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# Dependence of anuran diversity on environmental descriptors in farmland ponds

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**Abstract** In the Neotropics, conversion of natural habitats into agricultural areas is occurring at a high rate, with consequent reduction of habitat complexity in anuran breeding ponds. Identifying features of farmland ponds that allow them to support a high diversity of species is fundamental for successful management and conservation policies and is especially important in Neotropical regions that harbor the highest anuran species richness in the world. Here, we aimed to investigate which environmental descriptors correlate the occurrence of anuran species in tropical farmland ponds in southeastern Brazil. We found that environmental descriptors reflecting the complexity of vegetation in farmland ponds primarily predict the diversity of anuran species in these habitats. Species richness was correlated mainly by vegetation height in the margin, with ponds that exhibit greater stratification harboring a larger number of species. Vegetation height in the interior of ponds, diversity of vegetation in the margin, pond area and hydroperiod were also important variables predicting the abundance of six of 10 anuran species analyzed. Our results show that features of farmland ponds representing increased habitat complexity are key factors in maintaining a high diversity of species, providing a greater variety of microhabitats, both in vertical and horizontal strata, and thus meeting diverse speciesspecific requirements.

**Keywords** Amphibian · Generalized linear models · Hierarchical partition · Heterogeneity · Mesophytic semideciduous forest

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## Introduction

Farmland ponds are widely distributed in agricultural landscapes and contribute significantly to regional biodiversity as they support heterogeneous communities of aquatic organisms (Santi et al. 2010). Despite this, their small size has made them highly vulnerable to human activities, and they are threatened in many regions (Snodgrass et al. 2000; Beja and Alcazar 2003). Investigation of relationships between properties of farmland ponds and diversity of amphibians has long attracted the attention of researchers (Beebee 1977, 1985; Diaz-Paniagua 1987), as these ponds provide potential breeding sites for most anuran species. Habitat complexity of breeding sites is important to the structure of anuran assemblages; however these studies have yielded divergent results concerning which environmental descriptors of breeding sites influence a given anuran assemblage (Vasconcelos et al. 2009).

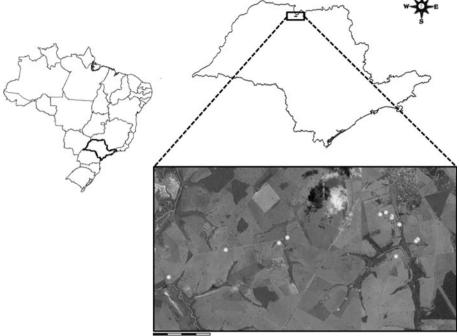
As a result of human land use, amphibians are among the most threatened animal groups (Cushman 2006). Destruction of their habitats is documented as the main threat to amphibians in Brazil (Eterovick et al. 2005; Silvano and Segalla 2005), which contains the greatest diversity of frog and toad species in the world (AmphibiaWeb 2011). Of particular concern is the inland region of southeastern Brazil, where native vegetation has been devastated by agricultural activities (Rodrigues et al. 2008). Recently, because of commercial demands from the ethanol market, an agro-ecological zoning ordinance was established in São Paulo state that prohibits sugarcane farming in some areas of Atlantic forest but allows it in inland areas (Joly et al. 2010). The vast majority of anurans recorded in inland São Paulo state breed in farmland ponds and these were eliminated due to the expansion of sugarcane fields. This is worrisome because of the deficiency of information on the importance of these ponds as breeding sites for anurans. This lack of information constrains efforts to develop effective and cost-efficient strategies to sustain both agricultural production and high species diversity within altered landscapes.

In this study, we evaluated what characteristics correlate the occurrence of anuran species in 12 farmland ponds located in an agricultural area in southeastern Brazil. Specifically, we aimed to answer the following questions: (i) what descriptors of farmland ponds are correlated with high anuran species richness; and (ii) which environmental descriptors of farmland ponds best predict the abundance distribution of anuran species? The understanding of which characteristics of farmland ponds correlate the occurrence of anuran species will allow us to determine which features should be preserved for the maintenance of species richness in agricultural areas.

### Materials and methods

#### Study area

This study was carried out in the municipality of Icém  $(20^{\circ}20'S, 49^{\circ}11'W)$ , in northwestern São Paulo state, Brazil (Fig. 1). This region was originally covered with semi-deciduous forest and patches of cerrado, which was removed for the establishment of agricultural crops that reduced the vegetation to 4% of its original extent (Rodrigues et al. 2008). As a result, this region is the most deforested and fragmented in the state, and has the fewest conservation areas (Rodrigues et al. 2008). At present, the region is characterized by an agricultural landscape dominated by small forest fragments embedded in grassland, sugarcane and rubber plantations (Rodrigues et al. 2008). Grasslands are still prevalent in the



0.5 1 1.5 2 km

Fig. 1 Satellite image of the location and distribution of 12 farmland ponds (*circles*) studied in Icém, northwestern São Paulo state, Brazil. Image from Google Earth

region, but recent sugarcane expansion (Rodrigues et al. 2008; Joly et al. 2010) has eliminated previously constructed ponds.

The climate of this region is characterized by two well-defined seasons during the year: hot and wet (September–March), during which about 85% of the annual rainfall occurs, and a pronounced dry season (April–August), with average precipitation of only 15% of the annual rainfall. Total annual rainfall varies from 1,110 to 1,250 mm ( $\pm$ 225 mm; Barcha and Arid 1971). Thirty-seven anuran species have been recorded in northwestern São Paulo state, corresponding to almost 15% of the anuran species and 5% of Brazil's anuran species richness (Rossa-Feres et al. 2011). Most of the anuran species of this region are considered habitat generalists and are not listed as threatened species. However, considering that four of the 37 species have been recorded only in the last 3 years (Prado et al. 2008; Silva et al. 2009, 2010), species richness is probably higher than previously thought.

# Species richness and abundance

We sampled 12 farmland ponds with different physiognomic characteristics, all located in pasture matrix and at least 1,000 m from sugarcane, orange and rubber plantations (Fig. 1). Field work was carried out every two weeks during the rainy season (September 2004–March 2005) and monthly during the dry season (April–August 2005), totaling 19 samples of each farmland pond.

Assessment of adult anurans was conducted during the period of greatest activity (from 7 pm until about 12 pm by survey at the breeding site (sensu Scott and Woodward 1994). Pond visits was conducted by two trained field personnel and lasted 30 min per survey. Acoustic surveys involved walking the perimeter of each pond and recording the number of individuals of each species that were heard calling at a radius of 5 m of the pond. Tadpoles were sampled with a hand net (between 2 p.m. and 6 p.m.) with a wire mesh of 3 mm<sup>2</sup> and a long cable. The hand net was passed intensively through the whole area of each breeding site, from the margins to the central area of the pond. Tadpoles were anesthetized in a 5% solution of benzocaine and fixed in 10% formalin immediately after collection. We sampled adults and tadpoles in each pond because both survey methods underestimated the number of species when used separately (Silva 2010). However, a close approximation of the actual number of species in each breeding pool is obtained when the methods are combined (Silva 2010). Therefore, data from tadpole surveys were used only for qualitative analyses of species richness, while data from acoustic surveys were used in both qualitative and quantitative analyses. Collected individuals were deposited in the DZSJRP—Amphibia adults and DZSJRP—Amphibia tadpoles collections of the Departamento de Zoologia e Botânica, UNESP, Campus São José do Rio Preto, Brazil.

#### Environmental descriptors

Several studies have demonstrated that combinations of environmental variables measured at local and regional scales are important drivers of the structure of frog and toad communities (Werner et al. 2009; Shulse et al. 2010; Hammer and Parris 2011; Silva and Rossa-Feres 2011; Silva et al. 2011, 2012). Considering the characteristics of the studied system: (i) anuran species with wide distribution and habitat generalists, (ii) ponds embedded in the same homogeneous landscape (pasture matrix) and, (iii) ponds separated by small distances from each other (minimum: 0.06 km-maximum: 8.7 km; Fig. 1); we did not considered regional descriptors and focused mainly on assessing how the structural characteristics of ponds predict the richness and abundance of frog and toad communities in a homogeneous landscape. For this, we investigated eight major environmental descriptors of ponds (Appendix Table 2) known to affect the structure of anuran communities (Beebee 1977, 1985; Eterovick and Sazima 2000; Hazell et al. 2001, 2004; Beja and Alcazar 2003; Van Buskirk 2005). All environmental descriptors (except for hydroperiod; see below) were measured through field inspection between December 2004 and January 2005 when rainfall volume and anuran diversity were highest in the region. These descriptors included: breeding pond area (AREA), calculated in the field using a 200 m tape to measure length and width and extrapolated to pool size based on the formula of an ellipse (area =  $a \times b \times \pi$ , where a = maximum pool length measured in meters and b = maximum pool width measured in meters) because all ponds were of this shape; maximum depth (DEPTH), the deepest part of the pond as measured in centimeters; hydroperiod (HDP), classified as short (3 or fewer months with water), intermediate (between 3 and 9 months with water) or permanent (containing water throughout the year) based on observations of ponds in the field every 2 weeks from September 2004 to August 2005; number of vegetation types in the pond interior (NVI), scored as one of four categories: (1) no vegetation, (2) emergent herbaceous vegetation, including floating aquatic pteridophytes (Salvinia auriculata) and/or umbellifers (Eringyum sp.) when present, (3) herbaceous vegetation and shrubs and (4) herbaceous vegetation, shrubs and sparse trees; number of vegetation types in the margin (NVM), also scored categorically: (1) no vegetation, (2) emergent herbaceous vegetation, (3) herbaceous vegetation and shrubs and (4) herbaceous vegetation, shrubs and sparse trees; categories of vegetation height in the interior (VHI) and in the margin (VHM) of the farmland ponds, scored as one of five categories: (1) vegetation height only up to 30 cm, (2) additional (most) vegetation between 31 and 60 cm in height, (3) additional vegetation up to 90 cm in height, (4) additional vegetation up to 120 cm in height, and (5) vegetation in all of the above categories; and percentage of vegetation cover on the pond surface (PVS), visually estimated: (1) no vegetation, (2) up to 25%, (3) 26–50%, (3) 51–75%, and (4) 76–100%.

### Statistical analysis

Predictor variables influencing response variables such as species richness are often significantly correlated, meaning that identifying the likely causal variables is problematic (Mac Nally 2002). The occurrence of such multicollinearity in our data was checked by calculating the variance inflation factor (VIF) using the package AED (Zuur et al. 2009) in the statistical software environment R (version 2.12.2; R Development Core Team 2011). According to Quinn and Keough (2002), high VIF values (>10) indicate high multicollinearity. Because we found no VIF values greater than 10 among the explanatory variables, all further analyses were performed without considering multicollinearity.

To investigate which variables correlate species richness (number of species) in farmland ponds, we fit generalized linear models (GLMs) to the data using the GLM function implemented in the NLME package (Pinheiro et al. 2009), with a Poisson distribution and the log link function. We detected overdispersion and corrected the standard errors using a Quasi-Poisson model. To determine the optimal model, we started with a model in which the fixed component contained all explanatory variables. Then we generated sub-model sets from the global model using the dredge function implemented in the MuMIn package (Barton 2009). We used Akaike's information criterion adjusted for overdispersion, corrected for small sample sizes (QAICc, Burnham and Anderson 2002), to select explanatory variables driving total species richness, and Akaike weights to evaluate model selection uncertainty.

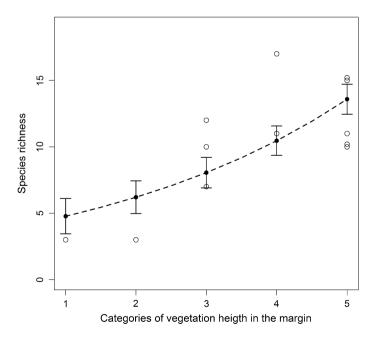
The relative importance of each environmental descriptor in predicting the abundance of each anuran species (adults only) was examined with hierarchical partitioning (Mac Nally 2000, 2002) using the hier.part package (Walsh and Mac Nally 2008). Because the data for species abundance were overdispersed, this analysis was performed with a Quasi-Poisson model. Hierarchical partitioning compares all possible models in a multiple regression setting and determines the independent capacities of the predictive variables to explain the patterns of variability in the corresponding response variable (Chevan and Sutherland 1991). The independent explanatory power of each predictor with respect to the dependent variable is characterized by an index I, which reflects the independent contribution of the predictor to the variance explained by the models. A second parameter, J, measures the interaction between each predictor and the others and, a third parameter,  $R^2$ , measures the percentage of total explained variance. Variables that independently explained a larger proportion of the variance than expected by chance were identified using randomization tests (Mac Nally 2002). For each predictor, the observed contribution to the explained variance (I) was compared to the distribution of I values resulting from 1,000 randomizations of the data matrix. Significance was accepted at the upper 95% confidence limit (Z score 1.65; Mac Nally 2002). For species abundance analysis, only anuran species of which adults occurred in at least six of the 12 farmland ponds studied were considered.

#### Results

We recorded 26 anuran species belonging to five families (Appendix Table 3): Bufonidae (1), Hylidae (10), Leiuperidae (7), Leptodactylidae (6) and Microhylidae (2). *Leptodactylus fuscus, Eupemphix nattereri, Pseudopaludicola falcipes* and *Physalaemus cuvieri* were recorded in at least nine of 12 farmland ponds, whereas 10 species were recorded in only one or two farmland ponds (Appendix Table 3).

The model with the environmental descriptor VHM, categories of vegetation height in the margin, was chosen as the most parsimonious (QAICc = 18.5), with deviance explaining 51.1% of variation in total anuran species richness (Fig. 2; Table 1). Farmland ponds with more categories of vegetation height in the margin contained higher species richness than habitats with vegetation in fewer height categories (Fig. 2).

Of the 24 anuran species with adult individuals recorded in the farmland ponds, only 10 were recorded in at least six ponds and thus used in the hierarchical partitioning analysis (Appendix Table 4). Abundance distributions of *Dendropsophus nanus, D. elianeae, Scinax fuscovarius* and *P. cuvieri* were not influenced by any of the explanatory variables (Appendix Table 4). Five environmental descriptors related to structural complexity of farmland ponds were important variables correlating the abundance distributions of the other six anuran species (Fig. 3). The occurrence of *Hypsiboas albopunctatus* was associated with higher numbers of vegetation types in pond interiors ( $R^2 = 33.63$ ), and the

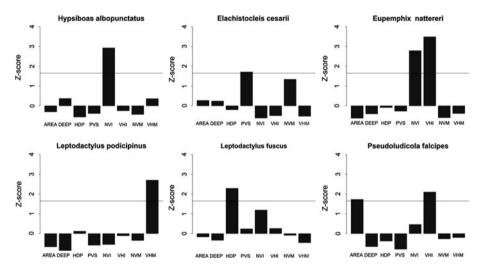


**Fig. 2** Predicted number of anuran species in 12 farmland ponds with different categories of vegetation height in the margin (VHM), sampled in the municipality of Icém, northwestern São Paulo state, Brazil. The *lines* GLM fit to the data, with standard error. *Open circles* observed species richness, *closed circles* estimated species richness. GLM (number of species) =  $1.3031 + 0.26711 \times VHM$ 

	QAICc	ΔQAICc	wQAICc	%DE
VHM	18.5	0	0.66	51.12
VHM + log(DEEP)	21.87	3.37	0.12	70.02
VHM + NVI	22.1	3.6	0.11	79.64
VHM + log(AREA)	22.16	3.66	0.11	79.00

 Table 1
 The four most parsimonious models predicting the relationship between anuran species richness (response variables) and environmental variables on 12 farmland ponds studied in Icém, northwestern São Paulo state, Brazil

*QAICc* Quasi-Akaike's information criterion,  $\Delta QAICc$  difference in Quasi-Akaike's information criterion, wQAICc QAICc weight, %DE percent deviance explained in the response variable by the model under consideration, *VHM* vegetation height in the margin, *DEPTH* maximum pond depth (cm), *NVI* number of vegetation types in the interior, *AREA* breeding area size (m<sup>2</sup>)



**Fig. 3** Plot of Z scores for independent contributions, based on randomizations of data matrices of potential explanatory predictor variables for species richness and abundance of six anuran species sampled in the municipality of Icém, northwestern São Paulo state, Brazil. The *horizontal line* upper 95% confidence limit. *AREA* Breeding area size, *DEEP* maximum pond depth, *HDP* hydroperiod, *PVS* percentage of vegetation cover on the pond surface, *NVI* number of vegetation types in the interior, *VHI* vegetation height in the pond interior, *NVM* number of vegetation types in the margin, *VHM* vegetation height in the margin

occurrence of *Elachistocleis cesarii* was associated with a greater PVS ( $R^2 = 26.49$ ). The occurrence of *E. nattereri* was associated with lower numbers of vegetation height categories in pond interiors ( $R^2 = 41.22$ ), whereas the occurrence of *L. podicipinus* was associated with higher numbers of vegetation height categories in pond margins ( $R^2 = 29.20$ ). *L. fuscus* occurred mainly in ponds showing intermediate or permanent hydroperiods ( $R^2 = 30.37$ ). *P. falcipes* was associated with large ponds ( $R^2 = 28.97$ ) and ponds with higher categories of vegetation height in the interior ( $R^2 = 30.12$ ).

## Discussion

Our results show that total anuran species richness in farmland ponds is mainly predicted by the number of categories of vegetation height in the pond margin, and five additional environmental descriptors correlate the variation in abundance of six anuran species. All of these descriptors are directly related to habitat heterogeneity and reflect the structural complexity in the breeding sites, in both vertical and horizontal strata. More heterogeneous ponds were found to harbor a greater number of species with diverse species-specific requirements.

Several studies previously conducted in tropical and temperate regions have found that anuran species richness is positively correlated with the quantity of vegetation and/or diversity of vegetation types within ponds (Diaz-Paniagua 1987; Eterovick and Sazima 2000; Weyrauch and Grubb Jr. 2004; Burne and Griffin 2005; Lichtenberg et al. 2006; Silva et al. 2011) and in pond margins (Hazell et al. 2004; Peltzer et al. 2006). The importance of vegetation height categories in farmland pond margins in explaining species richness is mainly due to the greater diversity of microhabitats provided by different levels of vertical stratification, which allows a greater number of species to coexist. Because most anuran species are specialized in their calling sites, an increase in the categories of vegetation height in pond margins increases anuran species richness. Menin et al. (2005), in a study conducted in another location within the same region, showed that vegetation species composition directly influences the occurrence and resources use of two closely related species of small anurans. According to these authors, the abundances of D. sanborni and D. nanus are related to the physical structure of the vegetation, as D. sanborni perches at higher sites and D. nanus perches at lower sites, and only rarely does D. sanborni occur with D. nanus in areas with only low vegetation.

Categories of vegetation height in both pond interiors and margins, number of vegetation types in the interior and percentage of vegetation in the interior predicted the abundance distributions of six anuran species in this study. These descriptors reflect the suitability of farmland ponds for anuran breeding, in particular the variety of calling sites and the amount of shelter from predators for tadpoles and young and newly metamorphosed adults (Hazell et al. 2001, 2004; Egan and Paton 2004; Welch and McMahon 2005; Kopp et al. 2006). Among the species correlated by these environmental descriptors, *H. albopunctatus* calls while perched on vegetation, whereas *P. falcipes* (Leuiperidae), *E. cesarii* (Microhilidae) and *L. podicipinus* (Leptodacylidae) vocalize while protected in tussocks on the banks. Therefore, farmland ponds that have a higher quantity and complexity of vegetation will harbor a higher number of species with different requirements and life histories.

The habitat heterogeneity hypothesis states that structurally complex habitats provide more niches and diverse ways to exploit environmental resources and thus increase species diversity (Bazzaz 1975). Here, increased structural complexity in vertical and horizontal strata of vegetation, in both the interior and the margin of farmland ponds, provides more diverse microhabitats that harbor a greater number of species with diverse species-specific requirements. Silva et al. (2012) in a study conducted within the same region with artificial ponds, showed that that breeding sites located both at the edge of and near to (within 50 m of) forest fragments supported greater abundance and species richness of frogs and toads than breeding sites located 100 and 200 m far from forest fragments. Thus, we do not intend to imply that other processes such as recolonization, extinction, dispersion and metapopulation dynamics (see Marsh and Trenham 2001; Cottenie 2005; Smith and Green

2005; Cushman 2006) are not important factors in explaining the distribution of anuran species, but our results provide evidence for the strong correlate of local descriptors.

Farmland ponds have been seriously affected by changes in human land use, and the recent sugarcane expansion (Rodrigues et al. 2008; Joly et al. 2010) is of concern because pond vegetation has been altered or even eliminated in sugarcane production areas. Our results show that environmental descriptors related to heterogeneity of vegetation, and thus the number of microhabitats present to meet diverse species-specific requirements, primarily predict the diversity of anuran species in farmland ponds. We would like to highlight the opportunity for the integration of anuran conservation with agricultural land use through the protection of environmental descriptors related to vegetation in farmland ponds, which will have minimal impact on agricultural crop yield and will promote the maintenance of a high diversity of anuran species.

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## Appendix

See Tables 2, 3 and 4.

	Latitude	Longitude	AREA	DEPTH	HDP	PVS	NVI	VHI	NVM	VHM
FP1	-20.366389	-49.256667	350	0.3	2	1	1	1	2	1
FP2	-20.356111	-49.201944	319	0.7	2	5	2	2	4	5
FP3	-20.355000	-49.203889	60	0.45	1	5	2	3	1	3
FP4	-20.356667	-49.201944	117	0.3	1	2	2	2	1	2
FP5	-20.368611	-49.200556	70	0.35	2	3	2	3	1	3
FP6	-20.363889	-49.238333	168	0.5	3	2	3	4	3	3
FP7	-20.375000	-49.275556	800	0.47	3	1	3	4	4	5
FP8	-20.355000	-49.204722	342	0.65	3	1	2	1	3	4
FP9	-20.363889	-49.193889	495	0.6	3	3	3	4	3	5
FP10	-20.362778	-49.236389	800	0.1	3	5	4	4	4	5
FP11	-20.358333	-49.198611	660	0.15	3	5	3	4	2	4
FP12	-20.363333	-49.193333	600	0.55	3	5	4	4	4	5

Table 2 Descriptors of the 12 farmland ponds (FP) studied in the Icém, São Paulo state, Brazil

AREA Breeding area size  $(m^2)$ , *DEPTH* maximum pond depth (cm), *HDP* hydroperiod, classified as: *1* short, 2 intermediate and 3 permanent, *PVS* scored as percentage of vegetation cover on the pond surface, *NVI* scored as number of vegetation types in the interior, *VHI* scored as vegetation height in the pond interior, *NVM* scored as number of vegetation types in the margin, *VHM* scored as vegetation height in the margin

recorded in 12 farmland nonds (FD) in Icém northwestern São Paulo state Brazil from Sentember 2004 to Auoust 2005 Table 3 Amiran species

	FP1	FP2	FP3	FP4	FP5	FP6	FP7	FP8	FP9	FP10	FP11	FP12	Total FP
Bufonidae													
Rhinella schneideri		Α						Т					7
Hylidae													
Dendropsophus elianeae		A/T	А			А		A/T	Α	А			9
Dendropsophus minutus		A/T				A/T		Α					
Dendropsophus nanus		A/T				A/T	A/T	A/T	A/T	А	А	А	8
Hypsiboas albopunctatus						A/T	A/T		A/T	A/T	A/T	A/T	9
Hypsiboas raniceps									А		А		7
Pseudis platensis		А											1
Scinax fuscomarginatus									A/T				1
Scinax fuscovarius	A/T	A/T	A/T	Т	A/T			A/T				А	7
Scinax similis		Т	Т		A/T	Α		Т	А				9
Trachycephalus venulosus		Τ											1
Microhylidae													
Elachistocleis cesarii			A/T		A/T		A	A	A/T	A/T	A/T	A/T	8
Dermatonotus muelleri		A/T	Т					A					3
Leptodactylidae													
Leptodactylus furnarius		Т								A/T			7
Leptodactylus fuscus	A/T	A/T	A/T	Τ	A/T	A/T	A	A/T	A/T	A/T	A/T	A/T	12
Leptodactylus labyrinthicus		А				Т		A	A/T	Т	Т	A/T	7
Leptodactylus mystacinus								A					1
Leptodactylus latrans								A					1
Leptodactylus podicipinus		А	А			Т	A	A	A		А	А	8
Leuperidae													
Physalaemus centralis									Ā				-

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Table	

	FP1	FP2	FP3	FP4	FP5	FP6	FP7	FP8	FP9	FP10	FP11	FP12	Total FP
Physalaemus cuvieri		A/T	A/T			A/T	A/T	A/T	A/T	A/T	A/T	A/T	6
Physalaemus marmoratus		Т			T		Т		Т	Т	Т		9
Pseudopaulicola falcipes		A	A		Т	A/T	A/T	A	A/T	A/T	A/T	A/T	10
Pseudopaludicola ternetzi							Т				A/T		7
Pseudopaludicola mystacalis						A/T		Т		A/T		Т	4
Eupemphix nattereri	A/T	A/T	A/T	Т	Т	A/T	A/T	A/T	Т		A/T		10
Total species richness	3	17	10	ю	7	12	10	17	15	11	12	10	
We followed the faxonomy as given in Frost (201	iven in Fro	st (2011)											

We followed the taxonomy as given in Frost (2011)

A Adult recorded in calling activity, T tadpoles

Bold values indicate the total number of farmland ponds that each species occurred (Total FP)

	Ι	J	$R^2$		Ι	J	$R^2$		Ι	J	$R^2$
Dendrop	sophus r	anus		Dendrop	osophus	elianeae		Scinax f	uscovar	ius	
AREA	0.08	0.06	11.34	AREA	0.04	-0.04	6.63	AREA	0.06	-0.02	6.10
DEEP	0.15	0.05	21.27	DEEP	0.20	0.23	29.75	DEEP	0.14	0.18	14.52
HDP	0.11	0.14	15.75	HDP	0.03	0.00	4.38	HDP	0.05	-0.01	5.66
PVI	0.01	-0.01	1.94	PVI	0.02	-0.01	3.48	PVI	0.14	-0.06	14.97
NVI	0.05	0.00	6.99	NVI	0.06	-0.06	9.63	NVI	0.16	-0.06	16.37
VHI	0.02	0.02	2.91	VHI	0.04	-0.02	6.07	VHI	0.12	0.05	12.97
NVM	0.09	0.07	11.87	NVM	0.08	0.07	11.41	NVM	0.15	-0.08	15.91
VHM	0.20	0.17	27.95	VHM	0.19	0.02	28.65	VHM	0.13	-0.07	13.50
Hypsibod	is albop	unctatus		Elachist	ocleis c	esarii		Eupemp	hix natt	ereri	
AREA	0.07	0.07	8.55	AREA	0.11	0.02	13.08	AREA	0.03	-0.01	2.85
DEEP	0.13	-0.10	15.79	DEEP	0.12	0.12	14.45	DEEP	0.05	0.06	5.36
HDP	0.04	0.13	4.62	HDP	0.07	-0.03	8.10	HDP	0.08	-0.08	8.66
PVI	0.06	0.04	7.58	PVI*	0.22	0.08	26.50	PVI	0.06	0.12	6.20
NVI*	0.28	0.15	33.64	NVI	0.04	0.06	4.38	NVI	0.23	0.15	24.79
VHI	0.08	0.14	8.97	VHI	0.05	0.11	5.46	VHI*	0.39	0.28	41.22
NVM	0.06	0.15	7.10	NVM	0.19	-0.16	22.18	NVM	0.05	-0.05	5.73
VHM	0.12	0.05	13.76	VHM	0.05	0.00	5.85	VHM	0.05	0.02	5.19
Pseudope	aludicold	a falcipes		Leptoda	ctylus fi	iscus		Leptoda	ctylus p	odicipinus	5
AREA*	0.26	0.23	28.98	AREA	0.07	-0.06	7.26	AREA	0.07	0.00	8.45
DEEP	0.04	-0.01	4.90	DEEP	0.06	0.00	5.96	DEEP	0.20	0.09	24.24
HDP	0.06	0.20	6.78	HDP*	0.30	-0.27	30.38	HDP	0.02	0.03	2.32
PVI	0.01	0.04	1.66	PVI	0.10	-0.10	10.36	PVI	0.06	0.01	7.01
NVI	0.10	0.25	11.00	NVI	0.22	-0.06	22.24	NVI	0.13	-0.12	15.12
VHI*	0.27	0.28	30.12	VHI	0.11	0.03	11.65	VHI	0.05	-0.02	5.68
NVM	0.07	0.03	7.93	NVM	0.08	-0.03	7.67	NVM	0.07	0.09	7.98
VHM	0.08	0.21	8.62	VHM	0.04	0.02	4.48	VHM*	0.24	0.14	29.20
Physalae	rmus cuv	ieri									
AREA	0.20	0.27	20.68								
DEEP	0.08	-0.01	8.20								
HDP	0.08	0.23	7.67								
PVI	0.07	-0.07	7.12								
NVI	0.08	0.19	8.57								
VHI	0.20	0.15	20.47								
NVM	0.10	0.29	10.10								
VHM	0.17	0.34	17.19								

 Table 4
 Hierarchical partition correlating the abundance of 10 anuran species in 12 farmland ponds Icém, northwestern São Paulo state, Brazil, from September 2004 to August 2005

I Reflects the independent contribution of the predictor, J measures the interaction between each predictor and the others predictors, and  $R^2$  percentage of total explained variance

*AREA* Breeding area size, *DEPTH* maximum depth, *HDP* hydroperiod, *PVI* percentage of vegetation cover on the surface of the farmland pond, *NVI* number of vegetation types in the interior, *VHI* vegetation height in the interior, *NVM* number of vegetation types in the margin, *VHM* vegetation height in the margin

\* Significance values from 1,000 randomizations of data

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