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RESEARCH ARTICLE

Anuran responses to spatial patterns of agricultural landscapes in Argentina

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Abstract

Context Amphibians are declining worldwide and land use change to agriculture is recognized as a leading cause. Argentina is undergoing an agriculturalization process with rapid changes in landscape structure.

Objectives We evaluated anuran response to landscape composition and configuration in two landscapes of east-central Argentina with different degrees of agriculturalization. We identified sensitive species and evaluated landscape influence on communities and individual species at two spatial scales.

Methods We compared anuran richness, frequency of occurrence, and activity between landscapes using call surveys data from 120 sampling points from 2007 to 2009. We evaluated anuran responses to landscape structure variables estimated within 250 and 500-m radius buffers using canonical correspondence analysis and multimodel inference from a set of candidate models.

Results Anuran richness was lower in the landscape with greater level of agriculturalization with reduced amount of forest cover and stream length. This pattern

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was driven by the lower occurrence and calling activity of seven out of the sixteen recorded species. Four species responded positively to the amount of forest cover and stream habitat. Three species responded positively to forest cohesion and negatively to rural housing. Two responded negatively to crop area and diversity of cover classes.

Conclusions Anurans within agricultural landscapes of east-central Argentina are responding to landscape structure. Responses varied depending on species and study scale. Life-history traits contribute to responses differences. Our study offers a better understanding of landscape effects on anurans and can be used for land management in other areas experiencing a similar agriculturalization process.

Keywords Amphibian conservation · Agriculture expansion and intensification · Entre Rios · Espinal · Landscape structure · Habitat loss · Forest connectivity · Landscape heterogeneity

Introduction

World population growth and food demand is leading to an agriculturalization process in many countries, which involves rapid changes in land use and promotes environmental degradation (Rabinovich and Torres 2004; Young 2006). This process is characterized by the expansion and intensification of land production areas that results in landscapes with reduced natural vegetation distributed in remnant patches and greater technology use to enhance production yields (Viglizzo et al. 2001; Aizen et al. 2009; Oesterheld 2008).

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In Argentina, agriculture expansion and intensification occurs primarily in the Pampas and Espinal ecoregions (Viglizzo et al. 2003), which are the most productive regions in the country. Natural vegetation, such as forests and grasslands are reduced and replaced by row crop production expansion (Tassi et al. 2011). Although there are several important crops in these regions, soybean production is the main driver of the agriculturalization process (Young 2006) and the dominant type of row crop (FAOSTAT 2014; SAGPYA 2014).

Therefore, agricultural landscapes show a lower land-use diversity and heterogeneity (Aizen et al. 2009). Also, greater input of agrochemical products to enhance production is observed (Pérez Leiva and Anastasio 2003; Zaccagnini et al. 2007a; Bernardos and Zaccagnini 2011; CASAFE 2014). As a consequence, the composition and spatial configuration of agricultural landscapes are changing, altering the integrity and sustainability of agroecosystems (Zaccagnini et al. 2007b; De la Fuente and Suárez 2008; Aizen et al. 2009) and resulting in loss of biodiversity in the region (Schrag et al. 2009; Gavier-Pizarro et al. 2012).

Biodiversity conservation is an essential consideration for sustainable agroecosystems (Altieri 1999). Of special concern in agroecosystems are amphibians, which play key ecological roles in ecosystem functioning (Seale 1980; Wyman 1998; Marcot and Vander Heyden 2001). In agroecosystems, adult stages are valuable as biological pest controllers for agriculture production (Attademo et al. 2005), and are considered good biological indicators because they respond quickly to environmental change (EPA 2002). Many amphibian species are declining worldwide and habitat loss, fragmentation and degradation by agriculture have been recognized as leading factors in several countries (Bishop and Pettit 1992; Sparling 2002). In Argentina, these factors are also expected to affect amphibian conservation in agroecosystems, but effects of landscape change through agriculturalization are still not clear. Agriculturalization generates landscapes with varying levels of transformation. By comparing these different landscapes, we can better understand how amphibians respond to agricultural expansion and intensification by identifying sensitive species and key factors that determine their persistence (Pulliam 1988; Opdam 1990).

Many amphibians have a biphasic life cycle requiring both aquatic and terrestrial natural habitats

for reproduction, larval development, feeding, hibernation and dispersal processes (Heyer et al. 1994). Thus, the availability, quality and connectivity of required habitats are fundamental for their persistence in agroecosystems. Recent international research on the relationships between amphibians and landscape attributes indicate that habitat loss and fragmentation exert strong negative effects on amphibians (Cushman 2006). Forest area surrounding ponds (Knutson et al. 1999; Houlahan et al. 2000; Herrmann et al. 2005), proximity of ponds to forests and distance among ponds (Guerry and Hunter 2002; Veysey et al. 2011) as well as connectivity of both ponds and forested habitats (Hecnar and M'Closkey 1996; Marsh and Trenham 2001; Rothermel 2004) were identified as key predictors of regional viability of amphibian populations. Several studies demonstrate that local and landscape changes resulting from agricultural expansion have negative effects on amphibian diversity (Babbitt et al. 2003; Silva et al. 2012). Further, crop expansion (Bonin et al. 1997; Mensing et al. 1998; Atauri and de Lucio 2001) and urban development (Carr and Fahrig 2001; Gagné and Fahrig 2007) can reduce amphibian richness and abundance.

Amphibian species respond differentially to landscape change in agricultural landscapes. Both negative and positive effects have been observed at species and guild levels (Bascompte and Solé 1996; Knutson et al. 1999; Joly et al. 2001). These studies suggest that amphibian response to landscape composition and configuration could depend on the interaction between species' life-history traits and the level of agricultural expansion. Anurans are the most diverse order of amphibians and include species with a variety of lifestyles from fully aquatic, semi-aquatic (aquatic and terrestrial), terrestrial, arboreal, and fossorial (Dodd 2010). Fully aquatic species may be more affected by direct changes to ponds than semi-aquatic or more terrestrial species that are not restricted to ponds and can move to find better habitat or shelter (Peltzer et al. 2006). These local scale impacts on reproductive habitat may have a stronger influence on species with low dispersal and low reproductive rates given their limited perception of space, low ability to colonize distant breeding sites, and thus, low population recruitment (Quesnelle et al. 2014). Alternatively, forest-dependent anurans may show greater sensitivity to forest habitat loss than habitat-generalist or open land species (Basso 1990). Also, more mobile forest-dependent anurans may show greater sensitivity to forest loss and fragmentation in the surrounding landscape matrix (Gibbs 1998) than highly mobile habitat-generalist species or less mobile forest-dependent species. Thus, it is important to study agricultural effects on anurans at the community and species levels at multiple scales to better understand the differential response of each species (Cushman 2006).

Our aim was to evaluate the effect of agriculturalization and resulting landscape structure on anurans in Argentina. Thus, we compared anuran responses patterns between two agricultural landscapes with different levels of agriculture expansion and intensification and evaluated the relation to landscape composition and configuration. We used these two agricultural landscapes as a proxy to represent a gradient of landscapes changes occurring during the agriculturalization process. Considering anuran life history traits mentioned above, we predicted the following relationships: (1) anuran richness, species frequency of occurrence and level of activity (anuran response variables) would be lower in highly transformed landscapes, (2) anuran response variables would be positively associated with landscapes having closer proximity of water bodies, greater amount of forest cover, greater proximity and connectivity of forest habitat patches and increased landscape heterogeneity, and conversely, negatively associated with greater row-crop production area and rural/urban housing density and proximity, and (3) individual species would show differential sensitivity to the agriculturalization process and show different associations to a different set of landscape variables based on their specific habitat requirements and life history traits.

Methods

Study area

We selected two primarily agricultural landscapes of 900 km^2 near the towns of Crespo (32°1′S, 60°17′W) and Cerrito (31°4′S, 60°1′W), in the west-central part of Entre Rios province, east Argentina (Fig. 1). These areas belong to the Espinal ecoregion where rapid agricultural expansion is occurring. The original vegetation of these landscapes are semi-xerophytic forests, characterized by tree species such as *Prosopis*
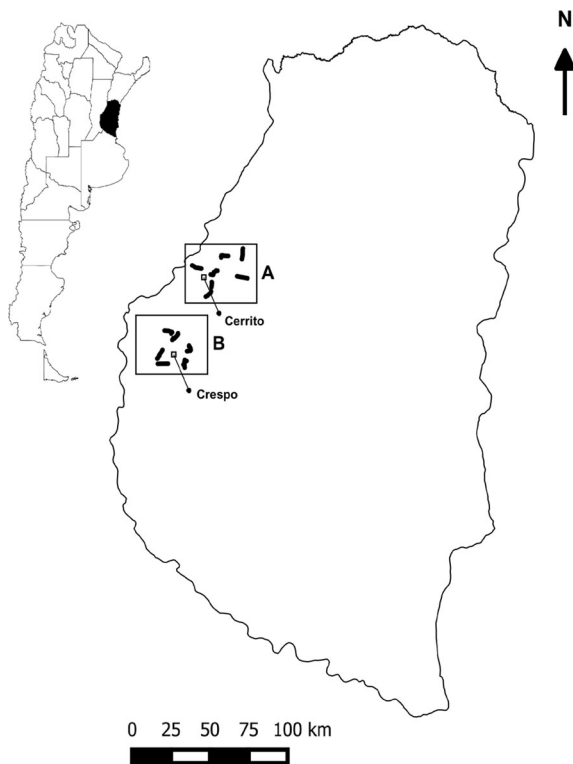
Fig. 1 Study area located in the west central portion of Entre Ríos province in Argentina. Selected landscapes with less (**a**) and more (**b**) agriculture expansion and intensification located near Cerrito (31°4′S, 60°1′W) and Crespo Towns (32°1′S, 60°17′W) respectively. Sampling transects are shown as black lines within study areas

affinis, *Acacia caven*, *Geoffroea decorticans*, *Celtis tala* and *Schinus longifolia*, intermixed with grasslands dominated by *Stipa* spp. and *Paspalum dilatatum* (Cabrera 1971; Sabattini et al. 1999, 2008). The climate is temperate with mean annual temperatures and precipitations ranging from 18 to 20 °C and 800 to 1000 mm respectively.

Landscapes represent two stages of the agriculturalization process and differ in the amount and connectivity of forests, degree of spatial heterogeneity (i.e. presence of different elements in the landscape), and environmental quality of aquatic and forest habitats as defined by their degree of contamination or composition and structure of their vegetation cover (Calamari et al. 2006; Sabattini et al. 2009; Tassi et al. 2011). More intensive agriculture occurs around Crespo, an area with a longer history of agricultural use resulting in severe landscape simplification due to the expansion of row crops such as soybean, wheat,

corn, and sunflower, planted pastures, and urban and large-rural settlements. Native forest cover has been greatly reduced and almost eliminated from this landscape (Sabatini et al. 2010). Forest environments consist primarily of remnant patches of native forest surrounding waterbodies, and small patches of exotic species planted for house landscaping and cattle shading. Less intensive agriculture occurs in the Cerrito landscape. This landscape has greater land-cover heterogeneity, forest connectivity and more and larger patches of native semi-xerophytic forests. Also most hedgerows, erosion control terraces and riparian strips are covered by native forest compared to those in Crespo dominated by herbaceous vegetation (Calamari et al. 2006). The hydrologic network is dense in both landscapes and several waterbodies with different hydrologic regimes are present, including streams (the most common), rivers, lagoons, temporary natural ponds, permanent artificial ponds, and roadside ditches.

Anuran survey

Call surveys are a cost-efficient means of assessing anuran distributions throughout large areas and are commonly used in large-scale monitoring projects (Bishop et al. 1997; Bonin et al. 1997; LePage et al. 1997). We used the anuran call catalog of Straneck et al. (1993) and the North American Amphibian Monitoring Program (NAAMP) protocol (Weir and Mossman 2005) to conduct frog and toad call surveys at 60 sampling points located systematically on six transects per landscape placed on secondary roads ($N = 120$) (Fig. 2). Call surveys were performed five times per point within 7-day sampling periods (two transects per night) across 3 years, beginning from spring 2007–summer 2009. In the southern hemisphere, most anurans breed from September to March (i.e. spring and summer seasons), so sampling periods followed rain events during months with higher amphibian activity, i.e. October–November and February–March. Unidentified calls were resolved by visual observations of the calling individual at the sampling point when possible.

We located sampling points at least 800 m apart to ensure spatial independence of amphibian detection (Semlitsch and Bodie 2003). Three observers conducted call surveys but the main observer was the same among sampling periods to minimize differences

in detection abilities. Call surveys lasted 3 min and were conducted after sunset and finished by midnight (Shirose et al. 1997; Gooch et al. 2006). Our sampling scheme did not allow us to meet the 'closed population' assumption necessary to calculate detection probabilities and occupancy because sampling occurred across years and migration and/or colonization processes might take place at sampled points (MacKenzie et al. 2003; Mackenzie and Royle 2005). Potential biases in occurrence estimation could be introduced by using naïve occurrence. However, we assert that five sampling periods per site within 7 days reduced bias. Thus, we obtained presence-absence data for each anuran species at each sampling point by pooling data from all sampling periods to calculate species richness, composition, frequency of occurrence and activity level. The presence of two pairs of species: (1) *Physalaemus biligonigerus* and *P. albonotatus* and (2) *Dendropsophus nanus* and *D. sanborni* were grouped for this study as *Physalaemus* spp. and *Dendropsophus* spp. respectively, because their calls are too similar to distinguish between in the field. We calculated species richness as the accumulated number of detected species after five surveys at each point. We used the proportion of sampling points occupied as a measure of each species frequency of occurrence within each landscape (i.e., high, moderate, and low frequency occurrence). We used the maximum activity-calling index value registered per sampling point after five surveys as an index of relative abundance of males (Weir and Mossman 2005). The activity calling index was 0 if no individual called, 1 when we could count the number of calling individuals, 2 if we could distinguish calls but they overlapped, and 3 when we detected a chorus of calling individuals. Maximum activity-calling index of 3 also implies breeding activity. Anuran richness and species presence-absence data at the sampling point were used to model their relationship with landscape structure variables. Only species detected by call surveys in at least 15 % of total sampling points in at least one of the studied landscapes were considered for presence-absence modelling.

Landscape analysis and explanatory variables

We used a Landsat satellite image obtained from a fusion process of one multispectral Landsat TM image of 30 m of spatial resolution (Path 226-Row 82 January 2007, including bands 1–5 and 7) and the panchromatic band from a Landsat ETM + image of 15 m of spatial resolution (January 2003) to increase the spatial resolution (Pohl and Van Genderen 1998; Calamari et al. 2006) for landscape analysis (Fig. 2). Those images were downloaded from INPE web site (Brazilian National Institute for Space Research). Before the fusion process the images were geometrically corrected using a first degree polynomial model because the topography of the study area is flat plain or with smooth undulations. Also, images were orthorectified using a digital elevation model (DEM) and nearest neighbor as resample method. Subsequently, we used Principal Component as a method for fusion process with nearest neighbor as resampling technique.

The resulting image was then classified using the parametric supervised classification algorithm maximum likelihood. Nine terrestrial land cover types were identified, and classification was validated with 100 points per land cover type randomly selected using Quickbird images (available in GoogleEarth TM, http://earth.google.com) and ground sampling (Congalton and Green 2009). Any pixel clump smaller than 0.5 ha was considered a classification artifact and was eliminated from the classified image. Overall classification accuracy was 82 % and the most misclassified cover type was corn (Supplementrary material Appendix 1). We grouped the nine land cover types into four classes: (1) row crops (soybean, corn, sunflower and sorghum), (2) forests, (3) grasslands, pastures and harvested fields with stubble cover, and (4) urban areas, roads, bare ground and harvested fields with no stubble cover (Fig. 2). The completed process was carried out in ERDAS imagine 9.2 (2008).

We established a 250 and 500-m buffer around each sampling point, and calculated landscape composition and configuration variables using FRAGSTAT (version 3.3, McGarigal et al. 2012) (Fig. 2, Supplementrary material Appendix 2). We selected these buffer sizes to include core terrestrial habitat and migration distances registered for anurans that range from 205 to 360 m (Semlitsch and Bodie 2003). Within each buffer, we calculated the Shannon diversity classes Index (SHDI) as a measure of landscape heterogeneity, total cover area of row crops (CA1) as a measure of row-crop production level, total forest cover (CA2), and number (NP2), cohesion (COHES2), mean area (AREA2) and mean euclidean distance (ENN2) of
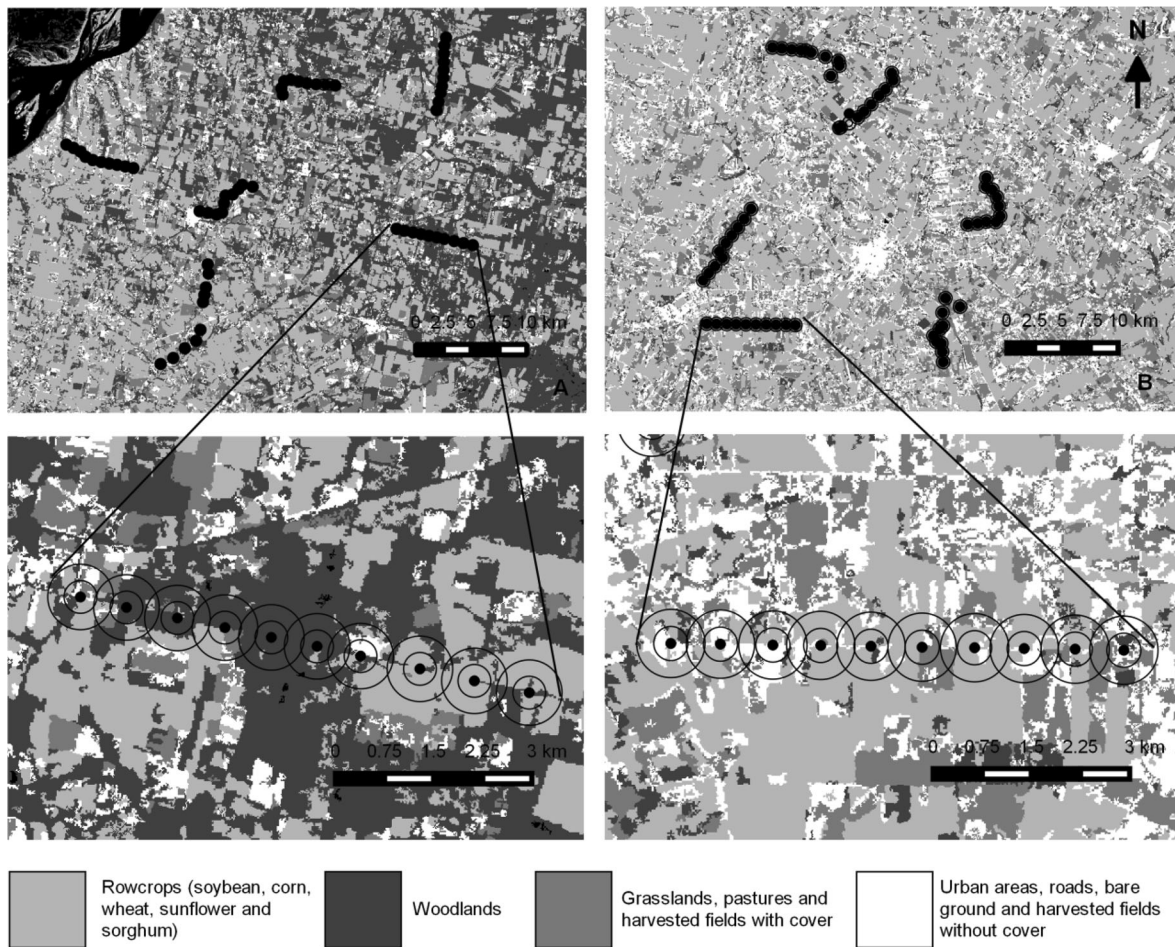
Fig. 2 Land cover classification of a Landsat TM image around (**a**) Cerrito and (**b**) Crespo towns showing distribution of sampling transects and points with 250–500 buffer areas

forest patches, as indicator of forested habitat loss and fragmentation for anurans.

To quantify the availability and proximity of potential aquatic breeding areas, we calculated the total number of different water bodies (WB), total length of stream sections (STREAM) within each buffer, and the distance to the nearest water body from the sampling site (DISTWB). We also measured rural-housing influence by quantifying total number of rural establishments, i.e. rural houses, within each buffer (RE) and distance to the nearest rural establishment (DISTRE). Visual recognition and quantification of these elements was performed using Quickbird imagery available through the Google Earth site (http://earth.google.com) using QGIS 2.0 (QGIS Development Team 2012) since most water bodies

and individual rural establishments could not be defined in the classified Landsat ETM + image.

Landscape structure and anuran diversity comparison between landscapes

To evaluate landscape structure and anuran status differences between the two landscapes, we compared landscape variables measured at two spatial scales (250 and 500 m), species richness and level of activity recorded at the sampling point using unpaired t-tests ($\alpha = 0.01$). To compare each species frequency of occurrence between the landscapes, we used Chi square (χ^2) tests. Statistical assumptions of normality, homoscedasticity and data independence were evaluated and met.

Response of anurans to landscape structure

We explored the association of each species presence to landscape structure variables using canonical correspondence analysis in R using vegan package (R Development Core Team 2013) to group species based on similar responses to the landscape structure (Legendre and Legendre 1998). We used univariate regression analyses to explore the relationship of species presence-absence and sampling point species richness (response variables) relationship with each landscape variable.

We examined the correlation among landscape explanatory variables by Pearson tests at each scale of analysis using a tolerance level of $r = 0.7$. Correlated variables with less statistical significance were discarded (Belsley et al. 1980). AREA2 was highly correlated with CA2 ($r = 0.981$) as well as WB and DISTWB ($r = 0.705$) at the 250 m-scale. AREA2 was also correlated with CA2 at 500 m ($r = 0.946$). Thus, we discarded AREA2 at both scales and WB at 250 m from further analyses. Final variables to include in further analyses were selected according to correlation analyses and the strength of their fit obtained by the univariate regression analysis with each response variable.

We analyzed anuran relationship with landscape composition and configuration at two spatial scales by fitting generalized linear mixed models for anuran richness and species presence in R version 3.2.1 (glmmML package, R Development Core Team 2013). Landscape and sampling transect entered the model as random effects (Zuur et al. 2009). We modeled richness as a poisson process (i.e. counts), and species presence as a binomial process, i.e. logistic regression. Species presence modeling was run only for the species whose frequency of occurrence differed between the landscapes but had at least 15 % of sampling points occupied within any of the studied landscapes.

We created a candidate set of a priori models for richness and species presence data using ecologically meaningful landscape variables at each scale (Table 1). Landscape variables were standardized before modeling. As we have a limited knowledge of the biology and ecology of several of the analyzed species, we fit the same set of models for all the species trying to represent all plausible relationships between anurans and landscape structure.

We used the second-order Akaike Information Criterion (AICc, recommended when $n/K < 40$, where n is the sample size and K is the number of estimated parameters) and Akaike weights (w_i) to choose best-fitting models from the candidate set of models (Burnham and Anderson 1998; Anderson et al. 2000; Burnham and Anderson 2001). The AIC belongs to a family of model selection criteria which consider model fit as well as complexity, and permits the simultaneous comparison of multiple models (Johnson and Omland 2004). AIC values reflect the amount of "lost information" when a model is used to approximate conceptual reality. Consequently, the model with the lowest AIC value is selected as the best model (Burnham and Anderson 1998). When differences between AIC values are small (i.e., less than 2 AIC units), Akaike weights can be used as a measure of the "weight of evidence" in favor of each model. Akaike weights are interpreted as the approximate probability that model i is the best-fitting model in the set of models being considered (Anderson et al. 2000).

To evaluate the effect of landscape composition and configuration, we used multi-model inference or "model averaging" (Burnham and Anderson 1998, 2001). For richness and individual species, we obtained model coefficient averages, interpreted as the average effects of each landscape predictor variable, weighted by Akaike weights. These model averages were obtained from the "confidence set" of models which was defined as those with less than 2 AIC units of difference with the best model (Burnham and Anderson 1998, 2001). Model selection parameters were calculated in R using MuMIn package (R Development Core Team 2013).

Results

Landscape composition and configuration

Less intensified landscape near Cerrito showed significantly greater forest cover (CA2) and mean area (AREA2), number (NP2) and cohesion (COHES2) of patches as well as lower cover of row crops (CA1) than the most intensified landscape found near Crespo at both spatial scales (Table 2). Density of rural establishments (RE) within 250 m, their proximity (DISTRE) and mean euclidean nearest-neighbour distance of forest patches (ENN2) within 500 m, also differed between landscapes, being greater in the more intensified landscapes around Crespo. The diversity of cover classes (SHIDI), total number of water bodies

Table 1 General structure of a priori models evaluated for anuran richness and species presence

Models	General model structure
Null	None
Single-factor	Aquatic habitat (STREAM; WB and/or DISTWB)
	Forested habitat (CA2)
	Row crop production (CA1)
	Heterogeneity (SHDI)
	Connectivity (COHES2, ENN2 and/or NP2)
	Rural housing (RE and DISTRE)
Multiple-factor	Aquatic habitat + forested habitat
	Aquatic habitat + row crop production
	Aquatic habitat + heterogeneity
	Aquatic habitat + connectivity
	Aquatic habitat + rural housing
	Forested habitat + heterogeneity
	Forested habitat + connectivity
	Forested habitat + connectivity + heterogeneity
	Forested habitat + heterogeneity + rural housing
	Forested habitat + connectivity + heterogeneity + rural housing
	Forested habitat + rural housing
	Aquatic habitat + forested habitat + heterogeneity
	Aquatic habitat + forested habitat + connectivity
	Aquatic habitat + forested habitat + rural housing
Full-Factor	Aquatic habitat + forested habitat + heterogeneity + connectivity + rural housing

(WB), total length of stream sections (STREAM) and distance to closest water bodies (DISTWB) did not differ between landscapes at either scale.

Anuran species presence, level of activity, and richness

We confirmed the presence of 18 species in the less intensified agricultural landscape near Cerrito area and 15 species in the more intensified landscape near Crespo by call surveys (Table 3). *Physalaemus riograndensis* and *S. acuminatus* were not detected in Crespo area and the presence of *P. albonotatus* and *Dendropsophus nanus* was uncertain in this area. The last two species show great calling similarity with *P. billigonigerus* and *D. sanborni* respectively, thus we decided to group these species as *Physalaemus* spp. and *Dendropsophus* spp. for further comparisons.

The less intensified landscape showed significantly greater mean total richness and less variability than within the more intensified landscape (t = 4.0526,

df = 116.48, p < 0.0001). Mean total richness at sampling points was 7.06 ±1.56 (mean ± SE) ranging from 5 to 12 species around Cerrito and 5.83 ± 1.66 ranging from 3 to12 species around Crespo.

The proportion of points occupied per species differed between landscapes as well (Fig. 3a). We distinguished three groups of species' frequency of occurrence: 1) high frequency of occurrence species in both landscapes with more than 75 % of sampling points occupied (n = 4: *Leptodactylus gracilis*, *L. mystacinus*, *L. latinasus*, *Hypsiboas pulchellus*), 2) moderate to low frequency of occurrence species that occupied between 15 and 75 % of sampling points showing a higher occurrence in the less intensified area (n = 7: *Rhinella schneideri*, *R. fernandezae*, *Scinax nasicus*, *S. squalirostris*, *Dendropsophus sp.*, *Pseudopaludicola falcipes* and *Physalaemus* spp.) and 3) rare frequency of occurrence species with less than 15 % of sampling points occupied in each landscape (n = 4), one species with a slightly higher occurrence in highly modified landscapes (*Odontophrynus americanus*) and three

Table 2 Description of landscape variables between less and more intensified landscapes near Cerrito and Crespo areas, respectively at 250 and 500 m buffers around sampling points in Entre Rios, Argentina

Landscape	Variables	Description	Agricultural landscapes			
			Less intensified (Cerrito)		More intensified (Crespo)	
			250	500	250	500
Aquatic habitat						
	WB	Total number of water bodies	1.03 (±0.17)[a]	3.89 (±0.42)[a]	1.17 (±0.16)[a]	4.71 (±0.31)[a]
	DISTWB	Mean distance to water bodies (m)	238.05 (±17.95)[a]	322.24 (±18.49)[a]	215.25 (±16.41)[a]	369.51 (±11.40)[a]
	STREAM	Total length of stream sections (m)	206.18 (±39.25)[a]	916.79 (±106.59)[a]	140.94 (±30.95)[a]	782.80 (±78.47)[a]
Forested habitat						
	CA2	Total cover of forest areas (ha)	6.45 (±0.70)[a]	40.11 (±2.39)[a]	1.11 (±0.23)[b]	16.92 (±0.81)[b]
	AREA2	Mean area of forest patches (ha)	5.67 (±0.72)[a]	20.71 (±2.59)[a]	0.89 (±0.19)[b]	2.51 (±0.34)[b]
Row crop production						
	CA1	Total cover of row-crops areas (ha)	7.39 (±0.69)[a]	44.62 (±2.14)[a]	9.36 (±0.63)[b]	52.99 (±2.06)[b]
Landscape heterogeneity						
	SHDI	Shannon's diversity index of cover classes	1.18 (±0.02)[a]	1.32 (±0.02)[a]	1.20 (±0.02)[a]	1.31 (±0.02)[a]
Forest connectivity						
	COHES2	Forest patch cohesion	91.79 (±1.08)[a]	95.63 (±0.51)[a]	72.78 (±±3.74)[b]	88.59 (±1.48)[b]
	ENN2	Mean euclidean distance among forest patches (m)	265.57 (±29.78)[a]	236.32 (±±41.55)[a]	352.63 (±37.55)[a]	345.57 (±45.37)[b]
	NP2	Number of forest patches	2.05 (±0.17)[a]	4.27 (±0.29)[a]	1.12 (±0.15)[b]	2.90 (±0.26)[b]
Rural housing						
	RE	Total number of individual rural establishments	0.4 (±0.13)[a]	1.47 (±0.31)[a]	0.55 (±0.09)[b]	1.67 (±0.19)[a]
	DISTRE	Distance to the closest rural establishment (m)	535.13 (±41.58)[a]	535.13 (±41.58)[a]	343.37 (±24.14)[b]	343.37 (±24.14)[b]

Superscripts a and b are used to indicate statistical differences of landscape variables between areas and scales at alpha = 0.01 by unpaired t-tests

species with a slightly higher frequency of occurrence in less modified landscapes (*R. arenarum*, *Elachistocleis bicolor* and *P. riograndensis*). Five species (33 %) were significantly found in more sampling points in the less intensified area: *R. schneideri* ($\chi^2 = 19.86$, p < 0.001), *R. fernandezae* ($\chi^2 = 6.4$, p < 0.05), *S. nasicus* ($\chi^2 = 8$, p < 0.005), *Physalaemus* spp. ($\chi^2 = 20.84$, p < 0.001) and *P. riograndensis* ($\chi^2 = 6.31$, p < 0.05). Finally, *S. squalirostris* and *Dendropsophus sp* showed a marginally higher occurrence in the less intensified area ($\chi^2 = 3.06$; p = 0.08 for both species).

Among the detected species, nine species (60 %) showed differences in the maximum activity level reached per sampling point between agricultural

Table 3 Anuran species detected by calling and visual surveys at sampling points in less and more intensified landscapes near Cerrito and Crespo areas

Species	Cerrito	Crespo
Bufonidae		
R. schneideri	X	X
R. fernandezae	X	X
R. arenarum	X	X
Cycloramphidae		
O. americanus	X	X
Hylidae		
S. nasicus	X	X
S. squalirostris	X	X
S. acuminatus	X	
Dendropsophus spp.**		
D. sanborni	X	X
D. nanus	X	
H. pulchellus	X	X
Leiuperidae		
Physalaemus spp.*		
P. albonotatus	X	
P. biligonigerus	X	X
P. riograndensis	X	
P. falcipes	X	X
Leptodactylidae		
L. latinasus	X	X
L. mystacinus	X	X
L. gracilis	X	X
Microhylidae		
E. bicolor	X	X

Species classified by family according to Vaira et al. 2012. * Grouped species: *P.albonotatus* and *P. biligonigerus*. ** Grouped species: *D. sanborni* and *D. nanus*

landscapes: *L. mystacinus* (t = 3.65, p < 0.001) and *O. americanus* (t = 2.53, p < 0.05) were more active in Crespo area (more intensified landscape) while *S. nasicus* (t = 6.83, p < 0.0001), *Physalaemus* spp. (t = 7.10, p < 0.0001), *R. schneideri* (t = 5.79, p < 0.0001), *Dendropsophus* spp. (t = 2.26, p < 0.05) y *P. falcipes* (t = 2.67, p < 0.01), *E. bicolor* (t = 2.19, p < 0.05) and *P. riograndensis* (Fig. 3B) were more active in Cerrito area (less intensified landscape). The calling activity level of species showed a very similar pattern than the one observed for the distribution of occurrence frequencies.

Landscape structure influence on anurans at community and species level

Richness

Site-level species richness was positively related to total cover of forests (CA2) at both buffer distances, and length of stream sections (STREAM) within 250-m (Fig. 4, Supplementrary material Appendix 3). STREAM_250 was present in 60 % of the best models while CA2_250 and CA2_500 were in 53 and 27 % respectively. Number of Forest patches at the 250-m scale (NP2_250), cohesion of forest patches at the 500-m scale (COHES2_500) and distance to rural establishments (DISTRE) also showed a positive influence on richness and were present in 13 % of the models (Fig. 4).

Species responses

Canonical correspondence analysis (CCA) axes explained 25 and 26 % of the variation at 250 and 500 m respectively indicating high variability in the data (Table 4). CCA axis 1 accounted for approximately 78 % of the constrained variability at both scales indicating a strong gradient, while CCA axis 2 accounted for 8 % of the constrained variability. CCA1 was most strongly influenced by total forest cover (CA2) and distance to rural establishments (DISTRE) at both scales.

Species formed two response groups in relation to the landscape variables. *L. latinasus*, *L. mystacinus*, *L. gracilis* and *H. pulchellus* (group 1) showed no association with any of the considered landscape variables. Due to this response pattern and the fact that they showed high frequency of occurrence and activity

Fig. 3 Proportion of occupied sampling points (**a**) and maximum activity level values (**b**) per site per species detected by calling surveys between less (Cerrito area, *white bars*) and more intensified landscapes (Crespo area, *black bars*). Species codes: *Leptodactylus latinasus* (*Ll*), *L. mystacinus* (*Lm*), *L. gracilis* (*Lg*), *Hypsiboas pulchellus* (*Hp*), *Scinax nasicus* (*Sn*), *Physalaemus* spp. (*Psp*: Physalaemus albonotatus and P. billigonigerus*), *Rhinella schneideri* (*Rs*), *R. fernandezae* (*Rf*), *S. squalirostris* (*Ss*), *Dendropsophus* spp. (*Dsp*: Dendropsophus sanborni and D. nanus*), *Pseudopaludicola falcipes* (*Pf*), *R. arenarum* (*Ra*), *Odontophrynus americanus* (*Oa*), *Elachistocleis bicolor* (*Eb*) y *Physalaemus riograndensis* (*Pr*). *P < 0.05, **P < 0.005, ***P < 0.0001
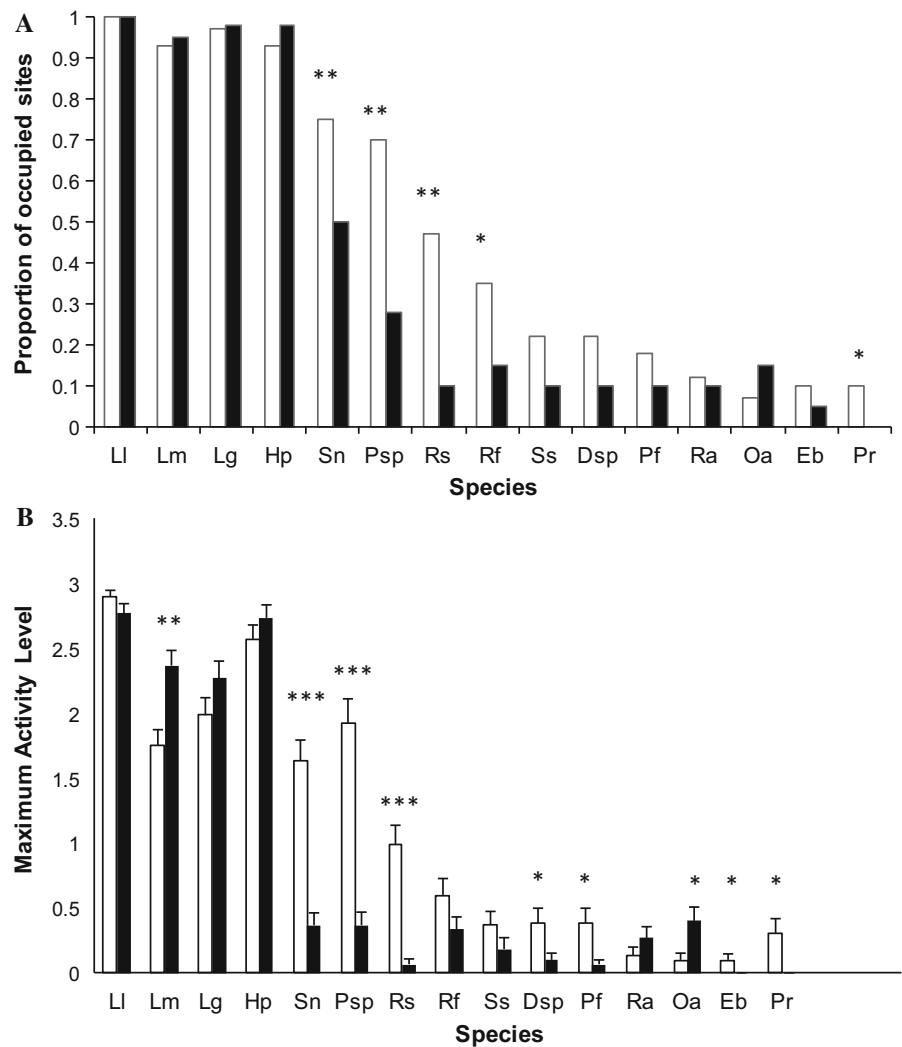

in both landscapes, these species were not analyzed further. The other group, *Dendropsophus* spp., *Physalaemus* spp., *R. schneideri* and *R. fernandezae* (group 2) showed an association to CA2 and DISTRE. Species in this group were more frequent in sampling points of less intensified landscape. *S. nasicus*, *S. squalirostris* and *P. falcipes* did not associate strongly with either group. However, *S. nasicus* showed similarities to both groups while *S. squalirostris* and *P. falcipes* were more similar to group 2 (Fig. 5).

According to individual species analyses, we observed that the presence of six out of seven amphibian species responded positively to aquatic habitat availability, where total length of stream (STREAM) was the more important type of aquatic

habitat. Also, four of these species (*S. nasicus*, *Dendropsophus* spp., *Physalaemus* spp. and *P. falcipes*) responded positively to forested habitat cover (CA2). Forest connectivity given by cohesion of forest patches (COHES2) was relevant for five species (*Rhinella schneideri*, *R. fernandezae*, *Dendropsophus* spp. *and Physalaemus* spp. and *P. falcipes*). *P. falcipes* was the only species that showed a negative response to this variable. Three species (*Rhinella schneideri*, *Physalaemus* spp. and *S. nasicus*) responded to landscape heterogeneity, i.e. diversity of cover classes (SHDI). *S. nasicus* was the only species that responded positively to this variable. In relation to human impact, rural housing (RE and DISTRE) and row crop production area (CA1) had

Fig. 4 Relationship between landscape variables and anuran species presence at two spatial scales (250 and 500 m). Averaged coefficients of more relevant variables that were included in the best set of models are shown (**a**) together with the proportion of models in the best set where those landscape variables were present (**b**). Position of averaged coefficients above or below zero indicates effect direction as positive or negative respectively
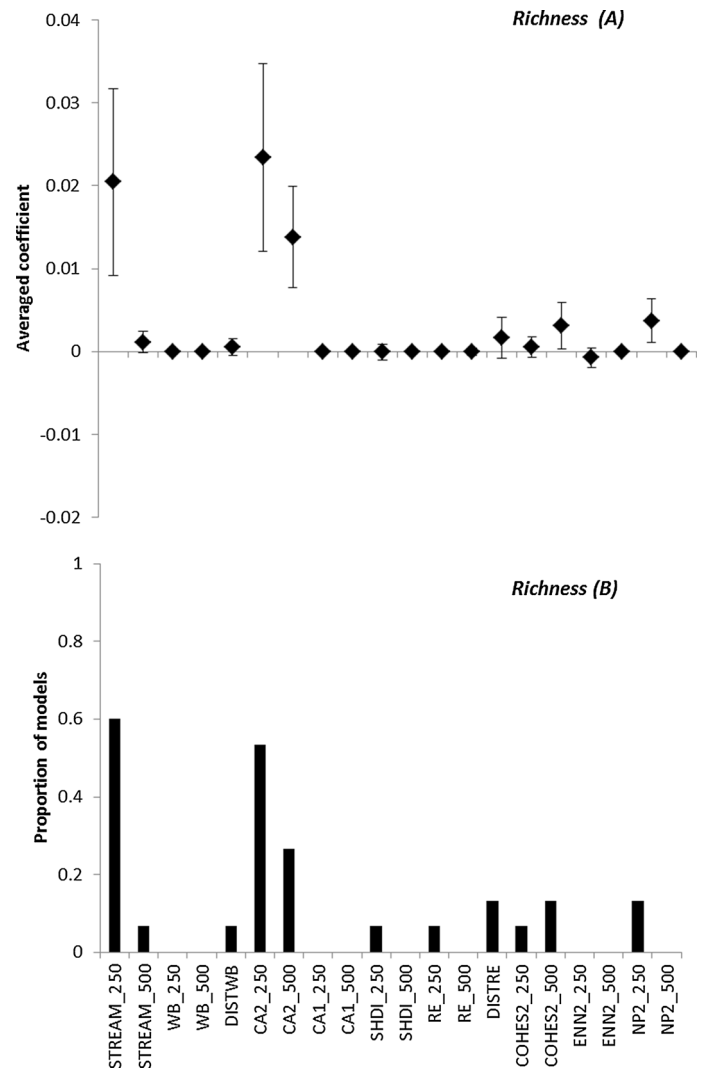
negative effects for two species (*Rhinella schneideri* and *Dendropsophus* spp.) (Fig. 6, Supplementrary material Appendix 3).

Regarding spatial scales we found that two species (*S. squalirostris* and *Physalaemus* spp.) were clearly related to landscape variables at the 250 m scale, four (*R. schneideri*, *R. fernandezae*, *S. nasica* and *P. falcipes*) at the 500 m scale and one (*Dendropsophus* spp.) to variables at both scales (Fig. 6, Supplementrary material Appendix 3).

R. schneideri was positively associated with the distance to rural establishments (DISTRE) and aquatic habitat availability (STREAM and WB) while

negatively associated with number of rural houses (RE), diversity of cover classes (SHDI) and row crop production (CA1). Other landscape variables that did not have significant coefficients but appeared within the best set of models for this species were forest cohesion (COHES2) and terrestrial habitat availability (CA2). The main scale of response for this species was 500 m.

R. fernandezae presence increased with forest cohesion (COHES2) within 500 m. According to the frequency of these variables in the best set of models it also showed an association at the same scale, i.e. 500 m, with aquatic (STREAM) and

Table 4 Summary information for Canonical Correspondence Analysis (CCA) obtained at both spatial scales (250 and 500 m). Output shows inertia (mean squared contingency coefficients) and proportion values that describe the explanatory power of the analysis given by considered landscape variables (constrained) and the unexplained "variance" (unconstrained), eigenvalues and importance of first and second CCA axes, and scores for landscape variables on CCA1 and CCA2

	250 m		500 m	
	Inertia	Proportion	Inertia	Proportion
Total	0.27	1.00	0.27	1.00
Constrained	0.07	0.25	0.07	0.26
Unconstrained	0.20	0.75	0.20	0.74
Eigenvalues	CCA1	CCA2	CCA1	CCA2
	0.05	0.005	0.05	0.005
	0.79	0.08	0.77	0.08
Landscape variables				
SHDI	0.11	−0.04	0.01	0.26
CA1	0.15	0.21	0.18	0.27
CA2	−0.50	−0.57	−0.59	−0.65
NP2	−0.31	−0.48	−0.23	−0.07
ENN2	0.10	0.19	0.12	0.02
COHES2	−0.28	−0.29	−0.27	−0.24
RE	0.13	0.43	0.06	0.33
DistRE	−0.29	−0.67	−0.29	−0.51
DistWB	−0.05	0.11	0.10	−0.08
STREAM	−0.19	−0.35	−0.14	−0.13

forested habitat availability (CA2), diversity of cover classes (SHDI) and distance to rural establishments (DISTRE).

Scinax nasicus showed a positive response to terrestrial habitat availability (CA2) and diversity of cover classes (SHDI) at 500 m scale. A response to aquatic (STREAM) and the distance to rural establishments (DISTRE) was also observed in the best set of models.

On the other hand, the presence of *S. squalirostris* was only positively related to stream length within 250 m (STREAM). However, forest cover (CA2), distance to water bodies (DISTWB) and diversity of cover classes (SHDI) appeared also in the best set of models.

Dendropsophus spp. responded to a great number of landscape variables at both spatial scales. It responded positively to total length of stream sections (STREAM), forest cover (CA2), forest patch cohesion (COHES2), and negatively to cover of row crops (CA1). Other variables in the best set of models were: number of water bodies (WB), diversity of cover classes (SHDI), forest patches (NP2), proximity of forest patches (ENN2) and distance to rural establishments (DISTRE).

Physalaemus spp. showed a similar response pattern than *Dendropsophus ssp* although it was limited to the 250 m scale. Landscape variables associated positively with this species were: number and proximity of water bodies (WB and DISTWB), total length of stream sections (STREAM), forest area (CA2), number and cohesion of forest patches (NP2 and COHES2) and diversity of cover classes (SHDI).

Finally, *P. falcipes* was associated positively with total number of water bodies (WB), forest cover (CA2) and patch cohesion (COHES2). Other relevant variables were: cover of row crops (CA1), number (RE) and proximity (DISTRE) of rural establishments. This species showed a clear association to the 500 m spatial scale (Fig. 6, Supplementary material Appendix 3).

Discussion

In west-central Entre Rios, landscape composition and configuration influenced the frequency of occurrence, and relative abundance of some anuran species, which influenced landscape-scale species richness patterns between two landscapes along the agricultural expansion and intensification gradient. The landscape with greater agricultural expansion and intensification had lower stream and forested habitats within 250 and 500 m of sampling points. While some species seems to be unaffected or adapting well to the new conditions, there is a subset of sensitive species that responded negatively to these reduced landscape features at different scales. Thus, changing anuran diversity patterns in east-central Argentina appear to be driven by the reduction in several key species, and at the sampling point scale, there is large diversity variation and potential for local extinctions that may result in more simplified anuran communities.

Fig. 5 Canonical correspondence analysis plots showing association of species presence data and landscape variables at two scales: 250 m (**a**) and 500 m (**b**)
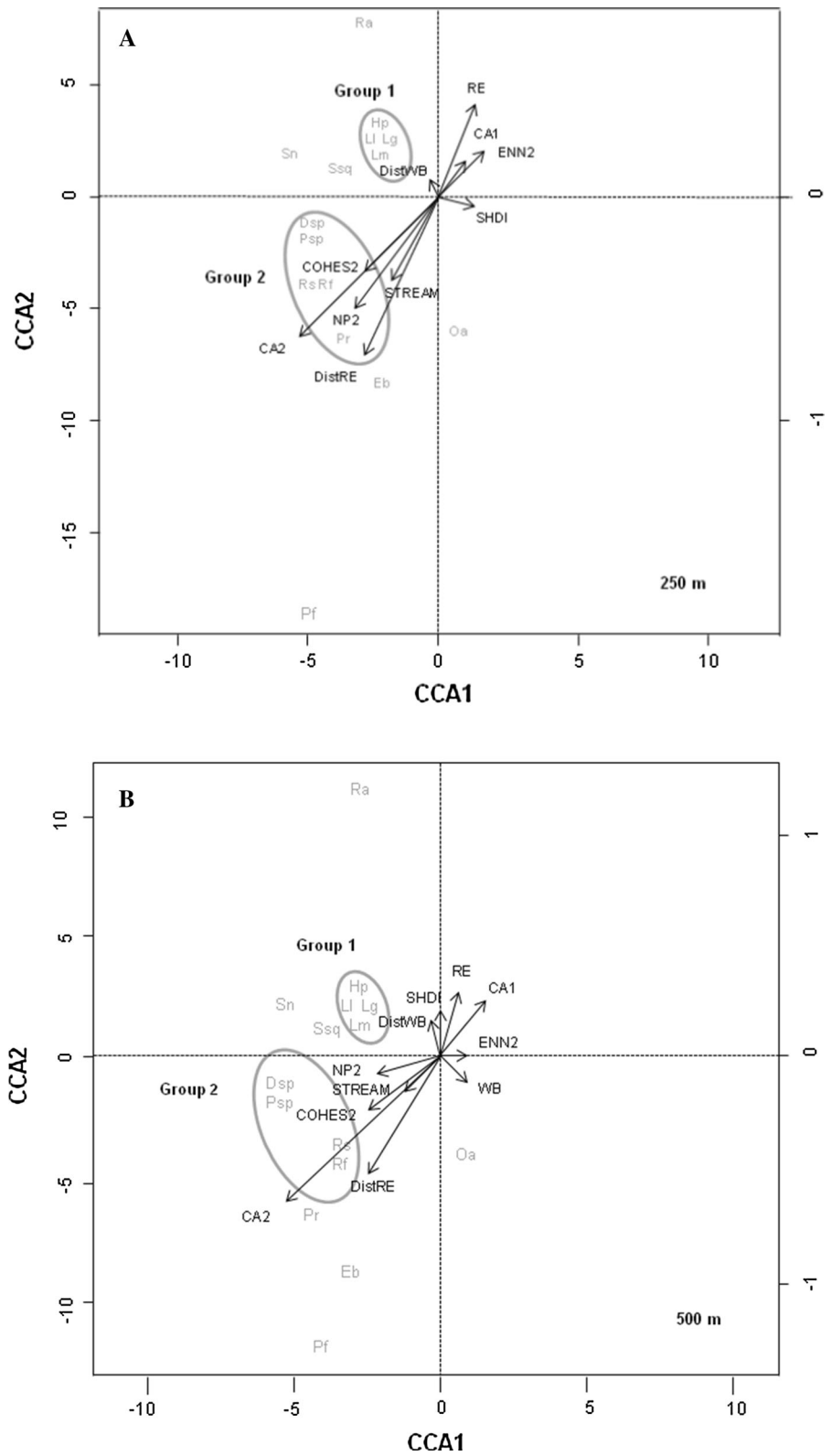
Fig. 6 Relationship between landscape variables and anuran species presence at two spatial scales (250 and 500 m). Averaged coefficients of more relevant variables that were included in the best set of models are shown per species (**a**) together with the proportion of models in the best set where those landscape variables were present (**b**). Position of averaged coefficients above or below zero indicates effect direction as positive or negative respectively
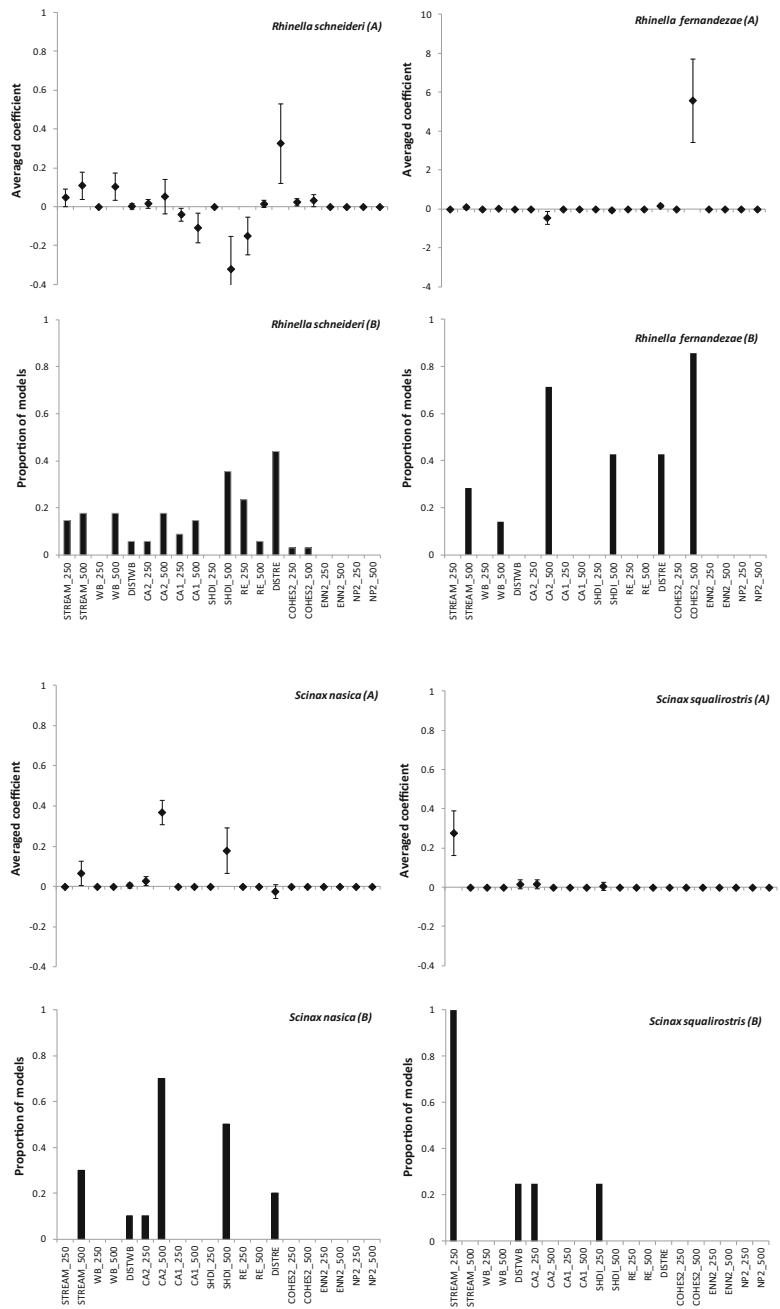
Anuran life history traits and landscape structure relationships

We identified four anuran species that tolerate high levels of agricultural expansion and intensification (*L. latinasus*, *L. mystacinus*, *L. gracilis* and *H. pulchellus*), seven 'sensitive' species (*R. shneideri*, *R. fernandezae*, *S. nasicus*, *S. squalirostris*, *Dendropsophus* spp., *Physalaemus* spp. and *Pseudopaludicola falcipes*) that respond negatively to high levels of agriculturalization, and four species that were 'rare' in both landscapes (i.e. *R. arenarum*, *O. americanus*, *E. bicolor* and *P. riograndensis*). In general, we observed that species within each group share common life history traits that may determine anurans response to landscape changes.
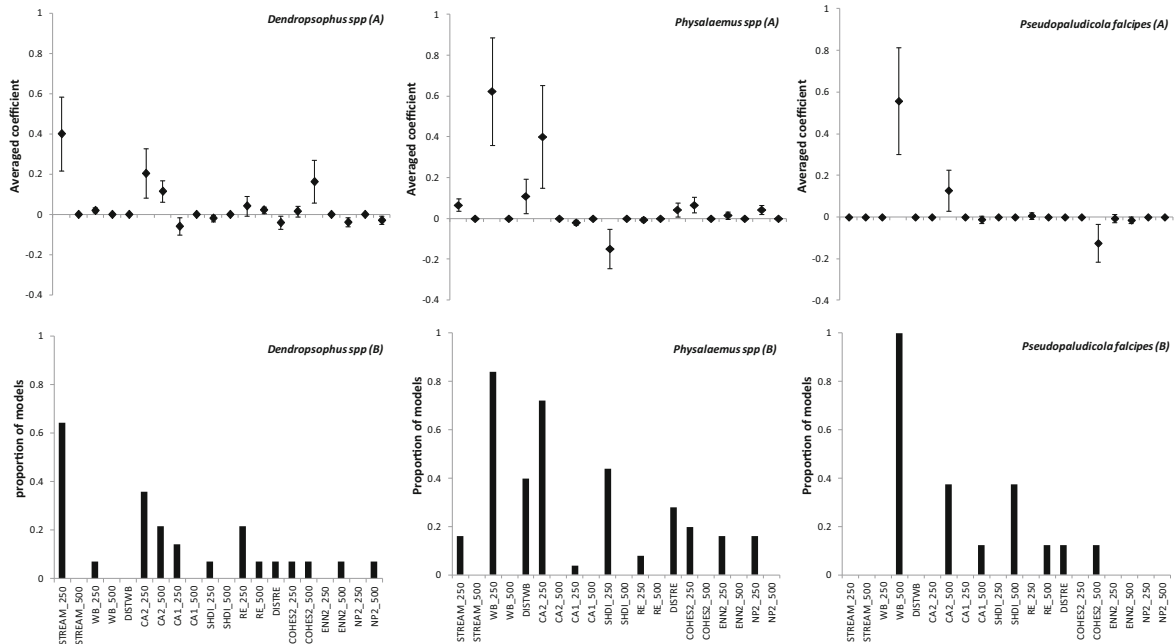
Fig. 6 continued

'Tolerant' species have life-history traits that might allow them to survive in intensified agricultural areas. Most are terrestrial-aquatic frogs (*L. latinasus*, *L. mystacinus* and *L. gracilis*), breeding in open land temporary ponds (Cei 1980; Basso 1990) or laying eggs in foam nests inside caves that develop rapidly after heavy rains (Gallardo 1972, 1974; Achaval and Olmos 2003). *H. pulchellus* is a treefrog with longer larval stages but is a continuous breeder that uses a variety of water bodies (Peltzer and Lajmanovich 2007). These 'tolerant' species are also generalist predators, medium-to-large in size, and potentially good dispersers (Gallardo 1987; Basso 1990). Thus, they might detect optimal habitat from a great distance and persist despite habitat transformation (Zollner 2000; Mech and Zollner 2002). The activity patterns of 'tolerant' species showed interesting differences between studied landscapes. For example, *L. mystacinus* was more active in highly modified agricultural areas, which might indicate that certain levels of agriculture could represent more resources for this species as observed for *H. pulchellus* and *L. gracilis*. On the contrary, *L. latinasus* was less active suggesting it may be less adapted to such landscapes (Suárez and Zaccagnini 2004).

'Rare' species included two terrestrial-aquatic anurans with explosive breeding events of short duration or with breeding periods taken place every 2 or more years. For example, *P. riograndensis* shows 1 or 2 days of high breeding activity only after very heavy rains events and *O. americanus* also shows this breeding activity pattern but also it occurs every two years because tadpoles overwinter and metamorphose the following season (Isacch and Barg 2002; Martori et al. 2005). This feature confers very low detectability to these species and may explain their very low frequency of occurrence and activity level in both landscapes. *R. arenarum* and *E. bicolor* are more terrestrial and their rarity in this study was difficult to explain. The biology of *E. bicolor* is not well known (Martori et al. 2005) and *R. arenarum* shows a more regular pattern of breeding activity (Isacch and Barg 2002) and resembles the other two toad species considered as sensitive.

Among 'sensitive' species we found terrestrial-aquatic frogs (*Physalaemus* spp., *P. falcipes*), toads (*R. schneideri* and *R. fernandezae*) and arboreal-aquatic species (*S. nasicus*, *S. squalirostris*, *Dendropsophus* spp.) (Lajmanovich and Peltzer 2004; Dodd 2010). Their diet specificity and longer development stages may explain their lower frequency of occurrence in

agricultural intensified landscapes as breeding habitat is lower and diversity of prey decreases (Lehtinen and Ramanamanjato 2006). Four 'sensitive' species (*R. schneideri*, *Physalaemus* spp., *P. falcipes* and *Dendropsophus* spp.) may require stream habitats surrounded by forest habitat to fulfill their life history needs. This may be an evidence of 'landscape complementation effect', in that the persistence of anurans in highly fragmented landscapes may be constrained by the need for connectivity between aquatic breeding sites (i.e. streams) and suitable terrestrial habitat (i.e. forests) (Dunning et al. 1992; Rothermel 2004). Landscapes extremely modified by agriculture have less landscape complementation of required habitat types and these anurans might be unable to fulfill their life requirements. Rural housing density and proximity might negatively affect *R. schneideri*, *Physalaemus* spp. and *Dendropsophus ssp* because they may depend on breeding habitat that is rare in residential areas and undergo domestic animals predation, road mortality or even stream pollution by waste disposal (Carr and Fahrig 2001; Suárez, pers.obs).

Landscapes including longer sections of streams, especially headwaters and low order streams may favor six out of seven sensitive species (*R. schneideri*, *S. nasica*, *S. squalirostris*, *Physalaemus* spp., *Dendrosophus* spp. and *P. falcipes*). Although these species are considered pond-breeding anurans, most have a long larval development, higher risk of desiccation and prolonged exposure to agrochemicals (particularly around Crespo town). Few natural ponds, most with altered physical and chemical conditions, are present in this area (Suarez R.P. pers. obs.). Streams surrounded by forests might substitute ponds as good quality aquatic habitat in these highly modified landscapes (Suarez pers. obs; Forman 1995; Naiman et al. 2005; Williams 2008). Forest connectivity along and between streams might favor toad species such as *R. fernandezae* and *R. schneideri* by providing favorable conditions to move between breeding sites (Sinsch 1990; Rothermel 2004; Cushman et al. 2009). Toads have longer migration distances than other anurans (Semlitsch and Bodie 2003) ranging from 250 to 1000 m (Forester et al. 2006) and avoid open habitats probably due to higher predation risks (Rothermel and Semlitsch 2002).

Landscape structure influenced anuran species at two spatial scales. Main effects were similar at 250 and 500 m scales. However, species showed specific associations to spatial scale (Johnson et al. 2002; Price et al. 2004). This specificity might have some relation to body size. Three of the largest sensitive species (*R. schneideri*, *R. fernandezae* and *S. nasicus*) showed stronger association to landscape variables at 500 m while two of the smallest species (*S. squalirostris* and *Physalaemus spp.*) did it at 250 m. Larger anurans tend to travel farther (Semlitsch and Bodie 2003; Forester et al. 2006; Daversa et al. 2012) and are able to detect preferred habitats at greater distances (Zollner 2000).

Landscape structure and anuran assemblages

The response of amphibian richness to landscape structure changes produced by the expansion of agriculture was determined by the observed individual relationships. In general terms, anuran richness would be reduced by the loss of forests and streams mainly at the 250 m scale as shown in other studies regarding forests cover (Kolozsvary and Swihart 1999; Houlahan et al. 2000; Trenham and Shaffer 2005). The moderate-low variation of richness explained in our models might be explained by the number of species that were not related to landscape pattern.

We suggest that if our observed patterns between landscape and anuran diversity are maintained through time and landscape changes such as lower forest cover continues, the anuran community may become less diverse. Several species, i.e. *Rhinella shneideri*, *R. fernandezae*, *Scinax nasicus*, *S. squalirostris*, *Dendropsophus* spp., *Physalaemus* spp. and *Pseudopaludicola falcipes,* would be further affected and could experience local extinctions in highly modified agricultural landscapes in east-central Argentina. For example, the presence of *S. acuminatus, P. limellum, L. elenae* and *T. typhonius* was recorded in Enrique Berduc Rural Educational Park, one of the last remnants of the historic landscape without agricultural use between Crespo and Cerrito areas. These anurans should be found across the study area based on historical ranges (IUCN 2015), but our inability to detect after multiple visits may indicate some of these species have already undergone local extinctions.

Conservation and management implications

Our results present baseline patterns that can be used to help mitigate landscape changes in a substantial area of Entre Rios and the Espinal eco-region under

heavy threat of rapid agricultural expansion and intensification, The future agricultural expansion in Entre Ríos will likely continue to exert negative impacts on anurans and the ecosystem services they provide (e.g. biological pest control, Attademo et al. 2005; Hocking and Babbitt 2014).

Based on our findings, landscapes that could provide more forest habitat within 500 m of streams would help mitigate local loss of species as this measure would assist the most sensitive species (*R. schneideri, R.fernandezae, Physalaemus* spp., *Dendropsophus* spp.). None of these species are categorized as vulnerable or threatened (Vaira et al. 2012; IUCN 2015). Thus, these species could be used as focus species in future monitoring studies to determine landscape change effects to provide valuable information for an accurate categorization.

Finally, recent development of the National Law 26331 on Minimum Standards for environment protection of native forests (Presupuestos Mínimos de Protección Ambiental de Bosques Nativos) provides a good opportunity to preserve and manage habitat for anuran conservation. Managers involved in land-use planning could include the relationships found in this study into landscape management recommendations to preserve the biodiversity of one of the most globally endangered biological groups.

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