

Our time will come: Is anuran community structure related to crop age?

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Abstract An ongoing controversy involves the debate about the effects of man-made land transformation on freshwater biodiversity. It has been suggested that agricultural areas provide habitats for many species of amphibians, but crop age may affect richness and community structure. In such modified landscapes, a nested structure has been commonly detected, although community structure may be season specific and guild specific. Here, we determined detectability associated with site-specific and survey-specific variables and examined nestedness patterns in anuran communities in natural areas and rice fields with different crop ages (10 and 20 years) in southern Brazil. We studied whether nestedness was associated with time since cultivation and whether these patterns were similar across guilds in these areas. Anuran detectability was related only with time after sunset. Community composition varied between crop ages. Aquatic and arboreal species were associated with native areas and showed a nested pattern. Fossorial species did not show significant nestedness. Our results showed that factors associated with crop age may affect guilds in different ways. These effects seem to be related to individual traits of species (habitat preferences, reproductive modes, plasticity). Incorporating species traits may enhance conservation strategies in agroecosystems.

Key words: anuran guild, detectability, nestedness, rice field, southern Brazil.

INTRODUCTION

Conversion of natural areas into agricultural areas or permanent pastures has considerably reduced the extent of natural environments in all Brazilian biomes (Ferreira *et al.* 2012). Many agricultural impacts are related to effects on matrix quality (Donald & Evans 2006), which could affect migration and dispersal processes (Knutson *et al.* 2004; Donald & Evans 2006; Ewers & Didham 2006). However, agricultural landscapes are characterized by marked changes in the matrix at different temporal scales, such as change in hydrological phases or crop rotation. Thus, some agricultural areas are better described as diversified instead of fragmented because the matrix is not necessarily hostile to all species (Ficetola & De Bernardi 2004; Lunt & Spooner 2005; Dixo & Metzger 2010).

Species distribution in agricultural areas is influenced by both current and historical characteristics of an area (Lunt & Spooner 2005; Piha *et al.* 2007). In this sense, areas with a long agricultural history are arguably habitats of lower quality than those with a shorter history of agricultural practices. This quality reduction is mainly related to structural alterations of

the soil and vegetation (Dupouey *et al.* 2002) and the accumulation of agrochemicals that could alter growth rates and parasite infections in resident species (Gray & Smith 2005; Peltzer *et al.* 2008). In such modified landscapes, local extinction is a common process and immigration is of major importance (Tscharntke *et al.* 2005). Both processes are recognized as possible causes of nestedness (Ulrich *et al.* 2009). Nestedness occurs in a community if species at low diversity localities are subsets of those at high diversity localities. These nestedness patterns may be generated by differential dispersal (McAbendroth *et al.* 2005), passive sampling (Higgins *et al.* 2006), habitat nesting (Whetered & Lawes 2005) or differential habitat quality (Hylander *et al.* 2005). In addition, several studies have showed that anthropogenic disturbances can also promote nestedness (Picazo *et al.* 2012; Gutiérrez-Cánovas *et al.* 2013; Zapponi *et al.* 2014). Human-induced gradients appeared to exclude specialist species while generalist species were present along the entire gradient. However the tolerance of species to disturbance may depend on certain biological traits (Martínez-Morales 2005; Cisneros *et al.* 2015), and the quantification of nestedness can be related to features of species or habitats, allowing tests for hypotheses about the extinction and colonization process (Ficetola & De Bernardi 2004; Tockner *et al.*

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2006; Simaiakis & Martínez-Morales 2010). Such information has important conservation implications, because nestedness can potentially identify risk prone species or groups of species.

Rice fields are considered important substitutes for natural wetlands in many regions of the world and certain fauna use these agricultural areas to forage and breed (Wilson *et al.* 2007; Duré *et al.* 2008; Machado & Maltchik 2010; Piatti *et al.* 2010). This importance is due to variation between aquatic and terrestrial phases of the crop cycle. However, our understanding of how these altered landscapes function as habitat for amphibians is limited, and the way in which crop age influences anuran community structure has received little attention. Rice fields differ from natural wetlands in the habitat heterogeneity and hydrological cycles. Hydroperiod is a major factor for amphibian communities (Both *et al.* 2009; Prado & Rossa-Feres 2014), and a pond must ideally hold water for enough time to allow species to reach metamorphosis. Human-induced changes in the hydroperiod could lead to successive reproductive failures and enhance the need for recolonization or rescue effects.

Various studies in modified landscapes have shown that the ability of amphibian populations to persist is related to individual species characteristics (dispersal ability, reproductive modes and habitat preference) (Ficetola & De Bernardi 2004; Cushman 2006; Dixo & Metzger 2010). Indeed, amphibians are a group with remarkable differences in life-history strategies. Arboreal species with aquatic larvae seem to be less tolerant of habitat alteration than species with terrestrial development (Becker *et al.* 2007). Thus, amphibian assemblages that use disparate resources may be affected differently by historic land use. Unfortunately, an imperfect detection of species is a pervasive issue in many studies addressing habitat use, relative abundance and colonization rates (MacKenzie *et al.* 2006; Durso *et al.* 2011). Although factors which influence anuran detectability depend on a myriad of conditions that vary through time or geographically (e.g. temperature, rainfall, vegetation cover) (Weir *et al.* 2005; Roloff *et al.* 2011), understanding the detection bias on the species occupancy is critical when habitat use is a concern.

In this study, we examined patterns of nestedness in anuran communities in natural areas and rice fields with different cultivation ages. First, we determined detectability associated with site-specific and survey-specific variables. Then, we verified differences in the composition and nestedness patterns between rice fields and natural ponds. Based on an increased gradient of disturbance (natural ponds → 10 years crops → 20 years crops), we predicted that areas with older crop ages have a different anuran composition and are depauperate in arboreal and semi-aquatic species. Fossorial species that are not directly associ-

ated with standing water availability and vegetative cover may be able to occupy rice fields.

METHODS

The state of Rio Grande do Sul produces more than 64% of the rice produced in Brazil, and the coastal plain region is an important area for irrigated rice production in South America (Azambuja *et al.* 2004). The study took place from August 2011 to August 2012 in an agricultural area (30.705° to 30.755°S, 51.630° to 51.700°W) dominated by rice production, in the central-west portion of the coastal plain. The climate is mildly humid subtropical and the average temperature is 18.5°C, with an average of 11°C in winter and 26°C in summer. Annual rainfall ranges from 1500 to 1700 mm year⁻¹.

Rice plantations at the study site are divided into multiple 1 ha plots that are interconnected by secondary roads and drainage canals. These drainage canals (2–5 m wide and 0.5–1.5 m deep) are filled with water from nearby streams. Water level in the canals is controlled by weirs, which supply the rice plots (about 10 cm water for 130 days) during the cultivation cycle. Sowing is manual or with the aid of machinery. Application of inorganic fertilizers, organophosphorus and carbamate insecticides, and glyphosate-based herbicides is concentrated in the initial growth stage (25–30 days after sowing). For the study, the rice fields were divided into two types according crop ages: areas cultivated for at least 20 years and areas cultivated for up to 10 years.

Three study plots (1 ha) in each of the two cultivation ages were sampled within a 10 km radius (Fig. 1). Plots next to other types of vegetation were avoided because we were interested in species associated with rice fields. We sampled three ponds to compare the composition between natural and modified areas. Study sites were at least 600 m from one another to minimize spatial autocorrelation. The spatial independence of the nine sampling areas was tested using principal coordinates of neighbour matrices (PCNM) analysis (Borcard & Legendre 2002). Latitude and longitude were converted into Cartesian coordinates. Prior to the PCNM analysis, species data were detrended by regressing all variables on the coordinates and retaining the residuals. We generated a set of four spatial variables from these coordinates with the 'pcnm' function of the vegan package (Oksanen *et al.* 2013). Two eigenvectors modelling positive spatial autocorrelation were identified by Moran's *I* statistic for the threshold distance (0–2.5 km). As the PCNM had not detected significant spatial structure ($F_{2,6} = 0.468$, $P = 0.98$), it was not included in the statistical analysis.

We sampled five times during the rice cultivation cycle: two samples in the off season (August 2011 and August 2012), one sample during the early growing period (January 2012), one sample during the late growing period (March 2012) and one sample during the post-harvest period (10 days after harvest) (June 2012). The off-season phase represents the period when the land is fallow, and the fields retain water only in the irrigation canals and scattered ephemeral pools. The early growing period is characterized by rice emergence (seedlings < 10 cm tall) and shallow water level, while in the late growing phase, rice can reach > 100 cm tall and water depth is increased to protect plants. Fields are dried

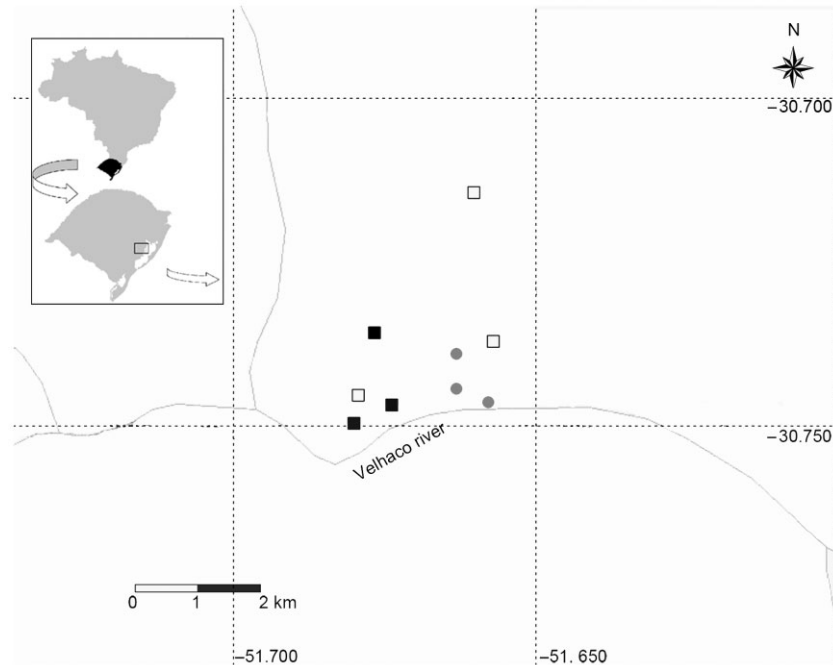


Fig. 1. Map of study area in the coastal plain of Rio Grande do Sul, Brazil. Clear squares: natural ponds, dark squares: 10 years rice, circles: 20 years rice.

completely before harvest (about 15 days) and post-harvest stubble is usually plowed. Harvesting of the rice results in a disturbance to potential anuran communities, where many of them either perish or escape into surrounding terrestrial areas.

Anuran richness and abundance were measured using visual and acoustic searches (Crump & Scott 1994). The sampling occurred between 19:00 h and 24:00 h, and the areas were sampled in a random order. In each sample, we followed a 100 m transect perpendicular to the edge of a field or pond. Each transect was sampled for 20 min. All of the individuals located visually or acoustically were recorded. The species were separated in guilds according to habit (Vallan 2000; Peltzer *et al.* 2006): (arboreal) species generally found in herbaceous, shrubby or low trees; (fossorial) species that excavate underground chambers for refuge or egg laying; and (semi-aquatic) species generally found in aquatic environment or in the interface between water and land.

Data in survey-specific factors thought to influence detection probability were collected (Weir *et al.* 2005; Kroll *et al.* 2008). These included information on time after sunset and Julian date. Time after sunset was registered in minutes from 18:00 h to the finish of each survey. We also considered habitat (pond or rice field) influence in site occupancy by amphibian species. For our analysis of occupancy estimates, we used a single season occupancy model (MacKenzie *et al.* 2006). A detection history was constructed for each species, assigning '1' to those sampling plots in which the species was detected and a '0' otherwise. We incorporated into the models the survey-specific and habitat type on occupancy (ψ) and detection probability (p), through a logit link function. We used 100 bootstrap iterations to compute standard errors of derived parameter estimates as recommended

by MacKenzie *et al.* (2006). For time after sunset and Julian date, both linear and quadratic effects were considered, allowing for the possibility of optimal calling conditions and hence optimal detection.

We followed a two-step process for building occupancy models (Kroll *et al.* 2008; Roloff *et al.* 2011). First, we defined a small set of five candidate models for detection probabilities (Appendix S1), in which ψ was held constant. Second, we examined occupancy models where ψ was allowed to vary with habitat type using the best model for detection probability. We used Akaike's information criteria (AIC; Burnham & Anderson 2002) to rank the candidate models for each species. We also calculated factors weights to gauge the overall importance of each covariate for each species. Analyses were carried out in statistical computing environment, R (R Development Core Team 2013), and its extension package unmarked (Fiske & Chandler 2011).

We used a permutational variance analysis (PERMANOVA) to assess differences in the anuran composition across natural ponds and rice fields, based on the Bray–Curtis dissimilarity. A non-metric multidimensional scaling (NMDS) plot was used to assist with interpretation. We used the 'ordihull' function to represent the projected two-dimensional ordination space occupied by each treatment (10 and 20 years rice, ponds). The analyses were conducted on the vegan package 2.0.3 for R (Oksanen *et al.* 2013). For nestedness analyses, we built presence and absence matrices where columns and rows were species and areas, respectively. Because the species groups could be subjected to different environmental pressures, we analysed nestedness in two ways: considering all species as equivalent and separating species into guilds. We quantified the nestedness based on overlap and decreasing fill (NODF)

(Almeida-Neto *et al.* 2008) as was recommended by Ulrich *et al.* (2009). NODF is a consistent metric that allows access to nestedness among locations only or among species only. NODF can range from 0 to 100, and higher values indicate more nested communities. Nestedness analyses require that the incidence matrix be ordered according to pre-defined criteria. Thus, we set the incidence matrix according to a gradient of disturbance (natural ponds→10 years crops→20 years crops). To evaluate the significance of nestedness, we used a null model that maintains observed row totals but allows column totals to vary randomly and 5000 simulations to validate the model significance. This algorithm preserves species occurrence frequencies (row totals), but allows species richness per site (column totals) to vary equiprobably. All of the analyses were carried out on vegan package 2.0.3 for R (Oksanen *et al.* 2013).

RESULTS

We recorded a total of 16 species of anurans that were distributed among four families (Table 1). Of the species found, five were classified as fossorial and five were classified as semi-aquatic. All six of seven species in the family Hylidae, with the exception of *Pseudis minuta*, were categorized as arboreal. *Pseudis minuta* was classified as semi-aquatic. For occupancy models, we focus on the species with a detection probability of ≥ 0.15 : *Dendropsophus sanborni*, *Hypsiboas pulchellus*, *Leptodactylus latrans*, *Pseudis minuta*, *Pseudopaludicola falcipes* and *Scinax squalirostris* (Table 1). Species with

detection < 0.15 were deemed unsuitable for occupancy modelling (O'Connell *et al.* 2006).

The full set of ranked candidate models is presented in Appendix S1. Overall, the best models for detection probability did not include survey-specific factors. Time after sunset was positively associated with *D. sanborni* and negatively with *P. falcipes* detection probabilities (Table 2). For three species, habitat type was included in the best model as a determinant of occupancy. Positive associations with natural ponds were found for *L. latrans*, *P. minuta* and *S. squalirostris*. The best model for *S. squalirostris* had 9.0 times more support than the second best model. However for *L. latrans* and *P. minuta*, the evidence ratio was lower (Table 2).

In the NMDS ordination (Fig. 2), rice fields and natural areas formed well-defined groups. Arboreal and semi-aquatic species were abundant in natural ponds. Small-sized arboreal species (snout-vent length < 20 mm) and fossorial species were associated with rice fields cultivated for 10 years. Small semi-aquatic species (snout-vent length < 25 mm) and fossorial species were more common in rice fields cultivated for 20 years. The PERMANOVA showed significant differences among amphibian communities of 20 years crops, 10 years crops and ponds ($F = 3.159$, $df = 2$, $P = 0.026$). When we separately assessed the composition differences by guild, only arboreal and semi-aquatic species showed significant differences (arboreal: $F = 2.636$, $df = 2$, $P = 0.002$; semi-aquatic: $F = 2.327$, $df = 2$, $P = 0.05$).

Table 1. Anuran species recorded in a rice cultivation area with different crop ages, Rio Grande do Sul, Brazil, and corresponding detection probabilities for constant occupancy, from August 2011 to August 2012

Species	Guild	$p(\cdot)$ [SE]	20 years crops			10 years crops			Natural ponds		
			1	2	3	1	2	3	1	2	3
Bufonidae											
<i>Rhinella dorbignyi</i>	F	0.11 [0.06]	x	x	x		x		x		
Hylidae											
<i>Dendropsophus minutus</i>	A	0.07 [0.04]							x	x	x
<i>Dendropsophus sanborni</i>	A	0.44 [0.11]		x	x	x	x	x	x	x	x
<i>Hypsiboas pulchellus</i>	A	0.39 [0.09]		x	x	x		x	x	x	x
<i>Pseudis minuta</i>	SA	0.41 [0.11]			x	x			x	x	x
<i>Scinax berthae</i>	A	0.04 [0.03]			x					x	
<i>Scinax granulatus</i>	A	0.07 [0.06]						x	x	x	
<i>Scinax squalirostris</i>	A	0.36 [0.12]				x			x	x	x
Leptodactylidae											
<i>Leptodactylus gracilis</i>	F	0.11 [0.05]		x		x	x	x		x	
<i>Leptodactylus latinasus</i>	F	0.17 [0.10]	x	x		x	x	x			
<i>Leptodactylus latrans</i>	SA	0.40 [0.10]		x	x	x		x	x	x	x
<i>Physalaemus biligonigerus</i>	F	0.09 [0.04]	x	x	x	x					
<i>Physalaemus cuvieri</i>	SA	0.02 [0.02]		x							
<i>Physalaemus henselii</i>	SA	0.02 [0.02]							x		
<i>Pseudopaludicola falcipes</i>	SA	0.38 [0.09]	x	x	x	x	x	x	x	x	x
Microhylidae											
<i>Elachistocleis bicolor</i>	F	0.13 [0.05]	x	x	x			x		x	x

A, arboreal; F, fossorial; SA, semi-aquatic.

Table 2. Parameter estimates contained in the best occupancy model adjusted by detection probability for six anuran species in a rice cultivation area in southern Brazil

Species × model	w_i	Evidence		Factor weight
		ratio	Estimates	
<i>Dendropsophus sanborni</i>				
Ψ (.), p(time)	0.82	4.82		
Time			0.02	0.99
<i>Hypsiboas pulchellus</i>				
Ψ (.), p(.)	0.43	1.34		
<i>Leptodactylus latinasus</i>				
Ψ (.), p(.)	0.51	1.50		
<i>Leptodactylus latrans</i>				
Ψ (habitat), p(.)	0.43	1.40		
Natural pond			8.60	0.43
<i>Pseudis minuta</i>				
Ψ (habitat), p(.)	0.58	3.20		
Natural pond			9.12	
<i>Pseudopaludicola falcipes</i>				
Ψ (.), p(time)	0.40	1.21		
Time			-0.01	0.55
<i>Scinax squalirostris</i>				
Ψ (habitat), p(.)	0.72	9.00		
Natural pond			11.5	0.72

w_i : model Akaike weight. Evidence ratio: ratio of Akaike weights between the two best ranked models. Factor weight: sum of Akaike weights over all models that include the explanatory variable. (.) The parameter was constant.

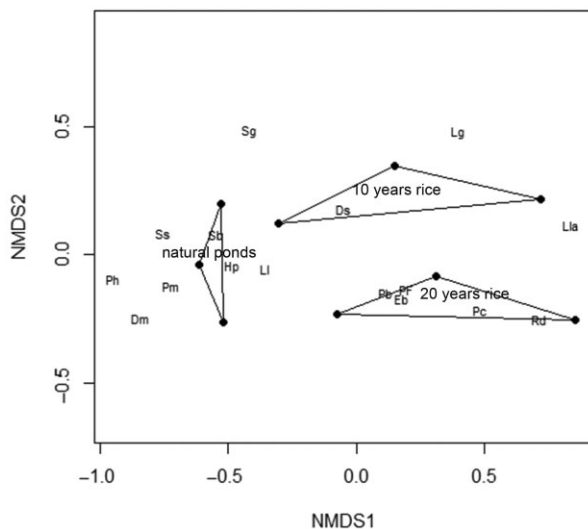


Fig. 2. Multidimensional scaling ordination for anuran assemblages in a rice paddy area with different crop ages (stress = 0.054), Rio Grande do Sul, Brazil, from August 2011 to August 2012. Black circles are sampling sites, and convex hulls are sites belonging to same treatment. Rd, *Rhinella dorbignyi*; Dm, *Dendropsophus minutus*; Ds, *D. sanborni*; Hp, *Hypsiboas pulchellus*; Pm, *Pseudis minuta*; Sb, *Scinax berthae*; Sg, *S. granulosus*; Ss, *S. squalirostris*; Pb, *Physalaemus biligonigerus*; Pc, *P. cuvieri*; Ph, *P. henselii*; Pf, *Pseudopaludicola falcipes*; Lg, *Leptodactylus gracilis*; Ll, *L. latrans*; Lla, *L. latinasus*; Eb, *Elachistocleis bicolor*.

The entire community of amphibians showed a significantly nested pattern (NODF = 59.22, $P < 0.001$) (Table 3). The degree of nestedness in species occupancy (N_{row}) was higher than the degree of nestedness among sampling sites (N_{col}). Arboreal and semi-aquatic species were nested according to NODF (Table 3). Arboreal species showed slightly higher degree of nestedness than semi-aquatic species. Fossorial species did not show significant nestedness.

DISCUSSION

Anuran species composition varied considerably between natural ponds and rice fields, and cultivated fields of different ages showed distinct patterns of community structure in an agricultural region in southern Brazil. Fossorial species seems to be the most resilient and arboreal/semi-aquatic species the most sensitive to disturbance associated with crop age. Anuran occupancy was correlated with natural ponds for some species (*L. latrans*, *P. minuta*, *S. squalirostris*), and detectability was related only to time after sunset. After conversion to rice fields, vegetation homogenization and alterations in the hydrological regimes were the immediate impacts on the anuran communities. Moreover, input of agrochemicals and periodic land preparation (i.e. ploughing the fields) may have a cumulative negative effect on species, as time since conversion increases. Cultivation age may explain differences in the anuran species composition through the effects on (1) habitat heterogeneity, (2) spawning site selection, and (3) population isolation.

Although there were low detection probabilities (0.02–0.44) of species in the study area, our results agree with other estimates for amphibians and other cryptic species of herpetofauna (Durso *et al.* 2011; Roloff *et al.* 2011). It is nevertheless interesting to note that our results of the detection probabilities were more associated with phenology of species than habitat characteristics. Many species with detection probability < 0.15 have also explosive breeding (Wells 1977) (*Rhinella dorbignyi*, *Scinax berthae*, *Physalaemus biligonigerus*, *Elachistocleis bicolor*). They are normally difficult to find during most of the year and are usually recorded after heavy rainfall events ($> 50 \text{ mm day}^{-1}$). Our results for time effects on *P. falcipes* and *D. sanborni* detectability are in agreement with species-specific traits. The former calls during daytime and decreases activity after nightfall, whereas in the latter, vocalization period is mainly crepuscular until 00:00 h (Maneyro & Carreira 2012).

Most of the differences in species composition detected between natural ponds and rice fields were a reflection of the greater abundance of arboreal and semi-aquatic species that called from floating vegetation (e.g. *P. minuta*, *L. latrans*) or herbaceous

Table 3. Measure of nestedness for anuran communities in a rice paddy area with different crop ages at southern Brazil

Matrix	N _{row}	N _{col}	NODF	NODF(q)	P(q)	S
Whole community	36.70	65.97	59.22	27.91	<0.001	16
Arboreal	58.33	81.11	65.03	42.84	<0.001	06
Semi-aquatic	46.30	80.00	53.62	30.07	<0.001	05
Fossorial	5.56	45.50	14.24	26.53	0.917	05

N_{row}, nestedness among all rows (study plots); N_{col}, nestedness among all columns (species); NODF, nestedness across all sites; NODF(q), nestedness of null model where presences are randomly assigned, but both row and column frequencies are maintained; P(q), significance of NODF based on this null model; S, species richness.

vegetation and shrubs (e.g. *H. pulchellus*, *S. squalirostris*). Habitat heterogeneity is an important parameter associated with species richness and occupancy, both in natural and agricultural areas (Both *et al.* 2009; Moreira *et al.* 2010; Prado & Rossa-Feres 2014). Although rice fields may create a mosaic of microhabitats suitable for the maintenance of anuran diversity, the number of vegetation types affects individual species occupancies, mainly anurans that vocalize perched on vegetation (Prado & Rossa-Feres 2014). As the cultivation age increases, we can expect a higher susceptibility to disturbances in the crop field and its boundary vegetation. These disturbances may be caused by close ploughing, misplacement of fertilizer or drift of herbicides, from the adjoining field, that affect richness and composition of the field vegetation boundary (Kleijn & Verbeek 2000). Thus, the lack of heterogeneous vegetation cover could explain the congruencies, regarding significant nestedness, between the whole community and two guilds (arboreal and semi-aquatic). Similar patterns have been seen in agroecosystems in central Brazil, where low anuran richness was considered to result from habitat simplification (Piatti *et al.* 2010; Souza *et al.* 2014).

There is a well-known trade-off between pond hydroperiod and predation by fish. In short-hydroperiod wetlands, amphibian communities are depauperate and low species richness is expected because of exclusion of amphibians with slow rates of development (Babbitt *et al.* 2003; Silva *et al.* 2011). In permanent wetlands, species are generally exposed to a wide variety of potential predators and competitors (Alford 1999; Werner *et al.* 2007). Amphibians species that can breed in fish-inhabited habitats have toxic/unpalatable tadpoles (i.e. bufonids), or tadpoles with anti predatory behaviour (i.e. leptodactylids). Although rice fields have a temporary hydroperiod (~130 days), organisms from permanent wetlands might be carried to cultivated fields by irrigation water. In the study area, the water used for crop irrigation comes from streams, and predatory fish such as wolf fish (*Hoplias malabaricus*) and catfish (*Rhamdia* sp.) are frequently found in the rice plots and irrigation canals. In addition to the predation on tadpoles and adults, the presence of fish influences the selection of breeding

sites by many anurans (Werner *et al.* 2007; Both *et al.* 2009). A plausible hypothesis is that the nestedness patterns observed can be due to the accumulation of species with traits that can achieve positive fitness along the predation pressures.

In agricultural landscapes, local extinctions are common and the biota depends on proximate semi-natural habitats functioning as populations sources (Tscharntke *et al.* 2005). Anurans may benefit from the presence of irrigation canals because these canals not only serve as breeding sites but also ensure moist conditions to facilitate movements of juveniles and adults (Mazerolle 2004; Duré *et al.* 2008). However, the suitability of a canal as habitat varies among species. Studies have indicated that post-metamorphic juvenile dispersal contributes more than adult dispersal to regional persistence (Guerry & Hunter 2002; Semlitsch 2008). Steep-side canals could act as barriers for non-arboreal anuran migration (Kato *et al.* 2010), which might be problematic because the connectivity between terrestrial and aquatic habitats is a key factor for the persistence of anuran populations (Becker *et al.* 2007). Fossorial species can burrow into the ground when the canals dry and persist until the canals refill. This may explain why fossorial species were associated with older rice fields and also did not exhibit patterns of nestedness related to crop age. However, semi-aquatic species would be more vulnerable to desiccation, relying only on soil cracks and crevices when the fields are drained. The association of only semi-aquatic species with small size (*P. falcipes* and *P. cuvieri*) and 20 years rice supports this assumption.

There are other factors related with crop age influencing anuran composition. Exactly what is most important is hard to identify; however of the many components associated with agronomic practices, agricultural chemicals accumulating have a major negative impact to biodiversity (Geiger *et al.* 2010; Jonason *et al.* 2011). There is a growing awareness that pesticide exposure has deleterious effects on amphibians, although we know very little about synergistic effects (Mann *et al.* 2009) or evolved resistance (Cothran *et al.* 2013). Because of the lack of information, it was complicated to estimate community patterns in rela-

tion to pesticide exposure. A cascade of events could affect anuran species through elimination of food resources, competitors or predators.

Differential nestedness within the guilds was consistent with previous studies for a variety of taxa including birds (Martínez-Morales 2005; Zapponi *et al.* 2014), insects (Hill *et al.* 2011) and mammals (Michalski & Peres 2005) within anthroposized landscapes. These studies, however, assume a hierarchical organization of niche relationships of species. On the other hand, phyllostomid bats and two of its constituent ensemble (frugivores and gleaning animalivores) did not have a nested arrangement associated with modified landscapes (Cisneros *et al.* 2015). Bats could obtain many critical resources from human-impacted environments, so a non-hierarchical organization of niche relationships could be a possible reason for the lack of nestedness. The lack of information on many Neotropical amphibian species did not allow consideration of species interactions (and niche relationships) on community dynamics. Although empirical evidence suggests that rice fields can help to conserve anurans (Duré *et al.* 2008; Machado & Maltchik 2010), we cannot be sure that some anuran species or even guilds may benefit from these agroecosystems.

To conclude, crop age was related to species nestedness in anuran communities in agricultural areas, and the patterns of variation between natural ponds and rice fields differed among guilds. It remains unclear which features linked with the dynamic conditions in rice fields were unsuitable to arboreal and semi-aquatic guilds, but the effects of crop age seem to be related to individual traits of species (habitat preferences, reproductive modes, plasticity). Our results provided important and useful information in the ecological and conservation field of herpetology. However, our study was undertaken in a small section of southern Brazil, and there is a need to replicate these studies across a broader range of species and landscapes. Grasslands of southern Brazil have exceptional conditions for rice expansion, but still, there is much work to be done. Understanding the factors regulating anuran abundance and diversity in agricultural areas will help to elucidate possible effects of relocation of the crop producing regions, because of climate change (Lobell *et al.* 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Occupancy and detection probability models for each species.