



Original article

Amphibian assemblages in dry forests: Multi-scale variables explain variations in species richness



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ABSTRACT

Pond-breeding amphibians depend on several habitats and scales throughout their complex life cycle. For pond-breeding amphibians inhabiting seasonal dry forests, landscape is composed of a set of scarce and ephemeral isolated ponds surrounded by a contrasting matrix. The Chaco ecoregion is one of the most extensive dry seasonal forests in South America. In the last four decades, agricultural expansion and transformation from subsistence livestock farming to commercial livestock production have triggered dramatic deforestation processes all across the region, changing landscape composition and configuration. We postulate that richness of pond-breeding amphibians in the Chaco dry forest is negatively associated with pond hydroperiod and isolation, and terrestrial matrix degradation. Pond attributes and landscape configuration and composition were used to fit a statistical model to predict amphibian species abundance and richness in Arid Chaco ponds. Our results show that amphibian abundance and species richness in Chaco ponds is related to local and landscape predictors. Isolated and ephemeral ponds located in degraded shrublands showed low species richness values in Chaco dry forests. These results suggest that present-day land-use changes in the Chaco will have important effects on amphibian assemblages from the region, because such changes imply not only the loss of native vegetation but also a reduction of rural people devoted to extensive livestock production, where the artificial ponds used for watering livestock are also used as breeding sites by Chaco amphibians.

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1. Introduction

Amphibians are undergoing a global conservation crisis (Houlahan et al., 2000; Stuart et al., 2004), with anthropogenic alterations to natural environments being the most important drivers of their global decline (Becker et al., 2007; Cushman, 2006; Gardner et al., 2007; Young et al., 2004). The sensitivity of Amphibians to habitat alterations is strongly related to their complex life cycle, since most species present an aquatic larval stage that metamorphoses into a terrestrial adult (Duellman and Trueb, 1994). Therefore, amphibian populations and assemblages usually respond to modifications in both aquatic and terrestrial habitats (Herrmann et al., 2005; Prevedello and Vieira, 2010; Rittenhouse and Semlitsch, 2007; Skelly, 2001).

Pond-breeding amphibians are dependent on availability of lentic aquatic habitats. From the landscape perspective, for pond-breeding amphibians, ponds can be considered habitat patches, embedded within a terrestrial matrix (Hamer and Parris, 2011; Marsh and Trenham, 2001; Mazerolle and Desrochers, 2005; Ribeiro et al., 2011). Therefore, amphibian assemblage attributes (e.g. species composition and richness) depend not only on pond characteristics (i.e. local patch characteristics) but also on terrestrial matrix attributes and pond connectivity in the landscape (Funk et al., 2005; Hanski, 1994; Prevedello and Vieira, 2010; Ribeiro et al., 2011).

Taking into account the different scales of influence and the multiple habitats used by amphibians throughout their complex life cycle, in the last decade researchers on amphibians ecology and conservation have turned their attention to the response of anuran assemblages to habitat variables that operate at the local and landscape scales. At the local scale, occurrence and abundance of many pond-breeding amphibians are strongly related to variations

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in characteristics of water bodies, such as hydroperiod, surface, water chemistry, predators, and vegetation cover (Blaustein, 1999; Heyer et al., 1975; Rodrigues da Silva et al., 2012; Skelly, 2001; Skelly et al., 1999). At the landscape scale, spatial arrangement of ponds has a strong influence on amphibian populations and assemblages (Funk et al., 2005; Guerry and Hunter, 2002; Rothermel, 2004). Frog populations in isolated ponds have less probabilities of being rescued from local extinctions (which are frequent in pond-breeding amphibians) by the arrival of individuals from nearby ponds (Funk et al., 2005; Sjögren Gulve, 1994; Skelly et al., 1999). Moreover, vegetation around ponds is crucial for the migration (periodic intra-populations movements) of amphibians (Pope et al., 2000; Semlitsch, 2008; Semlitsch and Bodie, 2003; Sinsch, 1990; Smith and Green, 2005). Since amphibians are very sensitive to desiccation and high temperatures, individuals avoid movements across surfaces without vegetation cover (Rothermel and Semlitsch, 2002). Matrix quality also affects assemblage diversity and composition of pond-breeding amphibians because altered vegetation offers more resistance to migratory events and to other terrestrial activities (Guerry and Hunter, 2002; Hecnar and M'Closkey, 1998; Hermann et al., 2005; Lehtinen et al., 1999; Mazerolle and Desrochers, 2005; Prevedello and Vieira, 2010; Rothermel and Semlitsch, 2002).

The relative importance of pond characteristics, matrix quality and pond isolation varies according to intrinsic environmental attributes of natural systems. For animals that inhabit landscapes with discrete and ephemeral patches inserted within a hostile matrix, patch isolation is an important factor influencing population permanence (Fahrig, 2007). For pond-breeding amphibians inhabiting drylands, landscape is composed of a set of scarce and ephemeral ponds surrounded by a contrasting matrix (i.e. a matrix dominated by drylands with low relative humidity and low vegetation cover). In addition, due to the low temporal and spatial availability of water bodies that characterize drylands, pond occurrence and hydroperiod result in a limiting factor for amphibian species abundance, composition and diversity (Beja and Alcazar, 2003; Dayton and Fitzgerald, 2001; Heyer et al., 1975; Welborn et al., 1996). Therefore, drylands subjected to human activities altering landscape features are an interesting model to test associations between populations and assemblages of pond breeding amphibians and environmental variables that operate at different scales, since amphibians have to deal with matrix degradation, pond availability and water permanence.

South America is the continent with the largest number of amphibian species (Stuart et al., 2004) and a large continental portion is occupied by dry forests. One of the most extensive dry seasonal forests of the continent is the Chaco ecoregion, which covers 1,200,000 km² in Argentina, Paraguay, Bolivia and Brazil (Bucher, 1982; Prado, 1993). In the arid portions of the ecoregion, most lentic water bodies are small summer rain ponds and temporary farm ponds created for watering livestock (Macchi and Grau, 2012; Morello and Saravia Toledo, 1959). Traditional land use in the Chaco is mostly limited to extensive cattle ranching, charcoal extraction and selective logging. However, in the last four decades, agricultural expansion and transformation from subsistence livestock farming to commercial livestock production have triggered dramatic deforestation processes all across the region (Hoyos, 2012; Zak et al., 2008). In the south of the Chaco ecoregion, current deforestation rate ranges from 2.75 to 3.13% year⁻¹, exceeding the rates of other dry seasonal forests (Trejo and Dirzo, 2010), tropical forests (Archard et al., 2002; Zak et al., 2008) and the global level of gross forest cover loss (Hansen et al., 2010). Therefore, areas that were originally undisturbed forests and halophytic shrublands are now occupied by degraded shrublands, crops and implanted pastures (Boletta et al., 2006; Gasparri and Grau, 2009; Hoyos,

2012; Zak et al., 2004).

The degradation of Chaco dry forests implies an increase in soil temperature and a decrease in relative humidity (Abril and Bucher, 1999). Although some Chaco amphibians presents strategies to avoid desiccation (e.g. *Lepidobatrachus* spp.; *Chacophrys pierottii*; *Ceratophrys cranwelli*; *Phyllomedusa sauvagii*; *Leptodactylus bufonius*) (Ceï, 1980; Faivovich et al., 2014; McClanahan et al., 1976, 1983), tadpoles of Chaco amphibians are highly susceptible to increases in normal temperatures of the area, since they live near their thermal tolerance thresholds (Duarte et al., 2012). For this reason it is plausible that tadpoles and post-metamorphic of some Chaco amphibians would be susceptible to degradation of Chaco dry forests. Moreover, due to the natural environmental conditions of the Chaco ecoregion (high temperatures and scarce and seasonal rains), pond availability and hydroperiod should be of major importance for the maintenance of pond-breeding amphibian populations and for local species richness.

Here we analyze the associations between amphibian richness patterns, species abundance and pond and landscape characteristics in the southernmost portion of Chaco dry forests. We postulate that species richness and abundance of pond-breeding Chaco amphibians is negatively associated with pond isolation and terrestrial matrix degradation. In addition, we propose that hydroperiod affects species differentially according to their larval development and, therefore, influences composition and richness of Chaco amphibian assemblages.

2. Materials and methods

2.1. Study area

The study area comprises a region of 13,400 km² located in the southernmost and driest portion of the Chaco ecoregion: the Arid Chaco sub-region (Hoyos et al., 2013; Morello et al., 1985) (Fig. 1). The original vegetation consists of a mosaic of xerophytic forest with a variable tree canopy cover (40–100%) and three well differentiated strata. The arboreal stratum is 7–8 m in height, with trees up to 15 m high, and is dominated by *Aspidosperma quebracho-blanco*. Forests alternate with halophytic shrublands in salt flats. Saline vegetation together with forests represents the original vegetation of the study area; however, forests have been drastically reduced and modified and currently the dominant matrix is composed of shrublands resulting from forest degradation. Degraded shrublands are characterized by the presence of isolated trees, rarely exceeding 15% of cover. The main stratum is composed of xerophytic shrubs (1.5–3 m high). Herbaceous vegetation is reduced or absent. For a detail of vegetation units in the study area, see Cabido and Zak (1999); Hoyos et al. (2013); Sayago (1969); Zak et al. (2004, 2008).

The climate is subtropical, with a mean annual temperature of 19.9 °C and maximum absolute temperatures that reach 47 °C. Rainfall is mainly concentrated in the warm season (October–April) and is approximately 450 mm yr⁻¹ (Morello et al., 1985; Zak and Cabido, 2002).

2.2. Ponds characteristics

Natural ponds are very scarce and ephemeral in the Arid Chaco region. Hence, local small-scale producers that raise cattle construct temporary farm ponds (locally known as “represas”, “aguadas” or “tajamares”) (Morello and Saravia Toledo, 1959). Farm ponds are important water reservoirs all across the Chaco, since water is a limiting resource in the ecoregion (Cavanna et al., 2009; Macchi and Grau, 2012; Morello and Saravia-Toledo, 1959; Morello et al., 1985). Artificial ponds are easily distinguishable from natural ponds, mainly by the contour shape (irregular in natural ponds and

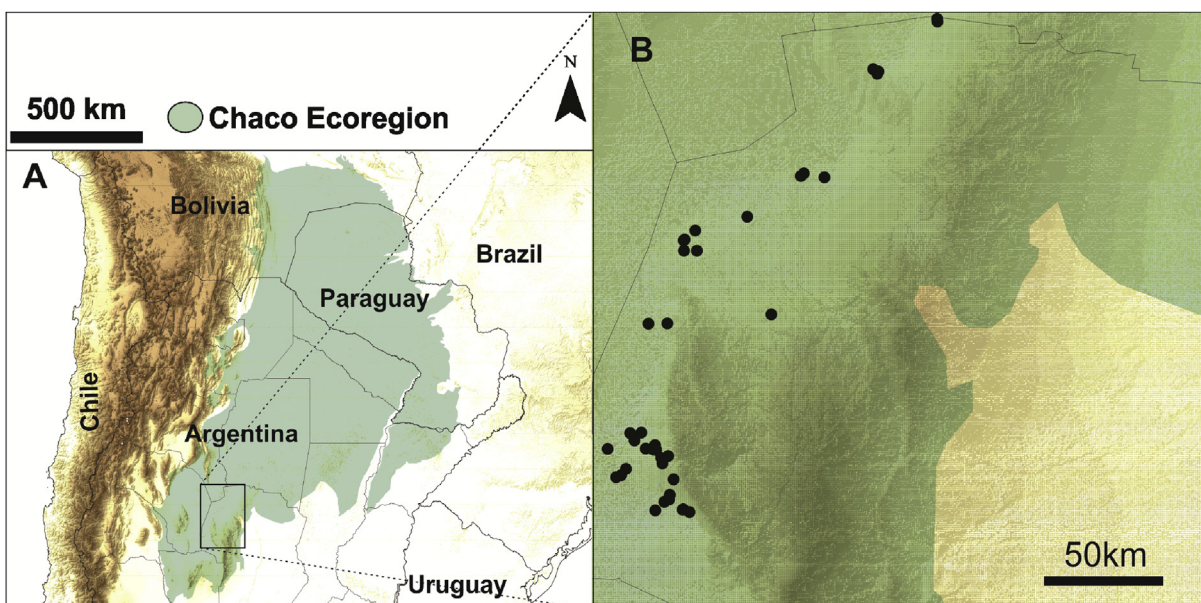


Fig. 1. A. Chaco ecoregion. B. Arid Chaco Sub-region. Black dots represent the surveyed ponds.

always regular rectangular or circular) in farm ponds. In addition, artificial ponds have an embankment with a pronounced edge, whereas natural ponds have gently sloping banks. Both natural and farm ponds are filled with summer rainwater and show similar arboreal and shrubby covers, indicating that both pond types are physiognomically similar (Lescano, 2011). The main difference between pond types is area (natural ponds are slightly smaller than farm ponds) and depth, which determines water permanence (or hydroperiod). Farm ponds in the sampling area contain water for 74.5 days on average (range: 45–155 days with water), whereas natural ponds contain water for 26.8 days on average (range: 12–40 days with water) (Lescano, 2011).

We selected 44 ponds (27 farm ponds and 17 natural ponds) within the study area in order to have a gradient of ponds in terms of water permanence. With the exception of two pairs of ponds that were separated from each other by 270 m and 315 m, the remaining sampled ponds were at a minimum distance of 2 km from one another and the most distant ponds were at a straight-line distance of 255 km (Fig. 1B).

2.3. Sampling of anurans

Samplings were conducted during the short wet season (summer season), which coincides with the activity period of amphibians in the study area (JNL pers. obs.). Amphibians were surveyed from November 2008 to February 2009, from November 2009 to March 2010, and from November 2010 to March 2011. We recorded all active adult amphibians present on the pond surface, pond bank area and shoreline vegetation of each surveyed pond using standard techniques (visual encounter and auditory surveys at breeding sites) (Crump and Scott, 1994; Dorcas et al., 2010; Scott and Woodward, 1994). Because all of the ponds analyzed had a relatively small area, we were able to survey each entire pond in less than two hours. Ponds were sampled after important rainfall events (>30 mm), since Arid Chaco amphibians are explosive breeders. Although we surveyed ponds in more than a single year, we did not detect any effect of survey period on species richness or assemblage composition (i.e. we did not record species turnover or changes in species richness among years in the surveyed ponds) (Lescano, 2011). Therefore, for each pond we obtained a single value

of species richness and a single value of abundance for each species coincident with the maximum abundance observed (Parris, 2004).

2.4. Habitat variables

We recorded five variables related to pond morphology and vegetation at each pond. *Pond area*: the area of small ponds (up to 100 m²) was calculated in the field. The surface area of bigger ponds was quantified using Google[®] satellite images in Quantum[®] Gis free software; *Pond type*: taking into account the differences in the hydroperiod between pond types, we used the categorical variable pond type (a binomial variable: natural or farm pond); *Herb cover*: the percentage of shoreline herbaceous vegetation cover was visually estimated at each pond; *Shrub and tree cover*: this variable was calculated as the percentage of shoreline cover based on visually estimated crown projection of trees and shrubs; *Pond depth*: the depth of the water bodies was quantified as the difference between edge and the bottom of ponds; this variable was recorded when the ponds were completely dry.

To measure terrestrial matrix composition we used a land cover map based on Landsat TM (Path-row: 230–82; 2004/12/26) (Hoyos, 2012; Hoyos et al., 2013). We measured three land cover units: forests, degraded shrublands, and halophytic shrublands. The forest variable included two vegetation types: closed and open forest (see Hoyos et al., 2013). Degraded shrublands are closed or open shrublands resulting from forest degradation. Land cover variables were quantified in circular areas of 1 km in diameter, with the center at each pond sampled (Fig. 2). The size of the area used to quantify matrix composition was selected based on previous studies (Guerry and Hunter, 2002; Lethinen et al., 1999; Rittenhouse and Semlitsch, 2007; Semlitsch, 2008).

Pond isolation was measured as the average straight-line distance of each pond to the three nearest ponds using a high resolution image (Google earth[®] satellite images) with the Quantum GIS V 1.8.0 software.

2.5. Data analyses

We used an information-theoretic approach (Burnham and Anderson, 2002) to evaluate the relative support of different *a*

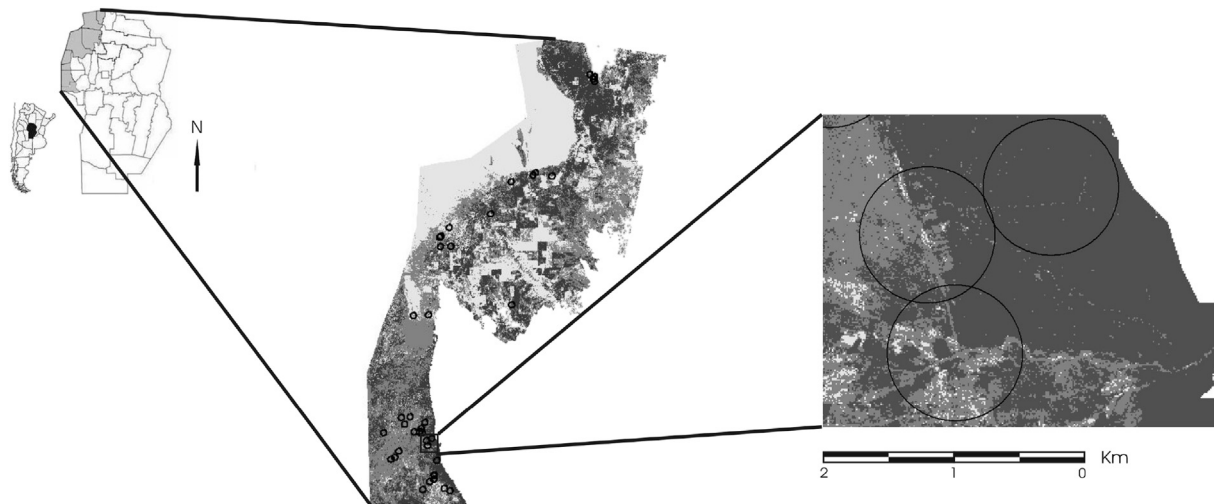


Fig. 2. Location of the study area in Córdoba province (Argentina) showing the sampling sites in the vegetation map developed by Hoyos (2012). In addition, three 1-km diameter circles centered in two farm ponds and one natural pond are indicated. Forest cover areas are indicated in dark grey; open vegetation areas (open and closed shrublands, halophytic shrublands, urbanized and cultivated lands) are indicated in grey.

a priori models (Burnham and Anderson, 2002; Manenti et al., 2009; Mazerolle, 2006; Popescu and Gibbs, 2009). First we formulated three *a priori* models to explain amphibian richness variations in ponds. According to the first model, species richness variations are explained only by local habitat variables, i.e. pond attributes (hereafter “pond model”). This model included four variables: pond area, pond type, tree and shrub cover, and herb cover. According to the second model (terrestrial matrix model, hereafter, matrix model), species richness variation is mainly related to terrestrial matrix characteristics. This model includes matrix composition variables (forest cover, halophytic shrublands and degraded shrublands). The third model tested whether variations in species richness are related to pond isolation and only included the variable distance to nearest ponds (hereafter “isolation model”). Finally, we made all possible combinations of models. Therefore, we tested a total of seven *a priori* models.

We used generalized linear models assuming normal distribution to relate amphibian richness to variables included in the seven *a priori* models (Guisan and Zimmermann, 2000; Herrmann et al., 2005; Manenti et al., 2009; McCullagh and Nelder, 1989). These seven models were compared using Akaike's information criterion (AIC) (Burnham and Anderson, 2002), with models with the smallest AIC values being considered the best models (Mazerolle, 2006). To compare candidate models we calculated delta AIC (ΔAIC) values, since models with similar AIC values ($\Delta AIC < 2$) are equally good candidates (Burnham and Anderson, 2002; Mazerolle, 2006). In addition, we calculated the Akaike's weight (ω_i) for each model, which represents the probability that a model is the best in the whole set of candidate models, as well as the evidence ratios $E = \omega_i/\omega_j$ to compare the relative support of the different models by the data (Mazerolle, 2006).

Statistical analyses were performed using the software InfoStat version 2012 (Di Rienzo et al., 2012). Multicollinearity did not bias our analyses because Pearson's correlation among independent variables were all $r < 0.60$. We used the Moran's I statistic to test for spatial autocorrelation in variables and model residuals. Species richness data and residuals of the final models obtained were not different from a normal distribution according to a Shapiro–Wilk test ($W = 0.992$; $p = 0.91$). We also checked for residual normality using a Q–Q plot and tested variance homogeneity by relating residuals and predicted values. All tests indicate that assumptions for using generalized linear models assuming normal distribution

were successfully met.

To relate amphibian species abundance to local and landscape variables we used generalized linear models assuming poisson distribution (log link function). The obtained models were compared using Akaike's information criterion (AIC) following the same procedure as that used for species richness. Statistical analyses were performed only for those species which occurs in at least 30% of the surveyed ponds and that are representative of different life habits: *Leptodactylus bufonius* (a terrestrial frog that finds refuge and reproduces in burrows); *Rhinella arenarum* (a terrestrial and generalist species); *Pleurodema guayapae* (a semi-fossorial frog with explosive reproduction); *Lepidobatrachus llanensis* (a semi-fossorial form during dry season and an aquatic and carnivorous frog with explosive reproduction during wet season) and *Phyllomedusa sauvagii* (an arboreal nester treefrog).

Rank abundance curves were performed to characterize amphibian assemblage structure and composition in water bodies with different hydroperiods. Rank abundance curves are useful to appreciate differences in the structure of assemblages associated to different environments (ponds with different hydroperiod in this case) by comparing the relative importance of species according to their abundance. A multivariate inference procedure (Multi-response permutation procedure; MRPP) was used to detect statistical differences in species composition between assemblages associated with pond types. With this nonparametric method, we tested the hypothesis that assemblages belonging to sites of different categories (ponds with different hydroperiod) would not differ significantly in structure and composition. Ecological distance for this test was measured using the Bray–Curtis index.

3. Results

We recorded 13 anuran species belonging to four families in the surveyed ponds. Farm ponds were used by 11 species (3–8 species per pond), whereas natural ponds were used by nine species (2–6 species per pond). A list of amphibian species recorded in this study as well as a brief description of the life history of adults and larval development is presented in Table 1.

3.1. Species richness models

We obtained a single candidate model (ΔAIC of the next model

Table 1

List of amphibian species recorded in the study area, indicating the life habits of adults and the time of larval development. Abbreviations: T: terrestrial species; SA: semi-aquatic species; T-F: terrestrial species with tendency to fossorial habits during dry periods; Ar: arboreal species; P: prolonged (1–3 months); S: short (15–30 days); VS: Very short (less than 15 days).

| Species | Habitat used by adults | Larval development |
|----------------------------------|------------------------|--------------------|
| <i>Rhinella arenarum</i> | T | P |
| <i>Rhinella schneideri</i> | T | P |
| <i>Leptodactylus latrans</i> | SA | P |
| <i>Leptodactylus mystacinus</i> | T | P |
| <i>Leptodactylus bufonius</i> | T | P |
| <i>Pleurodema guayapae</i> | T-F | VS |
| <i>Pleurodema nebulosum</i> | T-F | VS |
| <i>Pleurodema tucumanum</i> | T-F | S |
| <i>Physalaemus biligonigerus</i> | T-F | S |
| <i>Phyllomedusa sauvagii</i> | Ar | P |
| <i>Lepidobatrachus llanensis</i> | SA | VS |
| <i>Ceratophrys cranwelli</i> | T-F | S |
| <i>Chacophrys pierottii</i> | T-F | VS |

with the lowest AIC is 11.32), which includes variables related to pond characteristics, matrix composition and pond isolation (Tables 2 and 3). This model had a probability of 0.996 of being the best model in explaining variations in anuran species richness.

Species richness was associated with pond type and pond area (both pond attributes). Natural ponds had lower species richness (4.23 ± 1.15 species in average; range = 2–6 species per pond) than farm ponds (5.11 ± 1.28 species in average; range = 3–8 species per pond). Cumulative species richness was lower in natural ponds (9 species) than in farm ponds (12 species). Amphibian species richness showed a positive relationship with forest cover and a negative association with degraded shrubland cover in the terrestrial matrix. We also found a negative association between pond isolation and amphibian species richness (Table 3). Less isolated ponds (i.e. ponds located less than 1 km from the three nearest ponds) show more species richness in average (5.37 ± 1.15 species; range = 4 to 8 species per pond) than ponds located at more than 1.5 km from the three nearest ponds (3.75 ± 0.86 species; range = 2 to 5 species per pond). According to the best model obtained, species richness in a given pond would be maximum (i.e. 8 to 9 species) in big (around 20.000 m²) farm ponds, in which values of isolation and degraded shrubland cover in the matrix are minimum (450 m of average distance to nearest three ponds and 0% of shrubland cover respectively) and forest cover in the matrix reach 78%.

The alternative candidate models had much lower support than the best model obtained (Table 3).

Halophytic shrublands variable was spatially autocorrelated ($I = 0.14$; $Z = 5.01$; $p = 0.0001$). The remaining variables and the model residuals values were not spatially autocorrelated.

Table 2

Models ranked according to Akaike's Information Criterion (AIC). k: number of parameters used in each model; ΔAIC: difference between the AIC of the best model (ΔAIC = 0) and alternative models; L.Ratio: log-likelihood ratio; R²: coefficient of determination; ωi: Akaike's weight of the model. The variables included in each model are described in the text (data analyses section).

| Model | K | AIC | ΔAIC | L.Ratio | R ² | ωi | Evidence ratio |
|---------------------------|---|--------|-------|---------|----------------|-------|----------------|
| Pond + Matrix + Isolation | 8 | 108.38 | 0 | 51.21 | 0.61 | 0.996 | 1.00000 |
| Pond + Matrix | 7 | 119.71 | 11.32 | 36.36 | 0.47 | 0.003 | 0.00347 |
| Isolation + Matrix | 4 | 123.39 | 15.01 | 23.34 | 0.31 | 0.001 | 0.00055 |
| Pond + Isolation | 5 | 127.61 | 19.23 | 32.68 | 0.44 | 0.000 | 0.00007 |
| Matrix | 3 | 132.91 | 24.52 | 11.07 | 0.10 | 0.000 | 0.00000 |
| Isolation | 1 | 134.77 | 26.39 | 15.01 | 0.27 | 0.000 | 0.00000 |
| Pond | 4 | 140.53 | 32.14 | 16.92 | 0.29 | 0.000 | 0.00000 |

Table 3

Variables included in the best model explaining anuran species richness in the Arid Chaco region. Significant variables are highlighted in bold. β: estimate; L-R: log-likelihood ratio test; Lower CL: lower confidence limit of the interval; Upper CL: upper confidence limit of the interval.

| Variables | β | L-R χ ² | p | Lower CL | Upper CL |
|---------------------------------|---------------------------|--------------------|------------------|----------------------------|----------------|
| <i>Pond isolation</i> | | | | | |
| Distance to nearest pond | -0.974 | 14.852 | <0.001 | -1.437 | -0.512 |
| <i>Matrix composition</i> | | | | | |
| Degraded shrublands | -0.018 | 5.714 | 0.017 | -0.032 | -0.0034 |
| Forest | 0.018 | 4.142 | 0.042 | 0.001 | 0.036 |
| Halophytic shrublands | 0.008 | 0.584 | 0.445 | -0.015 | 0.033 |
| <i>Pond attributes</i> | | | | | |
| Tree and shrub cover | 0.004 | 1.283 | 0.257 | -0.003 | 0.012 |
| Herb cover | 0.004 | 1.465 | 0.226 | -0.002 | 0.009 |
| Pond area | 5.2¹⁰⁻⁵ | 4.027 | 0.045 | 1.36¹⁰⁻⁶ | 0.0001 |
| Pond type (natural) | -0.670 | 20.212 | <0.001 | -0.934 | -0.407 |

3.2. Species abundance models

Leptodactylus bufonius: *L. bufonius* was the most dominant species in both natural and farm ponds (Fig. 3) and was present in 95% of the ponds surveyed. Its raw abundance varied between 4 and 37 frogs per pond. We obtained two candidate models, which include variables related to pond characteristics, matrix composition and pond isolation (Table 4). However, although both models were statistically significant, the variables included in the models were not significant. Only a positive trend between the abundance of this species and the proportion of forests in the matrix was detected.

Rhinella arenarum: This was a common species in the study area and was abundant in both natural and farm ponds. This species showed an occurrence of 80% of surveyed ponds. The models obtained to explain the variations in abundance of *Rhinella arenarum* were not significant (Log-likelihood ratio test; $\chi^2 = 1.73$; $p = 0.19$ for the best fit model).

Pleurodema guayapae: The species was present in 52% of surveyed ponds and its abundance varied between 0 and 40 individuals per pond. Variations in abundance of *P. guayapae* were significant and negatively related with pond depth and isolation. In addition, one of the best models included a non-significant variable (Table 5). According to variations in the values of significant variables included the best model obtained, abundance of *P. guayapae* in a given pond would be maximum when values of isolation and pond depth are minimum (according to the sample values: 450 m of average distance to nearest three ponds and 15 cm of depth respectively).

Lepidobatrachus llanensis: The species was present in 39% of surveyed ponds and its abundance varied between 0 and 13 individuals per pond. Variations in abundance of *L. llanensis* were significantly explained by the variable depth (Table 6). The model included a variable that was non-significant (variable

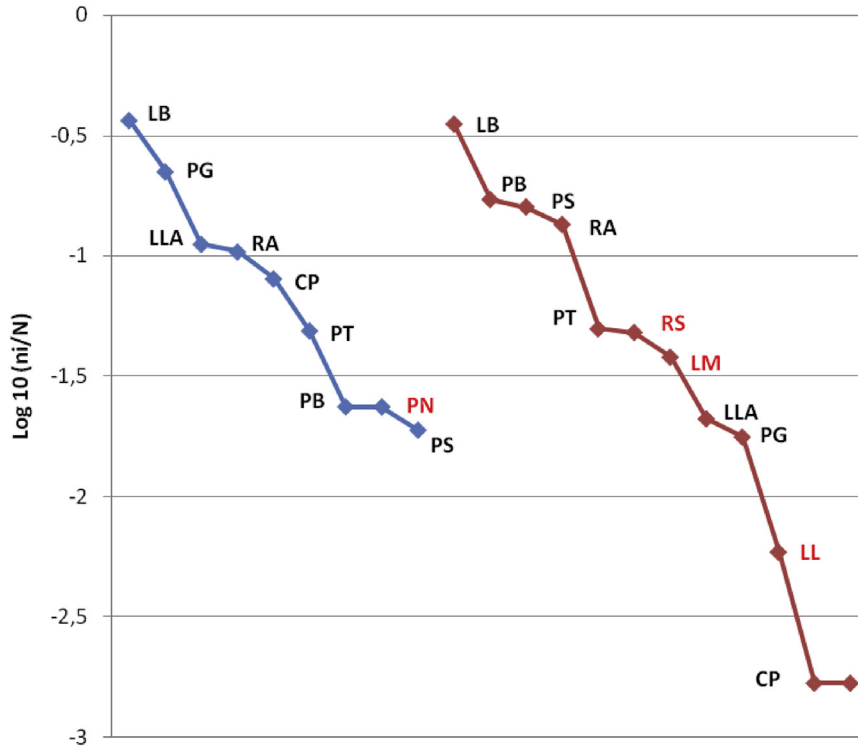


Fig. 3. Rank abundance curves for natural ponds (blue line) and artificial ponds (red line). Abbreviations: LB: *Leptodactylus bufonius*; PG: *Pleurodema guayapae*; LLA: *Lepidobatrachus llanensis*; RA: *Rhinella arenarum*; CP: *Chacophrys pierottii*; PT: *Pleurodema tucumanum*; PB: *Physalaemus biligonigerus*; PN: *Pleurodema nebulosum*; PS: *Phyllomedusa sauvagii*; RS: *Rhinella schneideri*; LM: *Leptodactylus mystacinus*; LL: *Leptodactylus latrans*; CC: *Ceratophrys cranwelli*. Abbreviations indicated in red represent species exclusive to each of the aquatic environments. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
List of the best models obtained to explain variations in abundance of *Leptodactylus bufonius*. The following values are indicated: coefficient (β), its significance according to the χ^2 test, and upper confidence limit (upper CL) and lower confidence limit (lower CL) of the interval for the estimated coefficient, as well as the χ^2 statistic for the Log-likelihood ratio ($\chi^2 LR$) test, its significance, AIC statistic, weight (ω) and Nagelkerke's R^2 (R_N^2).

| | Model terms | | | | | Model | | | | |
|--------------------|-------------|----------|-------|----------|----------|---------|-------------|--------|---------|------------|
| | β | χ^2 | p | Lower CL | Upper CL | AIC | $\chi^2 LR$ | p | R_N^2 | ω_i |
| <i>Model 1</i> | | | | | | | | | | |
| Forest | 0.009 | 3.447 | 0.063 | -0.0005 | 0.0175 | 386.43 | 35.99 | <0.001 | 0.58 | 0.52 |
| Isolation | -0.325 | 2.571 | 0.109 | -0.745 | 0.070 | | | | | |
| <i>Model 2</i> | | | | | | | | | | |
| Tree & shrub cover | 0.008 | 2.552 | 0.110 | -0.002 | 0.017 | 387.898 | 36.998 | <0.001 | 0.594 | 0.250 |
| Forest | -0.311 | 2.225 | 0.136 | -0.741 | 0.095 | | | | | |
| Isolation | 0.001 | 0.193 | 0.661 | -0.005 | 0.007 | | | | | |

forest cover; Table 6). According to the best model obtained, abundance of *L. llanensis* in a given pond would be maximum when values of pond depth are minimum (according to the sample values: 15 cm of depth).

Phyllomedusa sauvagii: The species was present in 60% of surveyed ponds and its abundance varied between 0 and 54 individuals per pond. The candidate model included two variables: depth and trees and shrub cover in ponds (Table 7).

Table 5
List of the best models obtained to explain variations in abundance of *Pleurodema guayapae*. The following values are indicated: coefficient (β), its significance according to the χ^2 test, and upper confidence limit (upper CL) and lower confidence limit (lower CL) of the interval for the estimated coefficient, as well as the χ^2 statistic for the Log-likelihood ratio ($\chi^2 LR$) test, its significance, AIC statistic, weight (ω) and Nagelkerke's R^2 (R_N^2).

| | Parameters | | | | | Model | | | | |
|------------------|--------------|--------------|------------------|--------------|---------------|-------|-------------|--------|---------|------------|
| | β | χ^2 | P | Lower CL | Upper CL | AIC | $\chi^2 LR$ | p | R_N^2 | ω_i |
| <i>Model 1</i> | | | | | | | | | | |
| Forest | 0.014 | 1.87 | 0.171 | -0.007 | 0.03 | 50.70 | 20.85 | <0.001 | 0.591 | 0.354 |
| Depth | -2.33 | 15.81 | <0.001 | -4.07 | -1.04 | | | | | |
| Isolation | -1.45 | 6.55 | 0.0105 | -2.81 | -0.31 | | | | | |
| <i>Model 2</i> | | | | | | | | | | |
| Depth | -2.22 | 16.22 | <0.001 | -3.81 | -1.01 | 52.60 | 18.63 | <0.001 | 0.551 | 0.184 |
| Isolation | -1.03 | 4.27 | 0.038 | -2.18 | -0.049 | | | | | |

Table 6

Best model obtained to explain variations in abundance of de *Lepidobatrachus llanensis*. The following values are indicated: coefficient (β), its significance according to the χ^2 test, and upper confidence limit (upper CL) and lower confidence limit (lower CL) of the interval for the estimated coefficient, as well as the χ^2 statistic for the Log-likelihood ratio (χ^2 LR) test, its significance, AIC statistic, weight (ω) and Nagelkerke's R^2 (R_N^2).

| | Parameters | | | | | Model | | | | |
|----------------|--------------|-------------|--------------|--------------|--------------|-------|-------------|-------|---------|----------|
| | β | χ^2 | P | Lower CL | Upper CL | AIC | χ^2 LR | p | r_N^2 | ω |
| <i>Model 1</i> | | | | | | | | | | |
| Depth | -1.13 | 5.07 | 0.024 | -2.39 | -0.13 | 52.8 | 7.31 | 0.026 | 0.157 | 0.136 |
| Forest | -0.03 | 3.24 | 0.072 | -0.037 | 0.014 | | | | | |

According to the model obtained, abundance of *P. sauvagii* in a given pond would be maximum in deep ponds (more than 200 cm of depth) with high values (100%) of shrubs and tree cover in the shoreline.

3.3. Pond types and assemblage composition

Qualitative differences between assemblage structures can be observed in the rank abundance curves for ponds with different hydroperiods (Fig. 3). While some species are equally ranked in both types of ponds (e.g. *Rhinella arenarum* and *Leptodactylus bufonius*), other species like *Chacophrys pierottii*, *Lepidobatrachus llanensis* or *Pleurodema guayapae* have more relative importance in terms of abundance in short hydroperiod ponds respect to farm ponds. These differences were statistically supported by MRPP analysis since results indicated that assemblage structure differed significantly among ponds types ($T = -8.41$; $A = 0.092$; $p = 0.00007$).

4. Discussion

The results obtained in this study indicate that in this subtropical seasonal dry forest environment, amphibian species richness patterns are strongly influenced by pond hydroperiod and landscape variables. Based in ours results, isolated ponds (i.e. ponds located at more than 1.5 km in average from the three nearest ponds) have fewer species than those ponds near to other bodies of water (3.75 species vs 5.37 species in average respectively). Therefore, this variable represents an important factor explaining variations in amphibian species richness in the Arid Chaco (see Tables 2 and 3, section 3.1). This result partially agrees with the island biogeography theory proposed by McArthur and Wilson (1963), which predicts that species richness is lower in isolated islands (in this case, isolated aquatic habitat patches). Isolation is significant for pond-breeding amphibians, since the rescue of local populations from extinction depends on the probability of the arrival of individuals dispersing from nearby ponds (Carlson and Edenhann, 2000; Funk et al., 2005; Semlitsch, 2008; Sjögren-Gulve, 1994; Skelly et al., 1999; Trenham et al., 2003). Therefore, the effect of pond isolation on species richness patterns observed in the Arid Chaco region would be related to the balance between the incidence of local extinctions and the probability of recolonization from nearby ponds.

Table 7

Best model obtained to explain variations in abundance of de *Phyllomedusa sauvagii*. The following values are indicated: coefficient (β), its significance according to the χ^2 test, and upper confidence limit (upper CL) and lower confidence limit (lower CL) of the interval for the estimated coefficient, as well as the χ^2 statistic for the Log-likelihood ratio (χ^2 LR) test, its significance, AIC statistic, weight (ω) and Nagelkerke's R^2 (R_N^2).

| | Parameters | | | | | Model | | | | |
|-------------------------------|--------------|--------------|-------------------|--------------|-------------|-------|-------------|--------|---------|----------|
| | β | χ^2 | p | Lower CL | Upper CL | AIC | χ^2 LR | p | r_N^2 | ω |
| <i>Model 1</i> | | | | | | | | | | |
| Tree & Shrub cover | 0.017 | 7.41 | 0.007 | 0.005 | 0.03 | 52.75 | 29.06 | <0.001 | 0.552 | 0.371 |
| Depth | 1.06 | 14.52 | <0.0001 | 0.519 | 1.62 | | | | | |

If this hypothesis were true, then pond isolation would affect the occurrence of local populations of low vagility species, such as the arboreal frog *Phyllomedusa sauvagii* (Neckel-Oliveira and Gascon, 2006) or the semi-aquatic frog *Lepidobatrachus llanensis*. The abundance of *Pleurodema guayapae* exhibited a negative response to pond isolation. According to model obtained, the abundance of this species reach maximum values (near 23 individuals per pond) in shallow ponds (less than 20 cm) located nearby to other bodies of water (less than 500 m from three nearest ponds). The fact that abundance of *P. guayapae* is positively associated to proximity to potential breeding sites suggests that ponds would not represent isolated patches for the species. By contrast, its populations would depend on a group of water bodies, suggesting frequent movements among ponds. While local populations of most pond-breeding amphibians are usually composed of individuals that reproduce and live around a single pond, the use of several nearby ponds has also been documented; and in this case, a single breeding population relies on a group of ponds in which frequent migratory events occurs (Marsh et al., 1999; Petranka et al., 2004; Semlitsch, 2008; Zamudio and Wicczorek, 2006). Although no quantitative studies on movements of *P. guayapae* or other related species have been conducted, this species was frequently observed (along with *Rhinella arenarum* and *Rhinella schneideri*) moving on land, suggesting active movements and migrations. In addition, mass migrations of *Chacophrys pierottii* were observed after the breeding period (early autumn) in the study area (Ceí, 1980). We highlight the need for studies addressing amphibian movements in dry seasonal forests (dispersal rates, gene flow, home range, migrations).

The theory of McArthur and Wilson (1963) predicts that large islands are more diverse than small ones. In the present study we detected an effect of pond area on amphibian richness. Although some works suggest a positive relationship between pond area and amphibian richness, other studies show that this variable has little or no effect on species richness (Babbitt, 2005; Hecnar and M'Closkey, 1998; Richter and Azous, 1995; Snodgrass et al., 2000). In the study area all ponds are relatively small wetlands (from 50 to 20,000 m²), and the smallest ones (small rainwater-fed ephemeral ponds) have a very short hydroperiod. Therefore, the experimental design used in this study makes it difficult to separate the effect of these variables on species richness, and further studies will be necessary to elucidate this aspect.

The terrestrial matrix around ponds also had an important effect on amphibian richness patterns of the Arid Chaco. Ponds

located in matrices with low shrublands coverage and elevated forest cover (i.e. near 0 and 80% of coverage respectively) had maximum values of species richness (eight to nine species in non-isolated farm ponds). The results obtained also showed a positive trend between forest cover in the matrix and the abundance of a terrestrial species that finds refuge in mammal burrows as well as under fallen logs in the forest (*Leptodactylus bufonius*) (see Table 4, section 3.2). In this region, soil moisture in degraded sites with low canopy cover is significantly lower than in sectors with greater forest cover (Abril and Bucher, 1999). These modified microclimatic conditions in the matrix surrounding water bodies might negatively influence those species that move across or seek refuge in terrestrial environments, resulting in reduced species richness in ponds with low surrounding native forest cover. However, Arid Chaco amphibians can tolerate high temperatures and have several strategies to avoid desiccation (Duarte et al., 2012; Faivovich et al., 2014; McClanahan et al., 1976, 1983; Ruibal, 1962). Therefore, it is possible that terrestrial matrix degradation would also affect Arid Chaco amphibians in other ways than via microclimatic alterations. For instance, oversimplification of forest structure results in a decrease in the availability of fallen logs, which are often used as refuge sites by several Chaco amphibians. Further analyses will be necessary to determine the processes that better explain the effect of terrestrial matrix degradation on changes in amphibian species richness.

Species richness and assemblage composition were both related to pond type. According to our results natural ponds had lower species richness (4.23 ± 1.15 species in average) than farm ponds (5.11 ± 1.28 species in average). Sites with a very short hydroperiod (i.e., natural ponds) were characterized by the presence of a few species with very rapid larval development (less than 30 days), such as *Chacophrys pierottii*, *Lepidobatrachus llanensis* and species of *Pleurodema* (Table 3 and Fig. 3) (Ceí, 1980; Fabrezi, 2011; Quinzio et al., 2006). According to the models obtained the abundance of *Lepidobatrachus llanensis* and *Pleurodema guayapae* was associated with shallow (less than 30 cm of depth) and, therefore, ephemeral ponds (Tables 5 and 6, and Fig. 3). In contrast species with longer larval development (such as *Phyllomedusa sauvagii*, *Leptodactylus mystacinus* or *Rhinella schneideri*) (Fabrezi, 2011; Kher and Gomez, 2009) were dominant in deep farm ponds (Table 3 and Fig. 3). Tadpoles of species with rapid development present high activity rates. This represents a competitive advantage for resource acquisition and a rapid growth. However tadpoles with high activity rates are more exposed to predators, which are more abundant in ponds with long hydroperiod (Dayton and Fitzgerald, 2001; Skelly, 1996; Welborn et al., 1996). Therefore, the observed patterns of richness distribution and segregation of amphibians species between ponds with different hydroperiod in Chaco would be related with desiccation risk and the trade-off between high activity levels and predator avoidance.

Changes in species composition among ponds with different hydroperiod also suggest that management and conservation of water bodies with contrasting duration would be important not only for the protection of regional amphibian diversity (Babbitt et al., 2003; Semlitsch, 2000; Snodgrass et al., 2000) but also for the conservation of amphibian species with contrasting life history.

Variations in abundance of *Phyllomedusa sauvagii* were explained only by local pond variables (i.e. deep sites with high proportion of trees and shrubs on the edges represent favorable sites for the abundance of this species) (Table 7). For *P. sauvagii*, the importance of pond characteristics would be directly related to the species' reproductive mode and strategies. Firstly, larvae of *P. sauvagii* have a prolonged development period (Fabrezi, 2011); therefore, larvae would be exposed to a high risk of desiccation in shallow ponds. Secondly, plants availability around ponds is

important for species reproduction, because in *P. sauvagii*, oviposition involves selection of trees and shrubs with broad leaves and crowns projecting on ponds (García et al., 2013). Similar results were reported for other species of the genus. For example, *Phyllomedusa tarsius* was found to lay a higher number of clutches in ponds densely vegetated ponds with long hydroperiod (Neckel-Oliveira, 2004).

The results of this study have potential implications for the conservation and management of habitats for amphibians in the Chaco ecoregion, as well as in other tropical and subtropical dry forests with similar land uses. Most Arid Chaco anurans use temporary ponds with long hydroperiod as reproductive sites. In the Arid Chaco, most farm ponds are sites with longer water permanence than natural ponds, providing favorable breeding habitats for more than 80% of the amphibian species of the entire area (Table 1 and Fig. 3). Moreover, some of these species are mainly distributed in Chacoan environments (*Phyllomedusa sauvagii*; *Leptodactylus bufonius*) or are endemic to the Chaco ecoregion (*Lepidobatrachus llanensis*; *Pleurodema guayapae*; *Chacophrys pierottii*) (Ceí, 1980; Faivovich, 1994). The use of farm ponds by these amphibians reveals the potential value and the compatibility of certain traditional activities (i.e. extensive production of livestock for subsistence) with the maintenance of Chaco amphibian reproductive habitats. This is particularly important in the southernmost portion of Chaco, since the rapid expansion of the agricultural frontier and intensive livestock production in the region have caused a marked reduction in the rural population dedicated to traditional activities (Britos and Barchuk, 2008; Zak et al., 2008). Changes in land use might negatively affect the availability of farm ponds suitable for amphibian reproduction in the Arid Chaco, increasing the effect of pond isolation on species richness. Accordingly, the loss of ponds associated with traditional rural activities has been shown to have a negative effect on amphibian populations in Europe (Curado et al., 2011; Hartel et al., 2010).

In addition, the generalized conversion of woodlands into croplands involves the use of agrochemicals, many of which have been found to have a negative effect on amphibians inhabiting agroecosystems in Argentina (Peltzer et al., 2008; Vera Candioti et al., 2010). Thus, in the Arid Chaco the current conversion of extensive livestock systems that depend on native forest to agricultural systems or intensive livestock production systems (which requires logging and generally the implantation of exotic pastures) would negatively affect amphibians due to a reduction of livestock activities that require farm ponds (and a consequent increase in pond isolation), the contamination of remnant artificial and natural wetlands, and the elimination of forests in the terrestrial matrix.

Although ponds are of great importance in terms of diversity (Céréghino et al., 2007), to our knowledge, in Argentina there are no regulations concerning the conservation of small temporary freshwater lentic habitats (i.e., temporary rainwater ponds, small temporary bogs or marshes and farmland ponds). We suggest that protecting ponds with different hydroperiod and terrestrial buffer zones covered with remnants of Arid Chaco native forest would be an effective strategy to ensure the conservation of breeding sites for numerous amphibian species of the Arid Chaco. By contrast, if no actions are taken, the rapid land-use changes in the Chaco region will increase the isolation of the remnant ponds (through the loss of neighbor ponds and forest cover), resulting in the decline of regional amphibian diversity mediated by the occurrence of multiple local extinctions.

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