlight that other mechanisms like negative biotic interaction may have contributed to our results. Two other subtle issues must be recognized here. First, it is possible that imperfect detectability could have influenced our results. For example, tadpoles that swim in head-up posture and form schools can be more easily sampled than solitary benthic species. Functional metrics seem to be robust to imperfect detection, although detectability has the potential to bias trait–environment relationships (Roth, Allan, Pearman, & Amrhein, 2017). We were not able to correct functional composition without repeated surveys in the same pond. Yet, detection-adjusted occupancy models indicated a relationship between occupancy and agricultural activities and/or livestock management in the study area (Moreira et al., 2016). Second, the unavailability of information before conversion to productive lands is another limitation of this study. This issue is particularly hard to consider when working in the Brazilian Pampa, because untouched native grasslands and forests have been reduced by almost 90% (Cordeiro & Hasenack, 2009) and most sampling designs, such as the one used in our study, usually underestimate biodiversity losses (França et al., 2016).

In conclusion, this study showed that phylogenetic relatedness mediates most responses of anuran species to land use intensification in South American subtropical grasslands. Because tadpoles are often key consumers in freshwater wetlands, our results have direct effects on ecosystem structure. Under a scenario of land sharing (i.e., integrating biodiversity conservation and food production on the same land), our observations highlight that extensive cattle grazing over wide native pastures may provide an alternative more compatible with conservation than intensive short-term crops. However, reconciling biodiversity conservation with economic gains is a tough task, which minimally should involve strategies of land sharing and land sparing (Phalan, Onial, Balmford, & Green, 2011). We hope that our results contribute to the current debate about management practices that help maintaining biodiversity in productive areas.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

LFBM and SCF conceived the project and coordinated several aspects of the study. LFBM collected and conducted the specimen identification, analyzed the data, and participated in the drafting of the manuscript. HZC analyzed the data and drafted the manuscript. All authors read and approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tdz08kpx4 (Moreira, de Castilhos, & Castroviejo-Fisher, 2020).

ORCID

Leonardo Felipe Bairos Moreira https://orcid.org/0000-0002-2753-9933

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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