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RESEARCH ARTICLE

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# Artificial aquatic habitats impoverish amphibian diversity in agricultural landscapes of central Argentina

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## Abstract

1. In central Argentina, agro-ecosystems constitute the dominant landscape, representing the replacement of extensive grassland areas by crops and pastures. Agriculture has caused the loss of extensive areas of Pampean inland wetlands through drainage and the construction of artificial aquatic habitats such as ditches and ponds.
2. This study evaluated the availability and amphibian breeding use of 194 natural and artificial open water habitats and identified those attributes that affect amphibian diversity (richness, abundance and species occurrence).
3. Interviews with farmers revealed that all artificial ditches, drainage channels and ponds were constructed directly or indirectly to support agricultural activities, and 61.5% of them were created at the expense of natural wetlands. The results from generalized linear mixed models) indicated a significant decrease ($P < 0.05$) in amphibian richness (14.2–35.7%) and abundance (35.3–86.6%) in artificial habitats compared with natural habitats.
4. Overall, vegetation cover, average depth and edge slope emerged as the most important attributes affecting amphibian diversity in artificial open water habitats. Vegetation cover had a significant ($P < 0.05$) positive influence on species richness and abundance, whereas average depth and edge slope had the opposite effect.
5. Given the substantial modification of inland wetlands in central Argentina, natural aquatic habitats should be considered top priorities for conservation, and law enforcement is urgently needed to control the drainage and levelling of lagoons, ponds and low-lying areas. The appropriate design and planning of constructed wetlands, including shallow depth and slightly sloping edges, could greatly improve the ability of artificial wetlands to favour native amphibians in these altered landscapes.
6. Artificial wetlands could offer complementary habitats to natural habitats for amphibians and aquatic wildlife if actions leading to sustainable management and territorial planning are applied.

**KEYWORDS**
agriculture, anurans, canal, conservation evaluation, ditch, habitat management, land drainage, land-use, pond

  

## 1 | INTRODUCTION

The conversion of natural biomes into agricultural lands is widely recognized as one of the most significant human alterations of the global environment (Song et al., 2018). One of the major threats to wildlife and their habitats comes from the rapid loss of natural ecosystems through their transformation into crop fields and pastures for livestock (Donald, 2004). Agriculture not only affects terrestrial biomes but is also suggested to be one of the main drivers of the deterioration and loss of different types of aquatic systems (Mitsch & Gosselink, 2007; Dahl, 2011).

Wetlands are unique ecological environments with an estimated total area of 1.53–14.86 million km$^2$, hosting approximately 40% of all global species and 12% of all animal species (Hu et al., 2017; Reis et al., 2017). In the twentieth century, agriculture and urbanization caused almost half of the worldwide wetland loss, with Asia, Europe and South America being the continents most affected (Hu et al., 2017). By reducing the distribution and abundance of wetlands, these activities contribute to habitat loss, degradation and reduced connectivity, which greatly impoverishes the associated biodiversity (Foley et al., 2005; Lougheed et al., 2008). In addition, agricultural practices also disrupt the most valuable ecosystem functions by compromising the goods and services that wetlands provide to society (e.g. attenuating flood flows, purifying water, contributing to carbon storage and providing important habitat for biodiversity; Mitsch & Gosselink, 2007).

Wetlands are critical habitats for amphibians, particularly for species with complex life cycles that use ponds, ditches, lagoons, marshes, fens and bogs for breeding (Wells, 2007). Breeding amphibians aggregate in wetlands to lay their eggs, and larvae remain in the aquatic environment until they metamorphose into terrestrial or semi-aquatic juveniles. During the non-breeding season, wetlands may also serve as a primary source of food and refuge for adults and juveniles (Semlitsch & Bodie, 2003). Therefore, habitat quality can be an important determinant of amphibian species richness and abundance (Brand & Snodgrass, 2009; Boissinot, Besnard & Lourdais, 2019). Most amphibians are small and have a relatively low capacity for migration and dispersal between aquatic breeding and terrestrial foraging habitats (Sinch, 1990). This behaviour makes them highly sensitive to habitat modifications, particularly land conversion (Blaustein et al., 2011). Studies focusing on the effects of habitat loss on amphibians have acquired relevance since this taxonomic group was suggested to be the most threatened and rapidly declining vertebrate taxon (Bishop et al., 2012). Although several factors contribute to the global amphibian decline, habitat loss and agrochemical contamination related to agricultural practices are widely considered to be the major threats (Blaustein et al., 2011).

Covering the great plain of central-eastern Argentina, the Pampean Region has been the scene of a notable expansion and intensification of agricultural production systems (Baldi & Paruelo, 2008). The Pampean Region covers about 52 million hectares of productive organic soils, which were originally covered by grasslands dominated by gramineous species of the genera *Stipa*, *Poa*, *Piptochaetium* and *Aristida* (Soriano, 1991). Nowadays, agro-ecosystems constitute the dominant landscape where the extensive native grassland has been replaced by crops (mostly soy, corn and wheat) and grazing lands (Baeza & Paruelo, 2020). Natural and artificial inland wetlands occurring in these landscapes are critically affected by the agricultural practices and management carried out in the surrounding areas (Herrera et al., 2013; Benzaquén et al., 2017).

In addition to the direct impacts that agricultural activities cause on aquatic habitats (e.g. pesticide and nutrient runoff, trampling by livestock), Pampean inland wetlands have been influenced by other factors. In recent decades, a progressive change in water balance has been detected, which, by becoming more positive (precipitation > evapotranspiration), has led to a rise in the water table throughout the entire region (Alsina, Nosetto & Jobbágy, 2020). This rise has increased areas affected by flooding and extended flooding periods (Viglizzo et al., 2009; Kuppel et al., 2015). In some areas, governments have encouraged the construction of artificial drainage channels to solve flooding problems. In addition, numerous illegal channels have been built by private owners (Blarasin et al., 2005). Consequently, several natural wetlands have been drained and the levelling of lagoons and floodplains has been carried out for conversion into croplands (Brandolin, Ávalos & de Angelo, 2013; Benzaquén et al., 2017). Moreover, the same land-use changes that are destroying Pampean inland wetlands result in the construction of many types of artificial water habitats. Therefore, agricultural practices have also involved the creation of artificial ponds, irrigation ditches and water reservoirs for livestock, which represent new open water habitats. Despite playing a key role in the regulation of ecosystems, few studies have explored the effect of conversion and wetland loss on freshwater organisms (Bazzuri, Gabellone & Solari, 2020; Corriale et al., 2021) and less is known about the potential of artificial wetlands to support native species in agro-ecosystems of central Argentina (Brandolin, Ávalos & de Angelo, 2013).

Many authors have already studied the relative importance of artificial wetlands in providing suitable habitat for amphibians, particularly those that retain water during dry periods when temporary natural ponds dry out (Brand & Snodgrass, 2009; Canals et al., 2011; Bellakhal, Neveu & Aleya, 2014; Rannap et al., 2020). Furthermore, the construction and management of artificial wetlands that mitigate the loss and deterioration of natural wetlands have been extensively suggested as an important conservation practice (Brown et al., 2012). Thus, there is growing evidence identifying which wetland features favour amphibian diversity in Europe, the United States and Australia (Knutson et al., 2004; Smith et al., 2007; Canals et al., 2011; Drayer & Richter, 2016). Despite this, there has been almost no research related to agro-ecosystems in South American biomes. Previous studies conducted in the Pampean Region have addressed ecological and conservation issues related to native amphibians occurring in agricultural landscapes (Brodeur et al., 2011; Agostini & Burrowes, 2015; Deutsch, Bilenca & Agostini, 2017). In the absence of native or undisturbed areas, amphibians from central

Argentina inhabit an agricultural landscape mosaic of cultivated and grazing lands and are inevitably affected by farming activities (Agostini et al., 2020; Agostini, Deutsch & Bilenca, 2021). Some amphibian species have been reported to use artificial open water habitats (ditches, drainage channels and ponds) immersed in or surrounded by agro-ecosystems for breeding and feeding (Agostini et al., 2016), even though there is still little knowledge about how these new landscape elements can affect populations. Therefore, it is essential to explore whether artificial open water wetlands are potential habitats for amphibians, hence mitigating the effects produced by agricultural practices.

This study was conducted in agro-ecosystems from central Argentina, involving 194 natural and artificial open water wetlands that provide breeding habitats for amphibians. The aim was to evaluate the availability and amphibian breeding use of artificial and natural open water habitats and identify the attributes of the artificial open water wetlands that favour amphibian diversity. The following research questions were addressed: (i) what was the purpose of constructing artificial open water habitats in the agro-ecosystems studied; (ii) do the artificial open water habitats support the same amphibian richness and abundance as the natural ones; (iii) what artificial open water wetlands influence the habitat quality of breeding amphibians; and (iv) what are the conservation outcomes of this work in contributing to agricultural sustainability?

## 2 | METHODS

### 2.1 | Study area

The study area occupies 37,200 km$^2$ of central Argentina and supports 87 farms located in Buenos Aires, La Pampa, Córdoba and Santa Fe provinces (Figure 1). The area belongs to the Inland Pampas, an ecological unit of the Pampean Region (Soriano, 1991). The climate is temperate and subhumid, with hot summers and an annual precipitation range of 750–900 mm (Sierra, Hurtado & Specha, 1993). The soils have developed from sandy materials of variable coarseness on top of sediments with a fine texture and low permeability. This, and the lack of watercourses, mean that surface water caused by heavy rain takes time to drain away (Taboada, Damiano & Lavado, 2009). Typical wetlands appear in the form of semi-permanent pools, drainage ponds, lagoons and other low-lying areas

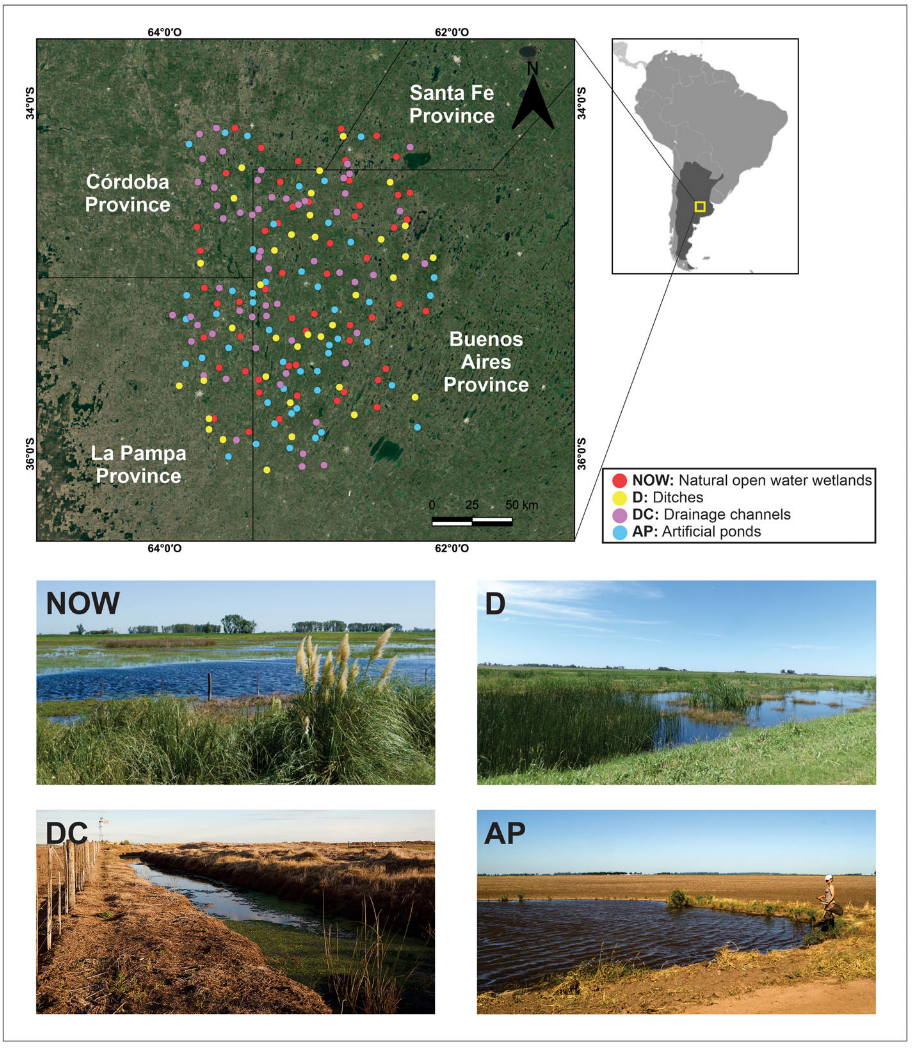


FIGURE 1 The study area in central Argentina, showing the locations (circles) of the 194 natural and open water habitats surveyed. The photographs show examples of these habitats

where the groundwater intercepts the soil surface or where precipitation sufficiently saturates the soil (Cabrera, 1973). The region was traditionally a livestock raising area but changes in land use began in the early 2000s with the introduction of both genetically modified soybeans tolerant to glyphosate and non-tillage systems (Baldi & Paruelo, 2008; Baeza & Paruelo, 2020). At present, the region is characterized by an agricultural mosaic dominated by cattle grazing lands and croplands (Baeza & Paruelo, 2020). The change in land use introduced new artificial open water habitats that retain water and might offer, especially in times of drought, habitats for the development of amphibian populations (Agostini et al., 2016).

## 2.2 | Farmer interviews and wetland selection

To understand why artificial open water habitats were created, semi-structured interviews (Young et al., 2018) with landowners were performed. The interviews were anonymous and covered three topics: (i) the purpose of artificial habitat construction, (ii) the date of construction; and (iii) whether open water habitats are/were subject to any management or intervention.

Working with farmers, a total of 221 open water habitats were identified. The natural open water wetlands were the typical temporary and semi-permanent ponds and low-lying areas of the region (Figure 1), while artificial open water habitats were classified into three categories: ditches, drainage channels and artificial ponds (Figure 1). None of the open water habitats studied dried out, at least during the sampling period. Both natural and artificial open water habitats were surrounded by soy crops and pastures for cattle grazing. Wetlands constructed less than 5 years previously were excluded from the analysis to avoid effects caused by colonization and early successional changes in aquatic communities (Scott & Woodward, 1994). Amphibians can respond adversely to co-occurrence with fish and proximity to roads (Hartel et al., 2007; Brown et al., 2012). Therefore, open water habitats less than 50 m away from main roads or containing large fish (e.g. *Hoplias argentinesis*, *Rhamdia quelem* or *Oligosarcus jenynsi*) were excluded from wetland selection. In total, 194 open water habitats (55 natural and 139 artificial) were included in the analyses.

## 2.3 | Amphibian surveys

Surveys were conducted during two breeding seasons in October to March 2016/2017 and October to March 2017/2018. To maintain independence, the open water habitats selected were more than 2.5 km apart and all of them were sampled twice each year. Standardized sampling techniques for breeding sites were used (Scott & Woodward, 1994) and were conducted primarily during wet periods. These periods coincide with the breeding seasons reported for all the species involved in the study area (Gallardo, 1974; Cei, 1980). To optimize species detection, surveys were conducted after heavy rainfall (Agostini et al., 2016; Agostini, Deutsch & Bilenca, 2021). Sampling was restricted to breeding sites combining two methods for detecting amphibians: (i) acoustic surveys were conducted for 5 min in three different locations around each open aquatic habitat; and (ii) visual encounter surveys were conducted using three fixed transects (30 $\times$ 2 m) per aquatic habitat. Each transect was randomly selected and covered both the edges and the centre of each wetland. Surveys were conducted by the same person during warm nights (22.00–02.00) with low wind ($\sim$10 km h$^{-1}$). The minimum air temperature for surveys was 15°C (measured *in situ* using a Kestrel 5500FW Weather Meter). The number of individuals observed was recorded for each species. The combination of these two methods is widely used to study amphibian communities (Petitot et al., 2014; Boissinot, Besnard & Lourdais, 2019; Agostini, Deutsch & Bilenca, 2021). For specific names and systematic approach, Frost (2021) was followed.

## 2.4 | Wetland attributes

In each of the selected open water wetlands, three sets of related habitat attributes were recorded *in situ*, including water quality (temperature, dissolved oxygen, conductivity and pH), wetland morphometry (area, average depth and edge slope), and wetland vegetation cover (submerged and emerged vegetation). Water quality parameters were measured using a Hanna VCx3 multiparameter. The area was estimated by measuring the length and width, which were then adjusted to calculate an ellipse or circle area. The average depth was obtained by measuring the depth at five randomly selected points across the length and width. The edge slope was measured at five different points around each wetland area using a clinometer (Suunto MC2). Vegetation cover was assessed using 10 randomly selected quadrats per water habitat; each quadrat was 50 $\times$ 50 cm. A vegetation cover index of submerged and emergent vegetation per open water habitat was calculated using the method of Yin, Winkelman & Langrehr (2000). The vegetation cover in each open water habitat ranged from 0 to 100 and was expressed as the average index values for both vegetation types.

## 2.5 | Statistical analyses

Mixed-effects models with normal error structure (identity link function) (Crawley, 2007) were used to determine whether habitat attributes varied among the open water wetlands assessed. Models were constructed considering temperature (T), dissolved oxygen (DO), conductivity (C), pH, area (A), average depth (AD), edge slope (ES) and vegetation cover (VC) as response variables and the type of water habitat as a fixed effect: natural open water wetlands (NOW), ditches (D), drainage channels (DC) and artificial ponds (AP). As previous studies detected land-use effects on amphibian diversity patterns (Agostini, Deutsch & Bilenca, 2021), plot identity (cropland and grazing land) was treated as a random effect. Breeding seasons 1 and 2 were also introduced to the model as random effects. Tukey's *post* *hoc* analysis was carried out to test the differences between natural (NOW) and artificial open water habitats (D, DC and AP).

Generalized linear mixed models (GLMMs; Zuur et al., 2009) were used to assess amphibian diversity patterns. Separate GLMMs were constructed, one for each response variable: species richness, count abundance and species occurrence (detected/not detected). The richness and species occurrence were determined based on acoustic and visual surveys, whereas count abundance was recorded only through visual surveys. Models were fixed to Poisson error structure (log link function, for count data = species richness and count abundance) and Bernoulli error structure (logit-link function, for binomial data = species detected/not detected).

To assess differences between amphibian assemblages inhabiting natural and artificial open water habitats, models were constructed considering richness and abundance as response variables and the type of open water habitat (NOW, D, DC and AP) as a fixed effect. Plot identity (cropland and grazing land) was treated as a random effect in each global model. To detect differences in amphibian activity between years, the breeding season (season 1 or 2) was also treated as a fixed effect.

To identify those artificial wetland attributes that influence amphibian richness, abundance and species occurrence, separate GLMMs were performed considering the following predictor variables: T, DO, C, pH, A, ES and VC. The species occurrence analysis was limited to those species with a presence in between 10 and 90% of the wetlands sampled (Peduzzi et al., 1996). The breeding season and plot identity (cropland and grazing land) were introduced to the model as random effects.

The fit of each global model (GLMMs) was checked before conducting model selection using the DHARMa package (Harting, 2020) for the Poisson and Bernoulli data distributions. The significance of the random effects was evaluated with a likelihood ratio (LR), and a stepwise backward deletion procedure was used to derive the minimum adequate model from the saturated model (i.e. one with all explanatory variables). The stepwise procedure is based on deletion tests, removing non-significant variables at $\alpha = 0.05$, that assess the significance of the increase in deviance that results when a given term is removed from the current model (Crawley, 2007). All analyses were conducted in the R environment, version 3.6.3 (R Core Team, 2020). A summary of the full models constructed in this study is provided in the Supplementary material: Appendix S1.

# 3 | RESULTS

## 3.1 | Construction of the artificial open water habitats

Interviews with landowners showed that 166 artificial open water wetlands had been created as a consequence of soil excavation for road construction and levelling of natural wetlands, construction of water reservoirs for livestock and channelization for drainage of natural wetlands (Table 1). Of these artificial open water habitats, 38.5% ($n = 64$) represent new aquatic surfaces whereas 61.5% ($n = 102$) were constructed to replace natural wetlands. The time elapsed since the construction of artificial wetlands ranged from 5 to 11 years. None of the interviewees stated that they had any conservation intentions at the time the wetlands were created. Two interviewees indicated that they intended to intervene or manage the wetlands by introducing ornamental (non-native) fishes.

## 3.2 | Amphibian responses in natural and artificial open water wetlands

During two breeding seasons, 14 amphibian species were detected (Table 2). GLMM analyses showed that the type of open water habitat influenced amphibian richness and count abundance whereas the breeding season had no effect on the response variables (Table 3). Post-hoc comparisons showed that species richness in artificial open water habitat decreased significantly ($P < 0.05$) compared with natural wetlands (21.4% ditches, 35.7% drainage channels and 28.6% ponds). Similarly, count abundance was found to be significantly lower ($P < 0.05$) in artificial open water habitats (35.2% ditches, 86.6% drainage channels and 64.8% ponds). Among artificial habitats, higher values of amphibian richness and abundance were associated with ditches (Figure 2, Tables 2 and 4). The attributes that varied significantly among the open water habitats were average depth ($F$, 3.21; d.f., 3; $P < 0.05$), edge slope ($F$: 3.42, d.f., 3; $P < 0.05$) and vegetation cover ($F$, 5.04; d.f., 3; $P < 0.05$). Tukey's *post hoc* analyses showed that both drainage channels and artificial ponds were deeper ($P < 0.05$) and had a steeper slope ($P < 0.05$) compared with natural habitats. In addition,

**TABLE 1** Results of interviews with farmers. Values of construction purpose and management actions are expressed as percentages of the total artificial wetlands surveyed ($n = 166$). Years since construction are expressed as mean (and standard error)

| | Ditches | Drainage channels | Artificial ponds |
|---|---|---|---|
| 1. Construction purpose | | | |
| Road constructions | 19.1% | 10.7% | 17.7% |
| Wetland levelling | 18.3% | – | 43.3% |
| Livestock watering | 32.5% | – | 38.3% |
| Wetland drainage | 30.0% | 89.2% | – |
| Conservation | – | – | – |
| 2. Years since construction | 6.2 (±2.4) | 6.8 (±2.4) | 7.1 (±3.9) |
| 3. Management actions | – | – | 1.4% |

**TABLE 2** Species composition of the amphibian assemblages in 194 open water habitats from central Argentina. Species occurrence (SO) is expressed as a percentage of occupied wetlands and the abundance (Ab) is expressed as means (and standard errors) of the total individuals sampled

| | Natural open water habitats ($n = 55$) | | Ditches ($n = 47$) | | Drainage channels ($n = 56$) | | Artificial ponds ($n = 36$) | |
|---|---|---|---|---|---|---|---|---|
| Anuran species | SO | Ab | SO | Ab | SO | Ab | SO | Ab |
| Bufonidae | | | | | | | | |
| *Rhinella arenarum* | 4.5 | 3.3 (±1.4) | 12.8 | 4.7 (±0.8) | 1.8 | 4.0 (±1.2) | 5.6 | 4.5 (±2.5) |
| *Rhinella dorbignyi*[a] | 59.5 | 15.9 (±4.2) | 83.0 | 7.9 (±0.6) | 10.7 | 4.0 (±0.7) | 55.6 | 10.7 (±1.0) |
| Ceratophryidae | | | | | | | | |
| *Ceratophrys ornata* | 5.1 | 2.7 (±1.9) | 4.3 | 2.0 (±1.0) | – | – | – | – |
| *Ceratophrys cranwelli* | 2.6 | 3.2 (±2.8) | – | – | – | – | – | – |
| Hylidae | | | | | | | | |
| *Boana pulchella*[a] | 21.0 | 4.5 (±2.3) | 76.6 | 4.2 (±0.4) | 32.1 | 4.4 (±0.7) | 19.4 | 3.3 (±0.8) |
| *Scinax granulatus* | 1.2 | 2.5 (±1.7) | 14.9 | 4.9 (±0.8) | – | – | 2.8 | 7.0 (±1.2) |
| *Scinax nasicus* | 1.0 | 1.3 (±1.0) | – | – | 1.8 | 3.0 (±1.0) | – | – |
| *Scinax squalirostris* | 18.7 | 9.2 (±2.9) | 7.5 | 3.0 (±0.8) | – | – | – | – |
| Leptodactylidae | | | | | | | | |
| *Leptodactylus gracilis* | 19.3 | 3.5 (±1.6) | 12.8 | 3.0 (±0.4) | 10.7 | 3.0 (±0.9) | 2.8 | 3.0 (±0.0) |
| *Leptodactylus latinasus* | 16.9 | 4.0 (±1.8) | 19.1 | 3.4 (±0.4) | 14.3 | 3.5 (±0.9) | 16.7 | 3.3 (±0.6) |
| *Leptodactylus luctator* | 58.3 | 4.9 (±2.3) | 46.8 | 5.1 (±0.5) | – | – | 13.9 | 4.0 (±1.3) |
| *Physalaemus biligonigerus*[a] | 56.1 | 6.9 (±3.3) | 68.1 | 5.6 (±0.4) | 10.7 | 5.5 (±1.4) | 47.2 | 6.9 (±0.6) |
| *Pseudopaludicola falcipes* | 12.3 | 9.5 (±2.9) | 12.8 | 9.3 (±0.7) | 1.8 | 6.0 (±1.4) | 25.0 | 8.9 (±1.7) |
| Odontophrynidae | | | | | | | | |
| *Odontophrynus americanus*[a] | 45.0 | 5.6 (±3.0) | 68.1 | 6.2 (±0.4) | 16.1 | 3.9 (±0.5) | 44.4 | 7.2 (±0.4) |
| Total richness | 14 | | 12 | | 9 | | 10 | |
| Total abundance | 1,730 | | 1,120 | | 231 | | 608 | |

[a]Species used for models testing the influence of wetland attributes on amphibian species occurrence.

**TABLE 3** Summary of the generalized linear mixed models showing the effects of types of open water habitats and breeding season on amphibian richness and abundance obtained in 194 wetlands from central Argentina. Land-use was included as a random effect

| Parameter | Explanatory variable | d.f. | LRT | *P*-Value | Significance |
|---|---|---|---|---|---|
| Species richness | Wetland type | **3** | **224.674** | $\mathbf{2 \times 10^{-16}}$ | *** |
| | Breeding season | 1 | 0.856 | 0.3549 | n.s. |
| Abundance | Wetland type | **3** | **160.270** | $\mathbf{3 \times 10^{-4}}$ | *** |
| | Breeding season | 1 | 0.109 | 0.7415 | n.s. |

Significant explanatory variables are in bold: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$; n.s., not significant.

all artificial habitat types showed a lower ($P < 0.05$) vegetation index than natural aquatic habitats. Values of the open water habitat attributes are provided in Table 5.

### 3.3 | Artificial wetlands attributes and amphibian diversity

After background selection, vegetation cover (d.f., 1; LRT, 71.9; $P < 0.001$) average depth (d.f., 1; LRT, 13.5; $P < 0.01$) and slope (d.f., 1; LRT, 9.2; $P < 0.05$) were selected as the best predictors of amphibian richness in artificial habitats (Table 6). Vegetation cover had a significant positive effect on species richness whereas average depth and slope had the opposite effect (Figure 3a). Amphibian abundance in artificial wetlands was positively affected by vegetation cover (d.f., 1; LRT, 71.9; $P < 0.001$) and negatively affected by average depth (d.f., 1; LRT, 13.5; $P < 0.01$; Table 6, Figure 3b). (LRT = Likelihood Ratio Test). The results from GLMM saturated models including significant and non-significant terms are provided in the Supplementary Material: Appendix S2.

Four species occurred in all types of artificial open water habitat and were present in 10–90% of each type (Table 2). Amphibian

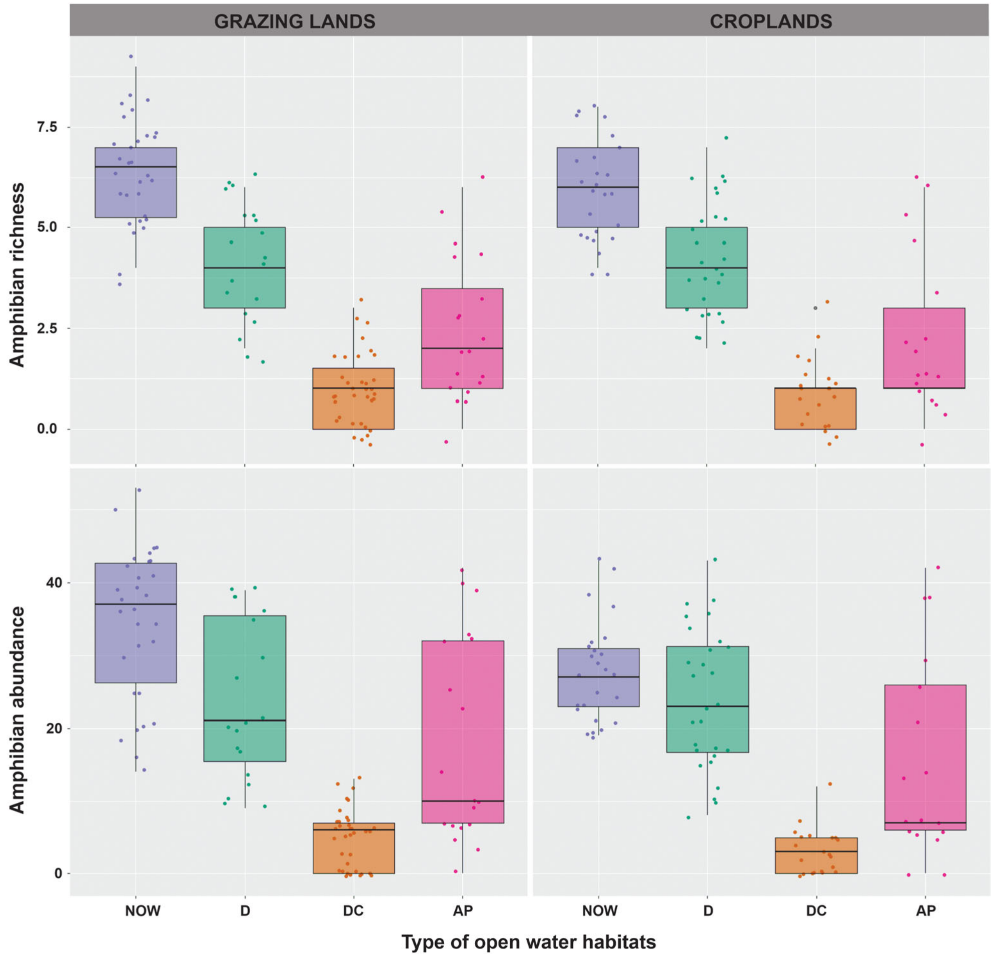


**FIGURE 2** Values of amphibian richness and abundance across the open water habitat types studied in crops and grazing lands. The transverse lines inside the boxes represent median values; lower and upper hinges correspond to the first and third quartiles. Whiskers represent the maximum and minimum range (excluding outlier values). NOW, Natural open water wetlands; D, ditches; DC, drainage channels; AP, artificial ponds

**TABLE 4** Coefficient estimates for significant explanatory variables identified by the generalized linear mixed model analyses (see Table 3). Coefficient estimates are expressed in terms of response variable. On the right, results of *a posteriori* comparisons using Tukey test are shown.

| | | | 95% confidence interval limits | | |
|---|---|---|---|---|---|
| **Parameter** | **Explanatory variable** | **Coefficient estimate** | **Lower** | **Upper** | **Significance** |
| Species richness | Intercept | 6.2 | 5.7 | 6.7 | |
| | Wetland type$_{(D)}$[a] | 0.7 | 0.6 | 0.8 | *** |
| | Wetland type$_{(DC)}$[a] | 0.2 | 0.1 | 0.2 | *** |
| | Wetland type$_{(AP)}$[a] | 0.4 | 0.3 | 0.4 | *** |
| Abundance | Intercept | 31.3 | 27.4 | 35.7 | |
| | Wetland type$_{(D)}$[a] | 0.8 | 0.6 | 0.9 | * |
| | Wetland type$_{(DC)}$[a] | 0.1 | 0.1 | 0.2 | *** |
| | Wetland type$_{(AP)}$[a] | 0.6 | 0.5 | 0.7 | n.s. |

Abbreviations: AP, artificial ponds; D, ditches; DC, drainage channels; NOW, Natural open water wetlands.
[a]Relative to level NOW of explanatory variable: open water habitat type.
$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$; n.s., not significant.

occurrence had no significant effect on the Hosmer–Lemeshow test and inflation for collinearity was not detected in any model. The occurrence of *Rhinella dorbignyi* was positively affected by the vegetation cover of wetlands (d.f., 1; LRT, 19.5; $P < 0.001$) and negatively associated with average depth and slope (d.f., 1; LRT, 25.9; $P < 0.001$; d.f., 1; LRT, 3.7; $P < 0.05$). The only wetland attribute affecting the occurrence of *Boana pulchella* was the average depth, showing a positive effect (d.f., 1; LRT, 53.6.9; $P < 0.001$). *Physalaemus biligonigerus* occurrence was positively related to vegetation cover (d.f., 1; LRT, 10.2; $P < 0.01$) and negatively affected by average depth

**TABLE 5** Mean values and standard errors of natural and artificial open water habitats attributes

| Attribute | Natural wetlands ($n = 55$) | Ditches ($n = 47$) | Drainage channels ($n = 56$) | Artificial ponds ($n = 36$) |
|---|---|---|---|---|
| Temperature (°C) | 21.9 ± 2.5 | 21.2 ± 3.7 | 19.2 ± 4.5 | 20.9 ± 2.6 |
| Dissolved oxygen (mg $L^{-1}$) | 10.3 ± 1.4 | 9.7 ± 1.3 | 10.8 ± 1.0 | 10.1 ± 1.5 |
| Conductivity (μS $cm^{-1}$) | 1.9 ± 1.1 | 1.7 ± 0.9 | 2.9 ± 1.3 | 2.5 ± 1.2 |
| pH | 7.2 ± 2.5 | 7.0 ± 2.1 | 6.5 ± 1.9 | 7.1 ± 2.7 |
| Area ($m^2$) | 1,578 ± 858 | 1,234 ± 858 | 1,045 ± 558 | 1,326 ± 745 |
| Average depth (cm) | 43.9 ± 8.1 | 41.5 ± 13.1 | 87.2 ± 21.1* | 44.6 ± 9.9* |
| Edge slope (deg) | 13.4 ± 1.2 | 20.4 ± 3.5 | 67.8 ± 9.0* | 34.6 ± 11.1* |
| Vegetation cover index | 59.2 ± 8.8 | 38.6 ± 3.2* | 12.8 ± 8.6* | 20.5 ± 9.3* |

*Significant differences (Tukey's *post hoc* analyses; $P < 0.05$) compared with natural open water habitats.

**TABLE 6** Coefficient estimates for significant explanatory variables identified by the generalized linear mixed model analyses. Coefficient estimates are expressed in terms of response variable. On the right, the results of *a posteriori* comparisons using Tukey test are shown

| | | | 95% confidence interval limits | | |
|---|---|---|---|---|---|
| Parameter | Explanatory variable | Coefficient estimate | Lower | Upper | Significance |
| Species richness | Intercept | 2.39 | 2.00 | 2.86 | *** |
| | Average depth | 0.64 | 0.47 | 0.87 | ** |
| | Vegetation cover | 6.14 | 4.40 | 8.57 | *** |
| | Slope | 5.12 | 3.12 | 7.95 | * |
| Abundance | Intercept | 5.53 | 4.45 | 6.87 | *** |
| | Average depth | 0.40 | 0.31 | 0.51 | *** |
| | Vegetation cover | 7.84 | 4.45 | 12.57 | *** |
| *Rhinella dorbignyi* | Intercept | 0.56 | 0.30 | 0.99 | * |
| | Vegetation cover | 91.82 | 29.65 | 158.36 | *** |
| | Average depth | 1.45 | 1.23 | 0.42 | *** |
| | Edge slope | 0.74 | 0.61 | 0.96 | ** |
| *Boana pulchella* | Intercept | 5.61 | 2.40 | 16.65 | *** |
| | Average depth | 0.95 | 0.24 | 2.03 | *** |
| *Physalaemus biligonigerus* | Intercept | 0.51 | 0.32 | 0.75 | ** |
| | Vegetation cover | 121.29 | 54.32 | 298.07 | *** |
| | Average depth | 1.12 | 0.98 | 0.19 | * |
| *Odontophrynus americanus* | Intercept | 0.65 | 0.36 | 0.98 | ** |
| | Vegetation cover | 2874.36 | 207.12 | 62.308.01 | *** |
| | Edge slope | 2.44 | 1.78 | 3.60 | * |

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

(d.f., 1; LRT, 8.6; $P < 0.01$). Vegetation cover also positively influenced *Odontophrynus americanus* occurrence (d.f., 1; LRT, 19.2; $P < 0.001$), while a negative effect of slope was found (d.f., 1; LRT, 8.8; $P < 0.01$). The results of the coefficient estimates for each significant explanatory variable are shown in Table 6, and GLMM saturated models including significant and non-significant terms are shown in the Supplementary material: Appendix S3. The probabilities of occurrence as a function of the significant variables selected by the models are shown in Figure 4.

# 4 | DISCUSSION

## 4.1 | Construction of artificial habitats

Interviews with farmers revealed that all of the artificial habitats included in the present study were constructed directly or indirectly to support agricultural activities. Furthermore, 61.5% of these artificial habitats had led to the disappearance of natural wetlands as a direct consequence of their construction. This is consistent with studies

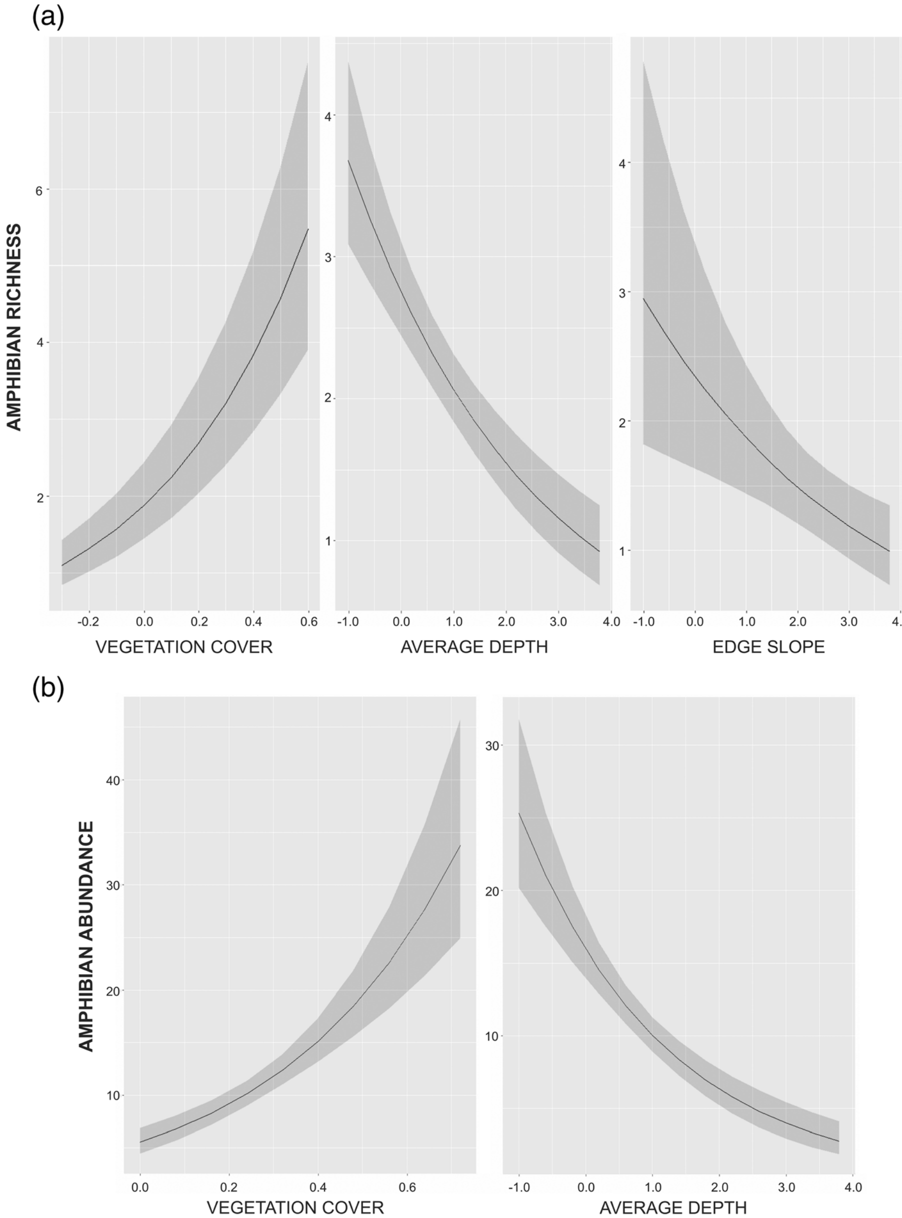


**FIGURE 3** The influence of average water depth, vegetation cover index and edge slope on (a) amphibian species richness and (b) abundance. See the Methods section for an explanation of how the graphs were derived. Only variables with significant influence are plotted

conducted in the Pampa and Chaco Ecoregions, in which the drainage of small wetlands and the increasingly frequent canalization of lagoons and marshlands are leading to the disappearance of a large number of wetlands to make the land available for agricultural use (Brandolin, Ávalos & de Angelo, 2013; Benzaquén et al., 2017). Further studies will be necessary to evaluate the effects of increased rainfall (Viglizzo et al., 2009; Kuppel et al., 2015), rising water tables (Alsina, Nosetto & Jobbágy, 2020) and canalization on the extent of natural wetlands.

Developed countries have used policies and regulations to promote the construction of artificial aquatic habitats to encourage landowners to offset the loss of natural wetlands in agricultural landscapes (Brown et al., 2012; Hansson, Pedersen & Weisner, 2012). In the present study, interviews showed that farmers usually regard natural wetlands as a nuisance, as they reduce the arable land surfaces and yields. Therefore, the introduction of agro-environment subsidy schemes and more government interventions on farmers' decisions might lead to more effective conservation and sustainable management of wetlands in central Argentina.

## 4.2 | Artificial wetlands as breeding habitat for amphibians

A growing volume of literature indicates that artificial wetlands are expected to offer suitable habitats for amphibian populations while providing benefits to agricultural activities (Knutson et al., 2004; Canals et al., 2011; Rannap et al., 2020). However, the results obtained in different biomes around the world are not conclusive. A review summarizing data on amphibian use of created and restored wetlands showed that amphibian species richness or abundance was either similar to or greater than reference wetlands in 89% of studies

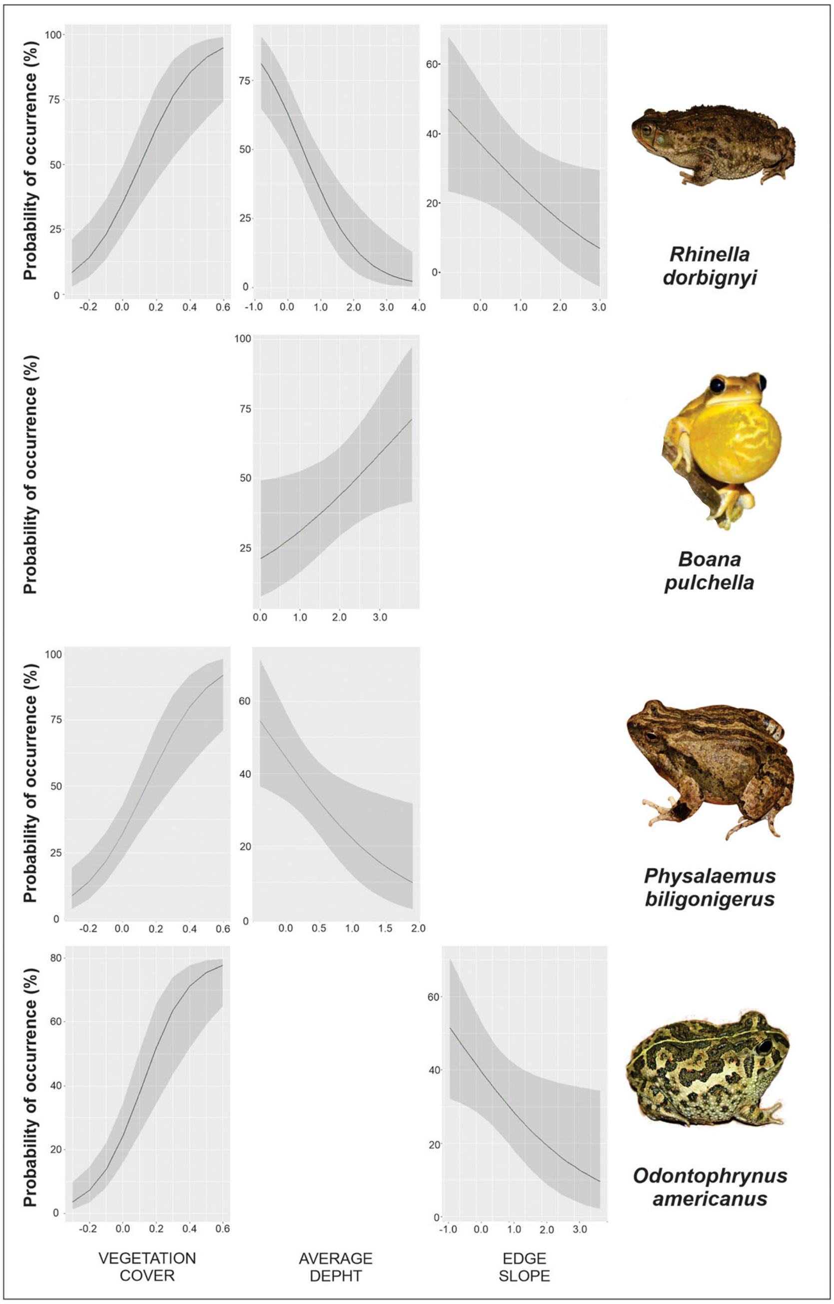


**FIGURE 4** The probability of occurrence of four common amphibians in the study area in relation to average water depth, vegetation cover index and edge slope. See the Methods section for an explanation of how the graphs were derived. Only variables with significant influence were plotted

(Brown et al., 2012). Other authors have concluded that the change from temporary to permanent artificial wetlands affects amphibians adversely (Beja & Alcazar, 2003). Similarly, studies conducted in agricultural and urban areas revealed that artificial pools do not always provide suitable habitats for amphibians and could act as ecological traps (Babbitt, 2005; Brand & Snodgrass, 2009). In the present study, artificial habitats hosted impoverished amphibian fauna compared with natural wetlands, confirming that the construction of channels and ditches to drain the natural wetlands or level low-lying areas adversely affects amphibians.

Results also showed that, among artificial open water habitats, ditches seem to be more effective in supporting amphibian breeding assemblages than artificial ponds and channels. As suggested by other authors (Cayuela et al., 2012; Shulse et al., 2012), this can be related to some characteristics of these environments resembling natural wetlands (e.g. shallow depth, short hydroperiod, and filled with rain water; Table 5). Well-managed ditches may facilitate metapopulation dynamics and promote the persistence of amphibian populations beyond remaining natural wetlands.

## 4.3 | Artificial habitat attributes favouring amphibian diversity

The most important water habitat attribute that best predicts amphibian richness and abundance is vegetation cover. Several authors have obtained similar results based on research conducted in wetlands related to agricultural landscapes worldwide (Knutson et al., 2004;

Shulse et al., 2010; Brown et al., 2012; Shulse et al., 2012; Boissinot, Besnard & Lourdais, 2019). The role of aquatic vegetation as a major modulator of amphibian diversity has also been observed in natural ponds of the Argentinean Pampean Region (Agostini, Deutsch & Bilenca, 2021). Aquatic vegetation increases habitat complexity and can reduce predation pressure by creating refuge zones for tadpoles (Shulse et al., 2010). The present study was conducted during the amphibian breeding season, and the vegetation cover index used combines the presence of both emergent and submerged macrophytes. Therefore, a high index value reflects the existence of different micro-habitats for breeding use by native amphibian species.

The average depth of the open water habitats also emerged as one of the best predictors of amphibian richness and abundance in central Argentina. Wetland depth has been extensively associated with hydroperiods (Wells, 2007; Shulse et al., 2010; Brown et al., 2012), and many authors have pointed out that larger and deeper wetlands typically hold high species richness (Pechmann et al., 2001; Drayer & Richter, 2016; Gonzalez Baffa-Trasci et al., 2020). In contrast, the present study showed that high values of amphibian diversity were associated with shallow constructed water habitats, with *B. pulchella* the only species strongly associated with deeper water. This can be explained by the fact that most amphibian species from the Pampean Region reproduce in temporary and semi-permanent wetlands and low-lying areas (Gallardo, 1974; Agostini et al., 2016). Moreover, the extensive formation of shallow temporary wetlands is typical of the region, as in most cases their water level depends on rainfall and phreatic discharges (Soriano, 1991; Viglizzo et al., 2009; Alsina, Nosetto & Jobbágy, 2020). Therefore, it is expected that the shallow depth of the artificial open water habitats favours native amphibian diversity.

The edge slope of the study sites also affected amphibian richness. Similar to many other habitat traits, the slope of wetlands seems to influence amphibians in a species-specific response (Drayer & Richter, 2016; Boissinot, Besnard & Lourdais, 2019; Agostini, Deutsch & Bilenca, 2021). The presence of shallow edges (or littoral zones) increases amphibian species richness in Ohio, USA (Porej & Hetherington, 2005). In contrast, the presence of deep littoral zones limits the abundance of American toad (*Bufo [Anaxyrus] americanus*) and boreal chorus frog (*Pseudacris maculata*) (Shulse et al., 2010). Results from this study showed a negative influence of edge slope for two species: *R. dorbignyi* and *O. americanus*. These results are consistent with the species' natural history traits as they use burrowing habitats and reproduce in shallow ponds, lowlands or the edges of small streams. Other component species of the assemblages, such as *Leptodactylus latinasus*, *Leptodactylus gracilis* and *Pseudopaludicola falcipes*, may use the shallow edges as breeding habitats (Gallardo, 1974; Cei, 1980).

Previous studies conducted in the area showed that parameters defining water quality did not vary significantly among natural wetlands associated with different land uses (Agostini et al., 2013; Agostini & Burrowes, 2015) and had no effects on amphibian diversity (Agostini, Deutsch & Bilenca, 2021). These results were explained as a possible consequence of the sampling design, which involved surveys after heavy rainfall masking the differences in water quality parameters among open water habitats. This is consistent with the results obtained in the present study showing that after rainfall, the values of pH, conductivity, temperature and dissolved oxygen did not affect amphibian diversity (see Supplementary material).

No dry aquatic habitats were found during the study period, which is expected considering that the surveys were carried out after heavy rainfall. This made it difficult to analyse the seasonality of aquatic habitats and the hydroperiod as one of the main factors affecting temperate amphibian assemblages (Beja & Alcazar, 2003; Babbitt, 2005). However, as most amphibian species in central Argentina breed in temporary and semi-permanent aquatic habitats (Gallardo, 1974; Cei, 1980), it is likely that hydroperiod acts as an important modulator of their diversity. Future studies should quantify in more detail the hydroperiod of artificial habitats in a species-specific response scheme.

### 4.4 | Conservation and management implications

The biodiversity of wetland and freshwater ecosystems is currently at high risk, with a very high proportion of species threatened with extinction (Hu et al., 2017; Reis et al., 2017). Consequently, the wetland management and conservation of agricultural landscapes is a huge challenge in the near future and effective conservation planning will require major improvements in the understanding of the factors that influence population viability in these complex landscapes.

In central Argentina, the Pampean Region combines the highest grassland replacement rates in South America, the lowest percentage of protected areas in the country and a lack of regulations and laws to protect biodiversity in agricultural lands (Viglizzo, Frank & Carreño, 2006; Herrera et al., 2013; Baeza & Paruelo, 2020). In this region, the loss and replacement of natural wetlands add to the already extensive list of threats facing amphibians in agricultural areas (e.g. pesticide exposure, pond-breeding eutrophication, population isolation). Thus, it is imperative to halt the loss of natural wetlands regardless of the potential for artificial open water habitats to maintain amphibian populations.

In human-altered landscapes facing the loss and modification of aquatic systems such as in central Argentina, the occurrence of artificial open water habitat may facilitate metapopulation dynamics and promote the persistence of sites for freshwater wildlife beyond remaining natural wetlands. Several studies of artificial wetlands suggest that these systems could contribute more to biodiversity, including amphibians, by optimizing pond designs and having the promotion of wildlife as one of the key management goals (Brown et al., 2012; Oertli, 2018). Therefore, well-managed artificial wetlands in central Argentina could provide suitable habitat (albeit sub-optimal) for aquatic species while increasing the productive value of the land. We conclude that shallow, well-vegetated wetlands with slightly sloping edges provide the best habitat for breeding amphibians and should receive priority for conservation in addition to natural wetlands. These wetlands could even provide potential habitat for threatened populations of *Ceratophrys ornata* (Deutsch, Bilenca & Agostini, 2017).

Some further considerations at the landscape level or areas surrounding the artificial wetlands should be addressed to maximize the effectiveness of amphibian conservation. Studies conducted in the region indicate that pesticides used on soybean crops and livestock access to wetlands cause high larval mortality and impoverishment of amphibian assemblages (Brodeur et al., 2011; Agostini et al., 2020; Agostini, Deutsch & Bilenca, 2021). In addition, it has been suggested that the artificial aquatic habitats should be placed in areas away from transit roads (Brown et al., 2012) since these can have substantial adverse effects on amphibian populations (Carr & Fahrig, 2001) and genetic diversity (Reh & Seitz, 1990). Likewise, the importance of spatial arrangements in the construction of wetlands has been emphasized in order to avoid population isolation and increase endogamy processes that may lead to possible local extinctions (Brown et al., 2012; Arntzen et al., 2017). As amphibians are valuable indicators of habitat quality (Blaustein et al., 2011), they could provide useful clues to identify agricultural land uses and management prescriptions that favour the overall conservation value of natural and artificial wetlands, particularly where information on other aquatic organisms is lacking (Beja & Alcazar, 2003). It is also important to manage these wetlands for breeding amphibians themselves, as there is concern over global declines in amphibian populations (Blaustein et al., 2011). This is particularly relevant in agricultural landscapes in central Argentina, where amphibians are strongly at risk from a wide range of impacts to their terrestrial and aquatic habitats.

In addition to effective government policies, some recommendations based on successful strategies from around the world, such as the National Wetland Policies of Canada and the Wise Use of Wetlands in the Mediterranean basin (The Ramsar Convention Secretariat, 2014a; The Ramsar Convention Secretariat, 2014b), can be made for setting conservation goals in central Argentina. Three important considerations are needed for successful implementation: (i) scientific and technical knowledge derived from the research and management of wetlands should be used to guide landowners, practitioners and decision-makers to enhance the conservation potential of artificial habitats; (ii) wetland conservation in agro-ecosystems must be pursued in the context of an integrated systems approach to environmental conservation and agricultural sustainable development; and (iii) government programmes should collaborate with the private sector and non-government organizations to promote public awareness and understanding of wetland functioning and human wellbeing and livelihood.

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## CONFLICT OF INTEREST

This work is all original research carried out by the authors (Perrone SM, Deutsch C, Lopez Etcheves AL, Bilenca D and Agostini MG). There are no interests, relationships, financial or otherwise that might be perceived as influencing any of the authors' objectivity.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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