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Differential responses of anuran assemblages to land use in agroecosystems of central Argentina

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ABSTRACT

Agriculture has been identified as one of the largest contributors to the current global biodiversity crisis. Amphibians are declining worldwide, and the loss of habitat and water contamination related to agricultural land uses have been suggested as the main drivers of this phenomenon. In central Argentina, the Pampean Region combines the highest rates of grassland replacement of South America, the lowest percentage of protected areas of the country, and the lack of studies exploring diversity patterns of native amphibians occurring in agroecosystems. To fill these gaps, we surveyed anuran (frogs and toads) assemblages from 342 breeding ponds located in three ecological units from central Argentina (Rolling, Flooding, and Inland Pampas) during three breeding seasons (2015–2018). We aimed to evaluate the importance of breeding habitat characteristics (ponds) and the surrounding landscape features as drivers of anuran diversity occurring in agricultural landscapes under the primary land uses of the region (cattle grazing and soybean cropping). We tested for the effects of breeding habitat characteristics and landscape features on anuran richness, abundance, and individual species occurrence, using GLMM models and information-theoretic procedures. Results indicated that species richness and total abundances were differently influenced by the habitat and landscape features across the ecological units. Overall, vegetation cover of the ponds and land use were the most important variables influencing richness and anuran abundance. The positive influence of pond vegetation cover on anuran assemblages was registered for all the ecological units, while different patterns emerged when we analyzed the effects of land use surrounding the ponds. Land use expressed as the percentage of soy crop surrounding the ponds negatively affected richness and abundance of anurans of the Flooding Pampas, but the inverse relation was found for assemblages occurring in the Inland Pampas. Moreover, multiple competing models suggested a positive correlation between anuran diversity and land-use heterogeneity, and pond density. The differential responses of anuran assemblages among the ecological units can be related to a combination of several factors encompassing regional soil characteristics (i.e., soil texture), land-use intensity as well as requirements of anuran species. We discussed the particularities of each ecological unit in order to recognize those conservation efforts that will favor anuran diversity in these altered landscapes and further contribute to achieving agricultural sustainability.

1. Introduction

Occupying 40% of Earth's land surface, global agriculture feeds over 7 billion people leading to profound global environmental impacts (FAO, 2019). Deforestation, land clearing, habitat fragmentation, and contamination as consequences of agricultural activities are among the major drivers of biodiversity loss (IPBES, 2019). The agricultural expansion and intensification worldwide are expected to undergo further increase, so a more accurate understanding of the effects of land use on biodiversity is, therefore, a critical conservation issue (Newbold et al., 2016).

The Rio de la Plata Grasslands are the main complex of grassland ecosystems in South America and constitute one of the most productive areas in the world (Bilenca and Miñarro, 2004). It includes the Pampas

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(central Argentina) and the Campos (Uruguay and the southern part of the Rio Grande do Sul State in Brazil) eco-regions. The entire region has been the scene of development, especially during the last century, of a vast livestock industry and a rapid increase in arable agriculture (Soriano, 1991). Notably, the Argentine Pampas has been received the most prominent land-use change related to the conversion of native grassland into agroecosystems, covering about fifty-two million hectares of productive organic soils (Baldi and Paruelo, 2008). This vast flat plain was primarily a livestock-grazing area, but significant land-use changes began between the 1960s and 1970s (Manuel-Navarrete et al., 2009). The most dramatic changes and impacts took place when technological innovation occurred in the 1990s with the introduction of both genetically modified soybeans tolerant to glyphosate in addition to non-tillage systems (Viglizzo et al., 2011).

Amphibians are experiencing population declines in all regions of the world. Nowadays, nearly 41% of amphibian species are threatened with extinction, being the group of vertebrates with more species under threat category in the IUCN Red List (Bishop et al., 2012; IUCN, 2020). The habitat loss associated with agricultural expansion and intensification is likely the single most important human activity affecting amphibian populations (Bishop et al., 2012). On the other hand, many amphibian species have been able to persist in agricultural landscapes around the world (Herzon and Helenius, 2008; Howell et al., 2019; Knutson et al., 2004; Pulsford et al., 2019). Moreover, some species have been found to be positively correlated with high intensity of crop cover and crop diversity (Collins and Fahrig, 2017; Koumaris and Fahrig, 2016), while others have benefited from the new habitats created around agricultural systems, including weirs, irrigation channels and dams (Brand and Snodgrass, 2009). Despite the evidence suggesting that the responses to land-use change could depend on species' life-history traits, several studies conducted in Europe and the USA identified the vegetation of wetlands and surrounding agricultural land uses as good predictors of anuran diversity (Boissinot et al., 2019; Koumaris and Fahrig, 2016). This growing body of literature also revealed that the amphibian species distribution and abundances might not be accurately predicted using variables describing the quality of a single habitat since amphibians requires a high level of habitat complementation (aquatic and terrestrial habitats) (Boissinot et al., 2019; Hartel et al., 2009). Thus, it is critical to combine multiple spatial scales (from microhabitat to landscapes) and different biological levels (community to species) in order to understand the effects of agricultural disturbance.

In South America, most of the studies that assessed the effects of land use on amphibian assemblages were mainly conducted in Amazonia, Atlantic Forest, and Cerrado Regions (e.g., Ferrante et al., 2017; Ribeiro et al., 2018) while few have explored agricultural impacts in formerly grassland landscapes. Some of them have reported adverse effects of pesticides on tadpoles (Agostini et al., 2020), changes in infection patterns of emerged diseases and abnormalities (Agostini and Burrowes, 2015; Agostini et al., 2013), and high frequency of abnormalities and enzymatic alterations (Brodeur et al., 2011). Other authors have reported detrimental effects at community and population levels in response to crops (Peltzer et al., 2006; Suárez et al., 2016) and differential effects of livestock grazing (Moreira et al., 2015; Verga et al., 2012). Nonetheless, these studies have been conducted at a local level and none of them allow to integrate the results on a more comprehensive scenario to understand how the most important agricultural activities carried out in the South American grasslands are affecting native amphibians.

The anuran diversity of the Pampean Region amounts to 34 species belonging to six families (Frost, 2020). The assemblages are composed of species with varied habitat requirements (terrestrial, burrowing, aquatic, and semi-aquatic habitats and species that climbed as the tree frogs) (Cei, 1980). Although these differences, all species reproduce in temporary and semi-temporary ponds, and their larvae are completely aquatic (Cei, 1980). A few species reproduce during winter, like *Boana pulchella* and *Physalaemus fernandezae* (Gallardo, 1974). Nonetheless, all species' reproductive activity peaks, including those that reproduce in winter, take place in spring and late summer rains (Gallardo, 1974). Especially in sectors with hydric limitations/warm summers and in the absence of hydrographic basins, reproductive choruses become particularly evident after intense rains events (Agostini et al., 2016).

This paper aims to evaluate the importance of breeding habitat characteristics (ponds), and the surrounding landscape features as drivers of anuran diversity occurring in agricultural landscapes under the primary land uses (cattle grazing and soybean cropping) of the Pampean Region. The extension of the Pampean Region is not uniform since differences in historical land-use patterns and the variation of climatic, edaphic, and biogeographic characteristics (Soriano, 1991). Therefore, we first characterized the amphibian assemblages in order to recognize the species composition for three ecological units (Rolling, Flooding, and Inland Pampas). Then, we hypothesize that pond vegetation and land use surrounding the ponds primarily affect anuran species richness and abundance. By contrast, we hypothesize that the contribution of habitat and landscape features to species occurrence varied among taxa. Several authors have reported that the quality of breeding sites is critical for reproduction and larval development (Wells, 2007). The vegetation of the ponds can reflect the quality of water bodies and has been extensively recognized as one of the most critical habitat features supporting amphibian reproduction (e.g., Boissinot et al., 2019; Hartel et al., 2009; Peltzer et al., 2006). Since we conducted the study during the anuran breeding season, we predicted that for all the ecological units, the richness and abundances should be notably favored by the vegetation cover of the ponds. Extensive crops represent the most modified scenario among the productive activities since the original biome is entirely replaced by a monoculture (Viglizzo et al., 2001). Additionally, wetlands occurring adjacent to soy crops are likely to receive high concentrations of pesticides and fertilizers as a result of run-off or spray-drift (Agostini et al., 2020; Carvalho, 2017; Herrera et al., 2013). Therefore, we expect that species richness and total abundance should be negatively related to the percentage of soy crops surrounding the ponds. Simultaneously, human-dominated landscapes with high diversity of patches (crops, pastures, non-grazed grassland, and wetlands) can provide landscape heterogeneity and connectivity (Collins and Fahrig, 2017; Ficetola and De Bernardi, 2004). Then, we predict that land-use heterogeneity and density of ponds should secondarily benefit anuran diversity. Finally, since species conformed anuran assemblages from the Pampean Region differ in life-history traits (Cei, 1980), we expect that habitat and landscape features should differently affect the anuran species. Based on the results obtained, we discuss the conservation outcomes of this work, contributing to agricultural sustainability.

2. Material and methods

2.1. Study area

Our study area (≅ 312,000 km^2) belongs to the Pampean Region and is located in the center of Argentina, extending to Buenos Aires, La Pampa, Córdoba, and Santa Fe Provinces (Fig. 1). The climate is warm-temperate, with mean temperatures varying between 15 °C in the south and 18 °C in the north. Annual rainfall decreases from 1000 mm in the NE to 800 mm in the SW, although inter-annual variability of rainfall is quite frequent in the Pampas with extensive rainfall or drought (Labraga et al., 2002; Scian et al., 2006). We conducted this study in three ecological units of the Pampas: Rolling Pampas (RP), Flooding Pampas (FP), and Inland Pampas (IP), which present differences in geomorphology, drainage, soils, physiography, and vegetation (Soriano, 1991). These ecological units also differ in land-use patterns resulting from different historical processes (Baeza and Paruelo, 2020). In the RP, cropland has replaced more than 75% of the native vegetation, and cattle breeding has progressively turned into an intensive activity, demanding the use of grain supplements for cattle and feedlots farms. By

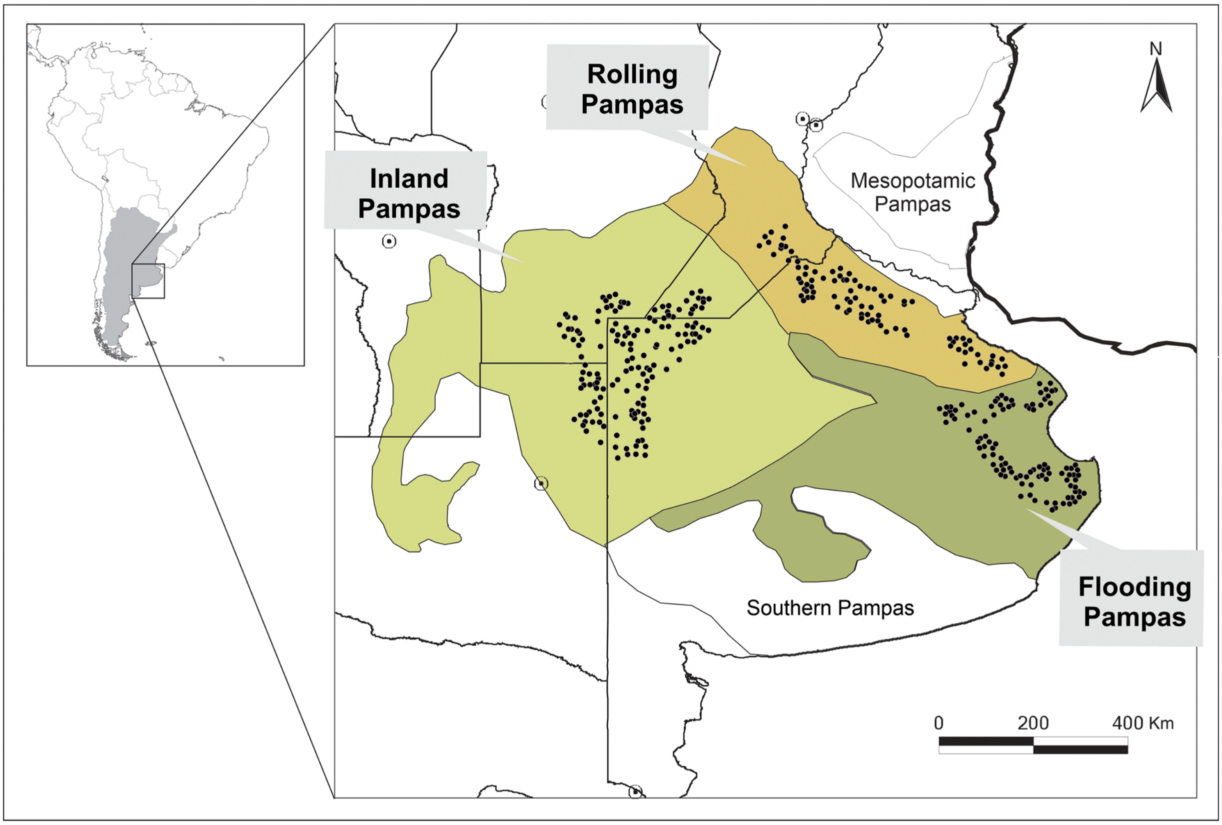

Fig. 1. Map of the study area. Circles are shown the 342 ponds surveyed.

contrast, in the FP, extensive cattle breeding in semi-natural grasslands is still the main farming activity (>85%), and the presence of summer crops is relatively low. Finally, the IP have mixed production systems devoted to both crops and animal husbandry (Baeza and Paruelo, 2020; INDEC, 2019).

Most amphibian species from the Pampean Region occur in ponds and temporary flooded areas (Cei, 1980), commonly related to agricultural lands. We created a wetland area dataset within the study area by digitizing 2013 aerial photographs in ArcGIS (ESRI, 2011) and recognizing those areas suitable to conduct the surveys. Then, we randomly selected the ponds when we reached the area, and the final selection was made based on accessibility and landowner permissions. We only included natural ponds between 1000 and 5000 m^2, surrounded by lands intended for soy cropping and cattle grazing (pastures and semi-natural grasslands). Several ponds were located in plots under unique land use. These ponds were then entirely surrounded by soybean crops or by pastures and semi-natural grasslands, while other ponds were located in plots with mixed land use.

2.2. Anuran sampling

We conducted a 3-years survey extended from October to November and February to March (2015–16, 2016–17, and 2017–18). These moments are coincident with the breeding seasons reported for all the species involved in this study (Cei, 1980; Maneyro and Carreira, 2016). To guarantee high species detection, we conducted surveys, especially after heavy rainfall (Agostini et al. 2006; 2020). Sampling was restricted to breeding sites, at which we employed survey techniques to detect amphibians during breeding seasons (Scott and Woodward, 1994). We conducted the surveys during warm nights (2200–0200 hrs.) with low wind (≅10 km/h). The minimum air temperature for surveys was 15 °C. We combined two methods to detect anurans. First, we conducted acoustic monitoring over 5 min recording the species calling. Then, we conducted a visual encounter survey, employing three fixed transects (30 × 2 m) per pond. In this case, we also recorded the number of observed individuals for each species (total abundance). For specific names and systematic proposal, we followed Frost (2020).

2.3. Breeding habitat characteristics and landscape features

We recorded *in situ* three sets of related habitat characteristics, including seven variables representing water quality (temperature, dissolved oxygen -DO-, conductivity, and pH), pond morphometry (area and average depth), and pond vegetation cover (submerged and emerged vegetation). Water quality parameters were measured using a Hanna VCx3 multiparameter. In the absence of aerial photographs available for each day and pond surveyed, we estimated the area of the ponds measuring the length and width, which were then adjusted to calculate the area of an ellipse or circle. We obtained the pond average depth by measuring the depth in five different sites across the length and width. To determine the vegetation cover of the ponds, we performed ten randomly selected quadrants/per (50 × 50 cm) and then constructed an index vegetation cover of submerged and emerged vegetation per pond, following Yin et al. (2000). The vegetation cover of each pond ranged from 0 to 100 and was expressed as the average of index values for both vegetation types. The landscape features included four variables measured *in situ*: land use, distance to the nearest pond, pond density, and land-use heterogeneity. The land use surrounding the ponds was visually estimated and expressed as the % of the edge of the pond covered by soy crops. In a 1 km-radio patch from the center of ponds, we measured the distance to the nearest pond and the density of ponds. We finally expressed the land-use heterogeneity as the Shannon diversity index of land use following Collins and Fahrig (2017). The index was build using the area of plots intended for intensive crops (soy, corn, wheat, sorghum, and sunflower), sown pastures, natural grasslands for livestock, and non-grazed natural grasslands. We measured breeding habitat characteristics and landscape features during the afternoon of the same day that the nocturnal anuran survey was conducted.

2.4. Statistical analysis

We used GLMM -Generalized Linear Mixed Models- (Zuur et al., 2009) to better understand the relative importance of habitat and landscape features in anurans assemblages occurring in agroecosystems with different land use from the Pampean Region. Response variables included species richness, total abundance of anurans, and species occurrence (presence/absence). The richness and species occurrence were determined based on acoustic and visual surveys, while total abundance was recorded only through visual surveys. The occurrence analysis was limited to those species with a presence between 90 and 10% of the ponds sampled (Peduzzi et al., 1996) and occurring in the three ecological units. Before conducting analyses, we test the spatial autocorrelation level for both response and explanatory variables employing the Mantel's Test (Mantel, 1967) (Supplemental materials: Appendix A). Models were fixed to Poisson error structure (log link function, for counting data = species richness and total abundance) and Binomial error structure (logit-link function, for binomial data = species presence/absence). The predictor variables were pond area (PA), pond average depth (PAvD), pond vegetation cover (PVC), land use (LU), distance to the nearest pond (DIS), pond density (PD), and land-use heterogeneity (LUH). We introduced to all models the breeding season (season 1, 2, and 3) as a random effect in order to control differences in anuran activity between years. Since differences in land use patterns and bioclimatic conditions across the Pampean Region (Soriano, 1991), we analyzed the effects of predictors on the anuran richness, abundance, and species occurrence separately for each ecological unit (RP, FP, and IP). We checked the fit of each global model before conducting model selection using graphical validation tools for the Poisson and Binomial data distributions (Zuur et al., 2009). Model performances were evaluated with information-theoretic procedures (Burnham and Anderson, 2002). Model selection was based on Akaike's information criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2002). We used two measures to provide further insight into the amount of uncertainty in model selection. The first measure was the difference in AICc between the best-approximating model and all the other models (ΔAIC_c). A ΔAICc score between 0 and 2 indicates substantial support for the model (Burnham and Anderson, 2002). Then, we obtained the relative importance of each variable retained in all the selected models (ΔAIC_c to the best model <3) using the sum of AIC weights of models, including the target variable. To estimate the relative effects of the predictors, we calculated the model weighted mean standardized coefficients from all the models selected. We calculated 95% confidence intervals for coefficients of explanatory variables so that when a confidence interval did not include zero indicated that the considered factor had a statistically significant effect on response variables (Burnham and Anderson, 2002). All statistical analyses and data manipulations were performed in the R environment (R Core Team, 2020).

Previous studies conducted in the area showed that water quality parameters did not vary significantly among ponds associated with different land uses (Agostini and Burrowes, 2015; Agostini et al., 2013, 2020). Considering that water quality values were within ranges leading to no detrimental effects on amphibians (Wells, 2007) (Supplemental materials: Appendix B), we informed these variables to describe and characterize the ponds. However, these data were not further included in statistical analyses for testing them as predictors of anuran richness, abundance, and occurrence.

3. Results

3.1. Assemblages' species composition

During three breeding seasons, we surveyed a total of 342 ponds (91 in RP, 102 in FP, and 149 in IP) in rural landscapes from the Pampean Region. The average of the minimum distance between ponds was 15.37 km (Min 7.92, Max 19.21). The maximum and the minimum number of ponds sampled in a single night were 4 and 1, respectively. We reported a total of 18 species (16 in RP, 13 in FP, and 13 in IP) belonging to six anuran families. *Rhinella fernandezae, Boana pulchella, Leptodactylus luctator, Pseudopaludicola falcipes,* and *Odontophrynus americanus* were the most common species at regional level, although ranking different in each ecological unit for the proportion of ponds occupied and total abundance (Table 1). The maximum number of species at the same pond was 10 (registered in 85 ponds), and no pond was founded unoccupied.

3.2. Assemblages responses

The Mantel's tests indicated that both response and explanatory variables did not show any significant spatial autocorrelation (Supplemental materials: Appendix A). Across the ecological units, species richness and total abundances were influenced differently by the habitat and landscape features. The values for all predictor variables are shown in Table 2.

3.2.1. The Rolling Pampas

Species richness was primarily associated with pond vegetation cover and land use (retained in 7 and 4 models, respectively). The relative influence (sum of AIC weights) of pond vegetation cover was 0.69, while for the land use surrounding the ponds was 0.31 (Table 3A). The model-averaged coefficients and 95% confidence intervals identified the pond vegetation cover as the only significant predictor for the species richness in the RP. Richness was positively related with pond vegetation cover (estimate 0.29 ± 0.13 SE, 95% [CI 0.13 – 0.45]) (Fig. 2A). The anuran abundance in this ecological unit was influenced by pond vegetation cover, land use, distance to the nearest pond, and density of the ponds. The relative influence of pond vegetation cover and land use was higher (0.61 and 0.48 respectively) than other predictors summing between 0.30 and 0.29 (Table 3A). The model-average coefficients indicated that anuran abundance was positively correlated to pond vegetation cover (estimate 0.31 ± 0.17 SE, 95% CI [0.19 – 0.43]) (Fig. 2A).

3.2.2. The Flooding Pampas

The variables that best predicted anuran richness and retained for the best models were pond vegetation cover, land use, and land-use heterogeneity, summing 0.47 and 0.52, and 0.39 of AIC weights, respectively (Table 3B). The model-average coefficients indicated significant effects of the three predictors on richness. Pond vegetation cover and land-use heterogeneity positively influenced the anuran riches (PVC estimate 0.59 ± 0.13 SE, 95% [CI 0.44 – 0.73], LUH estimate 0.35 ± 0.16 SE, 95% [CI 0.23 – 0.47]) while land use around the ponds expressed as the soy crop cover predicted a negative relation (estimate -0.26 ± 0.10 SE, 95% [CI -0.43, -0.09]) (Fig. 2B). We found that those variables affecting the anuran richness also influenced the anuran abundance. The vegetation cover of the ponds, land use, and land-use heterogeneity were retained for 6, 8, and 5 models, respectively (Table 3B). Land use had a strong influence on the anuran abundance (0.60), showing a negative effect (estimate -0.25 ± 0.11 SE, 95% [CI, -0.38, -0.14] (Table 3B, Fig. 2B). Pond vegetation cover and land-use heterogeneity followed to soy crop in relative influence (0.43 and 0.40) having positive effects on total abundance (PVC estimate 0.21 ± 0.09 SE, 95% [CI 0.12 – 0.30]; LUH: estimate 0.35 ± 0.15 SE, 95% [CI 0.13 – 0.51]) (Table 3B, Fig. 2B).

3.2.3. The Inland Pampas

Pond vegetation cover, pond density, and land-use heterogeneity resulted in the most influential variables predicting species richness showing similar influence (0.36, 0.40, and 0.39, respectively) (Table 3C). Only the density of ponds had a significatively positive effect

Table 1
Species composition of the anuran assemblages in three ecological units of the Pampas, central Argentina (2015-2018). Species occurrence is expressed as % of occupied ponds and the abundance is expressed as means (and standard errors) of the total individuals sampled.

Anuran species	Rolling Pampas (N = 91 ponds)		Flooding Pampas (N = 102 ponds)		Inland Pampas (N = 149 ponds)	
	Species occurrence	Abundance	Species occurrence	Abundance	Species occurrence	Abundance
Bufonidae						
Rhinella arenarum	6.5	5.3 (±2.4)	8.8	5.9 (±2.4)	8.7	3.9 (±2.9)
*Rhinella fernandezae**	58.2	13.3 (±5.4)	67.3	13.7 (±4.3)	63.0	21.9 (±7.7)
Ceratophryidae						
Ceratophrys ornata	–	–	5.9	3.5 (±1.6)	4.0	1.9 (±0.9)
Ceratophrys cranwelli	–	–	–	–	3.3	2.1 (±1.8)
Hylidae						
*Boana pulchella**	89.0	19.5 (±31.3)	88.1	25.2 (±13.9)	32.8	8.5 (±4.6)
Dendropsophus nanus	13.1	0.9 (±0.6)	–	–	–	–
Pseudis minuta	8.8	4.0 (±3.1)	38.2	6.8 (±7.5)	–	–
Scinax granulatus	16.5	2.9 (±1.1)	24.5	3.0 (±1.9)	5.3	0.8 (±0.5)
Scinax nasicus	12.0	1.6 (±2.3)	–	–	2.6	0.4 (±0.1)
Scinax squalirostris	31.9	11.1 (±3.6)	58.8	12.5 (±6.9)	–	–
Leptodactylidae						
Leptodactylus gracilis	16.5	1.9 (±1.7)	4.9	0.3 (±0.0)	36.9	6.3 (±1.5)
Leptodactylus latinasus	20.9	3.4 (±1.9)	10.7	0.4 (±0.0)	44.2	6.4 (±0.9)
*Leptodactylus luctator**	68.1	5.6 (2.4)	59.8	8.6 (±2.9)	44.9	12.8 (±6.2)
Physalaemus biligonigerus	46.1	5.3 (±3.0)	–	–	45.6	11.9 (±8.8)
Physalaemus fernandezae	26.8	4.0 (±2.8)	45.0	6.3 (±0.9)	–	–
*Pseudopaludicola falcipes**	31.9	3.7 (±1.1)	58.8	5.5 (±2.3)	13.2	4.9 (±1.5)
Microhylidae						
Elachistocleis bicolor	5.5	0.02 (±1.9)	–	–	–	–
Odontophrynidae						
*Odontophrynus americanus**	43.9	6.9 (±10.0)	60.7	7.8 (±3.7)	45.6	14.4 (±3.5)

* Species used for models testing the influence of habitat and landscapes features on anuran species occurrence. Species occurrence was obtained using acoustic and visual surveys and abundance was registered using visual encounter surveys.

Table 2
Mean values and standard errors of habitat and landscape features associated with ponds of the three ecological units assessed in the Pampean Region.

Breeding habitat and landscapes features	Ecological Unit		
	Rolling Pampas (N = 91 ponds)	Flooding Pampas (N = 102 ponds)	Inland Pampas (N = 149 ponds)
Pond area (m^2)	3452 ± 658	4045 ± 658	3024 ± 904
Pond average depth (cm)	45.2 ± 12.0	58.2 ± 21.1	39.2 ± 17.8
Pond vegetation cover index	44.3 ± 20.3	91.5 ± 10.4	67.3 ± 11.4
Soy crop cover (%)	78.7 ± 36.1	48.5 ± 29.7	51.5 ± 20.1
Distance to the nearest pond (m)	675.3 ± 316.5	208.9 ± 196.0	476.3 ± 267.3
Pond density	2.1 ± 4.8	10.5 ± 2.9	4.0 ± 2.1
Land-use heterogeneity (Shannon diversity index)	0.2 ± 0.1	1.4 ± 0.2	0.7 ± 0.2

on species richness (estimate 0.28 ± 0.15 SE, 95% [CI 0.11 – 0.45]) (Fig. 2.C). The anuran abundance was primarily associated with pond vegetation cover whit a high relative influence (0.49) and retained for 6 models (Table 3C). As in the other ecological units, this predictor was positively associated with anuran abundances (0.30 ± 0.12 SE, 95% [CI 0.10 – 0.50]) (Fig. 2C). The land use around the ponds also contributed to total abundance (retained for 4 and summing relative influence 0.35), but in this case, we found a positive relation between anuran abundance and soy crop cover (0.21 ± 0.16 SE, 95% [CI 0.10 – 0.32]) (Table 3C, Fig. 2C). Pond density and land-use heterogeneity were retained for 4 and 3 models and had intermediates contributions (0.28 and 0.25, respectively) but did not significantly influence anuran abundance (Table 3C, Fig. 2C).

3.3. Species responses

In the Rolling Pampas, pond characteristics appeared to influence species occurrence more than the landscape context. In this sense, pond vegetation cover and pond average depth were the most important predictors retained in the best models and showed high relative influence values (Table 4A). The occurrence of four species was positively related to pond vegetation cover: *B. pulchella* (estimate 0.45 ± 0.15 SE, 95% [CI 0.29 – 0.61]), *L. luctator* (estimate 0.22 ± 0.10 SE, 95% [CI 0.09 – 0.35]), *R. fernandezae* (estimate 0.38 ± 0.15 SE, 95% [CI 0.17 – 0.59]) and *O. americanus* (estimate 0.23 ± 0.09 SE, 95% [CI 0.03 – 0.43]) and (Fig. 2A). We also detected a marginal negative influence of land use over *B. pulchella* occurrence (Fig. 2A). The average depth positively affected the occurrence of *B. pulchella* (estimate 0.23 ± 0.13 SE, 95% [CI 0.09 – 0.37) (Table 4A, Fig. 2A). Regarding the Flooding Pampas, we found similar results of the habitat features influencing the occurrence of the five species and a more relevant influence of land-use heterogeneity (Table 4B, Fig. 2B). We found a negative influence of land use over the occurrence of *B. pulchella* (estimate -0.30 ± 0.12 SE, 95% [CI -0.45, -0.15]) and *L. luctator* (estimate -0.25 ± 0.16 SE, 95% [CI -0.42, -0.08]). The positive relation to land-use heterogeneity was detected for *B. pulchella* (estimate 0.19 ± 0.11 SE, 95% [CI 0.11 – 0.27]), *L. luctator* (estimate 0.35 ± 0.17 SE, 95% [CI 0.18 – 0.52]), *R. fernandezae* (estimate 0.24 ± 0.11 SE, 95% [CI 0.11 – 0.37]) and it was also marginal for and *O americanus* (Fig. 2B). Lastly, in the Inland Pampas, the landscape features measured acquired more relevance influencing the species occurrence compared to the other ecological units (Table 4C). The occurrence of two species was positively influenced by land-use heterogeneity: *L. luctator* (estimate 0.49 ± 0.23 SE, 95% [CI 0.29 – 0.69]) and *R. fernandezae* (estimate 0.35 ± 0.13 SE, 95% [CI 0.18 – 0.52]) (Fig. 2C). Additionally, pond density was positively related to *L. luctator* (estimate 0.25 ± 0.10 SE, 95% [CI 0.10 – 0.40]) and *O. americanus*

Table 3
Results obtained from the model selection procedure testing the effects of breeding habitat and landscape features on anuran richness and total abundance in three ecological units of the Pampas of central Argentina. **RI**: relative importance of each variable is reflecting the sum of AIC weights of all models, including the variable. **NM**: number of models in which variable was retained. Significant effects are bolded.

Response variables	PA		PAvD		PVC		LU		DIS		PD		LUH	
	RI	NM	RI	NM	RI	NM	RI	NM	RI	NM	RI	NM	RI	NM
A. Rolling Pampas														
Species richness	0.09	1	0.08	1	**0.69**	**7**	0.31	4	0.05	1			0.17	2
Total abundance	0.17	1	0.15	1	**0.61**	**8**	0.48	5	0.30	4	0.29	4	0.21	2
B. Flooding Pampas														
Species richness	0.16	2			**0.47**	**5**	**0.52**	**5**	0.05	1	0.05	1	**0.39**	**4**
Total abundance			0.05	1	**0.43**	**6**	**0.60**	**8**	0.02	1	0.11	2	**0.40**	**5**
C. Inland Pampas														
Species richness			0.07	1	0.36	4	0.10	1	0.16	2	**0.40**	**5**	0.21	2
Total abundance	0.09	1			**0.49**	**6**	**0.35**	**4**	0.09	1	0.28	4	0.25	3

Breeding habitat characteristics. PA = Pond area. PAvD = Pond average depth. PVC = Pond vegetation cover. **Landscapes features.** LU = Land use. DIS = Distance to the nearest pond. PD = Pond density. LUH = Land-use heterogeneity.

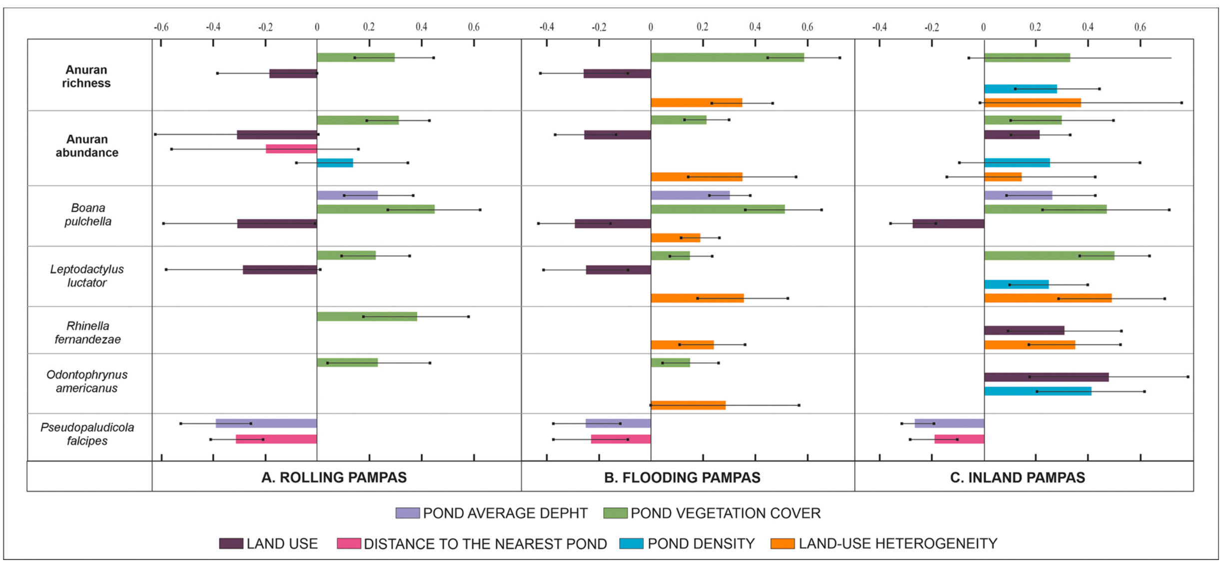

Fig. 2. Colored bars indicate the model-weighted means standardized coefficients and its 95% confidence intervals, showing the direction and magnitude of variable effects on anuran richness abundance and species occurrence in assemblages from the Argentinean Pampas. We only graph those variables that were selected for the best models (ΔAIC_c <3). A: Rolling Pampas. B: Flooding Pampas. C: Inland Pampas.

(estimate 0.42 ± 0.23 SE, 95% [CI 0.20 – 0.60]) (Fig. 2C). In contrast to results obtained for the other ecological units, two species responded positively to soy crops cover in the Inland Pampas: *R. fernandezae* (estimate 0.31 ± 0.12 SE, 95% [CI 0.09 – 0.53]) and O. *americanus* (estimate 0.48 ± 0.17 SE, 95% [CI 0.18 – 0.78]) (Fig. 2C).

Across the tree ecological units, *Pseudopaludicola falcipes* was the only species in which occurrence was influenced negatively by distance to the nearest pond and negatively related to the average depth of the ponds (Table 4, Fig. 2).

4. Discussion

This is the first study exploring how anurans occurring in agroecosystems from the Pampean Region respond to habitat and landscape attributes. Our study covering 342 ponds along more than 300,000 km^2 of agricultural lands from Central Argentina revealed that the responses are context-dependent and varied among ecological units. The responses also differed depending on the diversity measures (richness, abundance, and species occurrence) selected for testing the hypotheses. Overall, vegetation cover of the ponds and land use were the most important variables influencing richness and anuran abundance, while several combinations of different variables influenced the occurrence of the most representative anuran species of the region.

4.1. Breeding habitat characteristics

In concordance with our first prediction, vegetation cover of the ponds was the most important habitat characteristic supporting anuran richness and abundance, showing a positive influence across the three ecological units. The index we used to measure the vegetation of the ponds (Yin et al., 2000) combined the presence and cover of emerged and submerged macrophytes. Then, a high diversity index reflects the existence of breeding habitat for species with different reproduction strategies, e.g., Tree Frogs species vocalizing from emerged vegetation and species of Leptodactylidae family constructing floating foam nest using submerged and short emerged macrophytes (Wells, 2007). We conducted our study during breeding seasons; then, results may express that the vegetation cover is especially a good predictor for this particular moment of the anuran life cycle. Nonetheless, the aquatic vegetation not only offers a variety of microhabitat for reproduction but also could provide habitat for feeding and refuge of tadpoles (Hoff et al., 1999), reducing the toxicity of agrochemicals (Brogan and Relyea, 2014;

Table 4
Results obtained from the model selection procedure testing the effects of breeding habitat and landscape features on species occurrence in three ecological units of the Pampas of central Argentina. **RI**: relative importance of each variable is reflecting the sum of AIC weights of all models, including the variable. **NM**: number of models in which variable was retained. Significant effects are bolded.

Response variables	PA		PAvD		PVC		LU		DIS		PD		LUH	
	RI	NM	RI	NM	RI	NM	RI	NM	RI	NM	RI	NM	RI	NM
A. Rolling Pampas														
Boana pulchella	0.13	1	**0.42**	**4**	**0.60**	**7**	0.31	3					0.23	2
Rhinella fernandezae	0.06	1	0.17	2	**0.35**	**4**	0.15	2	0.07	1			0.21	2
Leptodactylus luctator	0.09	1	0.20	2	**0.63**	**8**	0.39	3	0.01	1	0.15	2	0.27	2
Odontophrynus americanus			0.04	1	**0.35**	**4**	0.10	1			0.12	2	0.09	1
Pseudopaludicola falcipes			**0.41**	**4**	0.16	1	0.15	1	**0.35**	**3**	0.09	1	0.11	1
B. Flooding Pampas														
Boana pulchella	0.11	1	**0.58**	**6**	**0.62**	**9**	**0.54**	**6**	0.20	2	0.23	2	**0.42**	**5**
Rhinella fernandezae					0.10	1	0.07	1	0.04	1			**0.42**	**5**
Leptodactylus luctator	0.12	2	0.03	1	**0.60**	**6**	**0.45**	**4**	0.06	1	0.08	1	**0.41**	**4**
Odontophrynus americanus			0.09	1	**0.48**	**3**	0.13	1			0.05	1	0.26	2
Pseudopaludicola falcipes			**0.36**	**4**	0.21	2	0.05	1	**0.48**	**5**	0.04	1	0.19	2
C. Inland Pampas														
Boana pulchella			**0.39**	**5**	**0.43**	**5**	**0.51**	**6**			0.07	1	0.09	1
Rhinella fernandezae			0.13	2	0.09	1	**0.46**	**4**	0.10	1	0.12	2	**05.1**	**5**
Leptodactylus luctator	0.07	1	0.09	1	**0.61**	**6**	0.13	2	0.23	3	**0.50**	**5**	**0.51**	**5**
Odontophrynus americanus	0.05	1			0.17	2	**0.41**	**4**			**0.30**	**3**	0.15	1
Pseudopaludicola falcipes	0.05	1	**0.41**	**4**	0.12	2	0.04	1	**0.43**	**4**	0.27	2	0.04	1

Breeding habitat characteristics. PA = Pond area. PAvD = Pond average depth. PVC = Pond vegetation cover. **Landscapes features.** LU = Land use. DIS = Distance to the nearest pond. PD = Pond density. LUH = Land-use heterogeneity.

Lizotte et al., 2011) and modulate the hydroperiod and physicochemical parameters of wetlands (Maisonneuve and Rioux, 2001). We argue that the presence and cover of aquatic vegetation can benefit anurans throughout the entire life cycle and guarantee populations' viability in these agricultural landscapes.

Worldwide, agricultural practices have caused severe wetlands degradation both in area and functionality (DeLucia et al., 2019). The contamination of wetlands from human-dominated landscapes has been associated with crop pest management involving broad-spectrum herbicides like glyphosate and 2,4- D (Agostini et al., 2020; Berman et al., 2018), which can directly cause the loss of aquatic vegetation (Ronco et al., 2008). Furthermore, livestock access to ponds has been shown to have adverse effects on reproduction in many amphibians by affecting water quality and coverage of submerged macrophytes (Howell et al., 2019; Knutson et al., 2004). We did not explore the individual effects of each land use practice and management on aquatic vegetation cover. However, we can expect that when intensively applied, both soy cropping and cattle grazing may reduce the breeding habitats and compromise anuran population viability.

Our models do not identify any of the morphometric variables of the ponds as predictors of anuran richness or abundance. Several studies outlined the scarce importance of wetland surface for the richness of animal communities in wetlands (e.g., Oertli et al., 2002), likely because other pond features have a more direct effect on the species presence (Ficetola and De Bernardi, 2004). Our results may be explained by the fact that we studied similar ponds concerning their areas and depth (see Supplemental materials: Appendix B).

4.2. Land-use effects across the ecological units

Among the landscape features studied, we identified the land use immediately surrounding the ponds as the best predictors of richness and anuran abundance. We had predicted that anuran assemblages from the three ecological units should respond negatively to the percentage of soy crops surrounding the ponds. This prediction was fulfilled in the Flooding Pampas. On the other hand, the negative effect of soy crops on anuran abundance from the Rolling Pampas was marginal but not significant and showed the inverse relationship with the abundance of anurans from the Inland Pampas (see Fig. 2). The differential responses among the ecological units could be related to a combination of several factors encompassing soil characteristics, history, the intensity of land use, and some particular requirements of anuran species conforming the assemblages.

Currently, the Rolling Pampas is the most intensive productive area of South America, and cropland has replaced more than 75% of the native vegetation affecting the integrity of the ecosystem (Baeza and Paruelo, 2020). The high productivity of the area allows the exploitation of soil resources mainly through summer crops (soybean, maize, and sunflower) (INDEC, 2019). This variety of crops is linked with agrochemicals used, which are massively applied and can reach the pond surface in high concentrations (Agostini et al., 2020; Viglizzo et al., 2011). Simultaneously, the intensification of livestock is reflected in the increased use of grains for supplemental feed and feedlots (Modernel et al., 2016). The growing presence of farms using feedlots and grain supplements for livestock means a severe threat because it increases the pressure levels in this already damaged system (García et al., 2013). The intensity of both agricultural practices, soy cropping and cattle grazing, can explain why we failed to identify the effects of land use on anuran richness and abundance. The little influence of the other landscape features may be explained by the fact that the agricultural intensification in this region decreased the inter-patch connectivity and lead to land homogenization (Baeza and Paruelo, 2020). In summary, our results reveal that anuran assemblages occurring in the Rolling Pampas are dealing with several issues related to both soy crop and cattle impacts that may reduce pond water quality, land-use heterogeneity, and compromise the connectivity between critical habitats.

In the Flooding Pampas, land use is still mostly extensive, resulting in highly diverse cultural/rural landscapes and determining that most of the land remains as semi-natural grassland (Baeza and Paruelo, 2020). The relatively low stocking rates and the limitations for cropping have determined that the Flooding Pampas units concentrate on one of the largest areas of native and semi-natural grasslands in South America (Bilenca and Miñarro, 2004). Under this scenario, it is not surprising that ponds surrounding by lands intended for cattle grazing supported the richest anuran assemblages, and the land use-heterogeneity emerged as good predictors for high anuran richness and abundance. We did not find effects of pond density or distance to the nearest ponds, and that could be related to the fact that this ecological unit is a vast region of a chain of interconnected natural ponds; therefore, wetlands are well represented, and its distribution is mostly uniform across the region (Soriano, 1991).

In the Inland Pampas, the agriculturalization process is relatively recent, having mixed production systems devoted to both crops and animal husbandry (Baldi and Paruelo, 2008; Viglizzo et al., 2011). This area presents good drainage conditions because the sandy nature of the soil and the lack of networks determine that ponds occur in low areas after the rains (Soriano, 1991). Typically, two rainy seasons in spring and fall occur between dry summers. Moreover, during late spring and summer, soils may be exposed due to loss of grass cover, which can be aggravated by overgrazing and soil compaction by cattle as was informed for other grassland regions of the world (Eldridge et al., 2016). This particular pattern of climatic and edaphic conditions may explain our results, indicating that ponds related to soy crops maintain anuran diversity. In this sense, summer crops like soy in the Inland Pampas can provide fresh and wet soil surfaces. Supporting this, the most common and well-distributed species in the Inland Pampas have burrowing habitats (*O. americanus*, *R. fernandezae*, *L. gracilis, and L. latinasus*, See Table 1) (Maneyro and Carreira, 2016). When landscape features were assessed, our results showed a positive influence of pond density and land-use heterogeneity of the patches. These findings may be explained by the recent expansion of summer crops over pastures identified as an increasing process leading to landscape homogenization and loss of wetlands (Herrera et al., 2013). If the process of patch degradation is not stopped, and if the landscape connectivity is not maintained, we can expect that the Inland Pampa landscapes will turn into profoundly impacted scenarios similar to those already observed in the Rolling Pampas.

Our work focused on the direct influence of breeding habitats and landscape features on anuran assemblages. Consequently, we did not attempt to consider the differential influence of management neither quantify how land use influenced other variables assessed at pond and landscape levels. Nonetheless, soy cropping and cattle grazing (the most important and extended productive activities in the Pampean Region) may ultimately define other landscape traits and impact pond characteristics. Further studies involving intensity, field slope, duration, timing, and frequency of the farming practices and introducing different landscapes scales will not only make it possible to recognize emergent response patterns of the anuran assemblages, but it may also aid in identifying alternative managements for increasing habitat complexity and connectivity.

4.3. Single species responses

Supporting our prediction about species occurrence, the role and importance of predictors differed from species to species based on its life-history traits. In our altered landscape, *B. pulchella* occurs in-depth and vegetated ponds and avoids those ponds surrounding by soy crops. *Leptodactylus luctator* also showed this preference. *Rhinella fernandezae* is a very plastic species that may colonize very heterogeneous habitats (Brodeur and Candioti, 2017), and the only significant selection was for those ponds related to soy crops in the Inland Pampa. We also identified the selection for ponds surrounding by soy crops in the case of *O. americanus* occurring in the Inland Pampas. Similar results were obtained by Peltzer et al. (2006), who demonstrated the presence of tadpoles of both species in ponds surrounded by soy croplands. *O. americanus* also needs well-developed and structured vegetation. Finally, *P. falcipes* showed very different ecological requirements from other analyzed species, preferring shallow water bodies. This habitat requirement was also mentioned in previous studies (Maneyro and Carreira, 2016). This species also resulted affected by the distance between ponds, which could be related to the low dispersal capacities of small species (Pabijan et al., 2012).

The differential contribution to landscape features on species occurrence is consistent with those particularities already discuses for each ecological unit. Finally, we should bear in mind that this study revealed only patterns of occurrence of the most common and well-represented species of the region. More studies are now needed to identify habitat and landscape features influencing the occurrence and distribution of rare and vulnerable species like *Ceratophrys ornata*.

4.4. Amphibian conservation in agro-ecosystems

Amphibians are experiencing population declines in all regions of the world, and several species are being affected by the loss of habitat and contamination related to agricultural development (Bishop et al., 2012). In the Pampean Region, the lack of long-term data on amphibian populations has been an obstacle to determine the impact of agricultural activities, and the absence of pristine areas also difficult the comparison between natural and altered scenarios (Agostini et al., 2013, 2016; Brodeur et al., 2011). Because this landscape is expected to keep undergo drastic changes in response to the increase in food demand, understanding how habitat and landscape traits influence native species is crucial. Our study represents the baseline for future long-term population dynamics to predict how anuran species might shift in response to habitat alteration in the Pampean Region.

Within ponds, species richness and abundance were highly associated with pond vegetation, and this association was represented in all the ecological units studied. These results are consistent with other studies suggesting that maintaining shore vegetation of ponds can increase anuran diversity within agricultural landscapes (Boissinot et al., 2019; Peltzer et al., 2006; Pulsford et al., 2019). Wetland management worldwide has proved the success of wetland buffers zones in maintaining the water quality by recovering native vegetation (Coukell et al., 2004; Semlitsch and Bodie, 2003). We argue that the creation of buffer zones around pods located in our agricultural landscapes may be acting directly on species richness via the provisioning of upland habitat and indirectly via influences on local pond habitat quality (by preventing livestock access and reducing nutrients and pesticides run-off). To our knowledge, there is not any study exploring the effects of wetland buffer zones in the agroecosystems of Argentina. Further studies on these fields are urgent to gain evidence about vegetation composition, dimensions, and other characteristics of the buffer zones for supporting effective management recommendations.

At the landscape level, intercropping, rotation, and preservation of hedgerows may prevent local declines (Knutson et al., 2004; Pulsford et al., 2019). Overall, these recommendations can maintain the connectivity between subpopulations and facilitates dispersal, protecting species against harmful effects and environmental impacts (Arntzen et al., 2017; Maes et al., 2008). Several authors also suggested that constructed farm ponds represent important alternative breeding habitats and may help sustain amphibian populations in agricultural landscapes (Knutson et al., 2004). In the Pampean Region, the need for increasing corridors and land heterogeneity seems to be more urgent in the Rolling Pampas. Meanwhile, the creation of artificial ponds under proper management could increase the connectivity of populations, mainly in those areas with dry seasons and where wetlands are drained as the Inland Pampas.

Particularly in Argentina, the lack of planning and economic interests leads to crop and livestock management with little to no attention to the conservation of natural resources, especially wetlands. Moreover, in most cases, the importance of wetland is unknown, even from a production perspective, resulting in severe degradation and environmental impacts (Herrera et al., 2013). Further studies should identify habitat and landscape elements favoring not only anuran diversity but also other taxa. This will lead to make scientific results available to landowners and involve landscape planners in the effective management and conservation of the grassland from South America. Future land use policy formulation needs to be addressed, and more government interventions on farmers' decisions will lead to achieving agricultural sustainability.

5. Conclusions

Our results revealed that the anuran assemblages from the Pampean Region respond differently to the effects of land use, suggesting that extrapolation of the effects obtained for a particular ecological unit could not be adequate to predict responses and impacts at regional level. In order to protect anuran diversity in the agroecosystems of the Pampean Region, conservation efforts must account for proper wetland management (including restoration and creation of ponds), preserve the remnant of grasslands vegetation as corridors or hedgerows, maintain land heterogeneity, and adjust the intensity of the practices according to each ecologic unit.

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Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2021.107323.

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