



Breeding Habitat and Landscape Correlates of Frog Diversity and Abundance in a Tropical Agricultural Landscape

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Abstract The biodiversity values of temporary pools in tropical ecosystems are poorly understood. Such wetlands are often threatened by agriculture. Constructed pools provide a means to mitigate for loss of natural pools but design features associated with restoration successful are not known. In this paper, we evaluated the effects of environmental variables at local (breeding pools) and regional spatial scales (landscape configuration) on species richness and abundance of anurans in heavily altered landscapes of southeastern Brazil. Frog and toad communities of 18 constructed temporary breeding pools were sampled every 2 weeks from October 2008 to March 2009. Two variables—hydroperiod and percentage of vegetation in the interior of the pools—explained 62% of species richness variation. Three other variables—pool area, distance of pools to forest fragments, and distance of pools to road—explained between 22 and 46% of the variation in

frog and toad abundance. Our results indicate that local- and regional-scale variables, and their interaction, are important drivers of the structure of frog and toad communities in these agricultural landscapes. To facilitate amphibian conservation we suggest that cattle ranchers create and maintain heavily vegetated temporary pools near protected forest reserves as both a water source for livestock and breeding habitat for amphibians.

Keywords Amphibians · Brazil, Conservation · Hierarchical partitioning · Scale · Temporary pools

Introduction

Amphibians are often the focus of studies to evaluate questions about the effects of local and regional variables on community structure (e.g., Babbitt et al. 2009; Karraker and Gibbs 2009; Werner et al. 2009; Bickford et al. 2010; Shulse et al. 2010; Wassens et al. 2010; Hamer and Parris 2011). Amphibian complex life cycles are typically affected by habitat changes operating at different spatial scales. Most studies relating environmental drivers to amphibian communities have focused on temperate zones (Burne and Griffin 2005; Van Buskirk 2005; Karraker and Gibbs 2009; Werner et al. 2009; Shulse et al. 2010; Wassens et al. 2010). Tropical Brazil supports the greatest frog and toad diversity in the World (AmphibiaWeb 2011), yet few studies have focused on environmental drivers of amphibian communities in this biodiversity hotspot (Myers et al. 2000). Of particular concern are amphibians in Mesophytic Semi-deciduous Forest, a subdivision of the Brazilian Atlantic Forest (Oliveira-Filho and Fontes 2000). Mesophytic Semi-deciduous Forest is one of the most threatened types of tropical forest in the world (Jansen 1997), and only 4% of

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original cover remains in the northwestern region of São Paulo State (SMA/IF 2005). This area is now largely a matrix of pasture with sparse trees converted for cattle ranching and sugar cane production (Rodrigues et al. 2008).

Landscape alteration can impact amphibian communities through habitat loss, fragmentation and isolation, and degradation of habitat quality (Hamer and Parris 2011). Agricultural ecosystems of the northwestern region of São Paulo State, Brazil, host 37 anuran species adapted to anthropogenic habitats (Vasconcelos and Rossa-Feres 2005; Santos et al. 2007; Prado et al. 2008; Silva et al. 2009; Silva et al. 2010). Constructed temporary ponds of this region provide breeding habitat for most anuran species (Santos et al. 2007), but are under threat from expansion of sugarcane production for ethanol production. Although ephemeral waters are threatened by human activities in many regions (Beja and Alcazar 2003), their biodiversity values are frequently overlooked (Snodgrass et al. 2000; Beja and Alcazar 2003). Lacking information on the species that depend on these wetlands and the wetland attributes important for maintaining their populations, conservation management is infeasible. Currently the Brazilian government has no conservation strategy to protect constructed temporary or permanent pools from sugarcane expansion or other human activities. Identification of the habitat features that are associated with the occurrence of anuran species is therefore important for predicting impacts of habitat change and identifying key habitats for conservation (Wassens et al. 2010).

To address this knowledge gap, we evaluated the effect of environmental variables measured at local and regional scales in determining species richness and abundance of anurans in 18 constructed temporary pools in a tropical agricultural landscape. Our research was guided by two questions: (1) What are the most important variables (local or regional) explaining distribution patterns of anurans in constructed temporary breeding pools in this agricultural landscape? and (2) How do the different species respond to these variables? Based on a review of the literature we hypothesized that constructed temporary pools that have extended hydroperiods, are heavily vegetated (Egan and Paton 2004), and are located near forest fragments (Silva and Rossa-Feres 2007, 2011) would harbor greater species diversity and abundance of anurans.

Study Area

This study was conducted in northwestern São Paulo State, Brazil (20° 33' S/50° 13' W to 21° 35' S, 48° 29' W, Online Fig. S1), an area of approximately 39 000 km² occupied by 64 inhabitants/km² (Nalon et al. 2008). Currently 37 anuran species have been recorded from the region, corresponding

to almost 15% of the State's species and 5% of Brazil's total anuran richness (Rossa-Feres et al. 2008). Most of the anuran species of this region are considered habitat generalists and are not listed as threatened species, although a lack of knowledge about species diversity in the region is of concern (Rodrigues et al. 2008). Four of the 37 species were only recently recorded (Prado et al. 2008; Silva et al. 2009; Silva et al. 2010).

The original vegetation of the region has been devastated by agricultural activities; indeed, the region is among the most deforested and fragmented within São Paulo State, with few conservation areas (Rodrigues et al. 2008). The agricultural landscape contains small forest fragments embedded in grasslands, and sugarcane and rubber plantations (Rodrigues et al. 2008). Recent sugarcane expansion (Rodrigues et al. 2008; Joly et al. 2010) is of special concern because constructed temporary pools, formerly retained as a water source for cattle production, tend to be eliminated from sugarcane production areas.

The region's climate is seasonal tropical with annual mean temperature between 22 and 23°C with a well-defined rainy season between October and March, and a pronounced dry season between April and September, when only 15% of the total annual rainfall of 1,100 mm (± 225 mm) occurs (Barcha and Arid 1971). The region's temporary pools dry between April and September. Rainfall in the first month of the rainy season is unpredictable, so temporary pools may dry once or twice after the first rains commence (Santos et al. 2007). Most constructed temporary pools (hereafter temporary pools) in the region were designed as cattle tank or irrigation channels by farmers.

Methods

Sampling

Sampling sites were located by field reconnaissance because most pools used by anurans in the region are small (<400 m²) and difficult to detect by satellite images. The field reconnaissance was performed on farms whose owners had given permission for the study. We chose 18 non-randomly selected pools distributed in six municipalities (Online Table S1, Fig. S1) based on the following criteria: pools were (1) located in a pasture matrix; (2) not in contact with permanently flooded habitats; (3) lacking fish; and (4) were >500 m distant from sugarcane, orange, or rubber plantations. The minimum and maximum distances between any two sites were 0.15 and 201.4 km, respectively (mean distance=85.8 km).

Population surveys of pools were conducted every 2 weeks during the rainy season, October 2008 to March 2009, for a total of 12 surveys per pool. This period is when

most anuran species in the region are active (Vasconcelos and Rossa-Feres 2005; Santos et al. 2007). Sampling was conducted between 1900 to 2400 h, and site visits lasted 30 min. Visual and acoustic surveys involved walking the perimeter of each pool upon arrival and recording the number of each species observed or heard calling. Abundance of each species was recorded by listening for calling males. Individuals not recorded calling were included in species richness analyses but excluded from the abundance analysis. Voucher specimens were collected and deposited in the amphibian collection of the Departamento de Zoologia e Botânica of UNESP, São José do Rio Preto, São Paulo.

We measured nine local- and regional-scale variables that potentially could affect the structure of anuran communities. All local variables were measured through field inspection between December 2008 and January 2009 when rainfall volume and anuran diversity was highest in the region. Local-scale variables (see Table 1) included: i) temporary pool size (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 (all pools were elliptically shaped) given a = pool length and b = pool width, such that pool area = $a \times b \times \pi$; ii) hydroperiod (HDP): short (≤ 3 months with water) or long (> 3 months with water) based on observations of the pools in the field every 2 weeks from October 2008 to March 2009; iii)

percentage of vegetation in the interior of the temporary pool (PVI): measured in increments of 0–20%, 21–50%, 51–80%, and 81–100%; iv) percentage of vegetation in the pool margins (PVM): measured in increments of 0–20%, 21–50%, 51–80%, 81–100%; v) heterogeneity of vegetation in the interior of the temporary pool (HVI): classified according to prevalence of a single type of vegetation, by emergent herbaceous vegetation, including aquatic pteridophytes (*Salvinia auriculata* Aubl.) and/or umbellifers (*Eriogonum* sp.), by herbaceous and shrubs vegetation, or by herbaceous and shrubs vegetation and sparse trees; vi) heterogeneity of vegetation in the margin (HVM): classified according to prevalence of grassland, grassland and other herbaceous vegetation, herbaceous and shrub vegetation, and herbaceous and shrub vegetation and sparse trees. For each pool, PVI, PVM, HVI, and HVM were visually estimated.

Landscape-scale variables (see Table 1) included: i) distance from the pool to the nearest forest fragment (DFR); ii) distance to the nearest breeding pool (DBA) (nearest focal pool with calling anurans); and iii) distance to the nearest paved road (DR) (only paved roads were considered because unpaved roads had low traffic volumes). All landscape-level variables were determined from recent high-resolution aerial photographs of the region (available from Google Earth: <http://earth.google.com/>) combined with field inspection.

Table 1 Summary of local- and regional-scale environmental variables for 18 temporary breeding pools in the northwestern São Paulo State, Brazil. See text for details

	Area (m ²)	Hydroperiod	% Vegetation Interior	% Vegetation Margin	Heterogeneity Vegetation Interior	Heterogeneity Vegetation Margin	Distance nearest forest (m)	Distance nearest pool (m)	Distance nearest road (m)
P1	775.1	2	2	3	1	1	5	82	215
P2	37.5	1	2	3	1	1	306	115	196
P3	102.3	1	2	2	1	1	163	22	140
P4	339.1	2	3	4	3	4	0	102	20
P5	256.3	2	2	2	2	3	133	800	15
P6	676.0	2	2	4	1	4	0	290	10
P7	348.5	2	1	3	1	1	800	50	5
P8	231.6	2	3	4	3	4	45	485	89
P9	400.3	1	1	2	1	2	855	55	20
P10	618.4	2	3	4	2	4	45	80	85
P11	123.4	1	1	2	1	1	710	103	120
P12	152.0	1	4	4	1	1	550	245	25
P13	337.4	2	2	4	3	4	0	80	258
P14	300.7	2	2	3	2	2	210	50	118
P15	384.6	1	3	2	1	1	70	391	40
P16	73.4	1	2	3	1	2	10	175	0
P17	539.0	2	2	4	2	3	77	300	25
P18	86.3	2	2	3	2	2	60	250	5

Statistical Analysis

To evaluate if pools were satisfactorily sampled to measure species richness, we compare species richness recorded in all pools based on two estimators (Jackknife I and II), using EstimateS 8.20 program (Colwell 2004). Estimators were generated as a function of accumulated number of samples in 500 randomizations (Colwell 2004).

Because ecological variables often do not constitute spatially independent observations due to the spatial structure of abiotic factors operating at different scales (Legendre 1993), we inspected all variables for spatial autocorrelation (through Moran's I test) using the package *spdep* (Bivand et al. 2009); none showed any evidence of spatial structure. Multi-collinearity among variables was examined with the variance inflation factor (VIF) (Zuur et al. 2009); this identified HVM with a high VIF value (>.0), and thus it was excluded from the analysis. All VIF values for other factors were <4.0.

To investigate which variables best explained species richness (number of species) of anurans in the 18 temporary pools, we fitted generalized linear models (GLMs) to the data using the GLM function in the *nlme* package (Pinheiro et al. 2009). To determine the optimal model, we started with a model in which the fixed component contained all explanatory variables. We used Akaike's information criterion, corrected for small sample sizes (AICc, Burnham and Anderson 1998), to select variables best explaining total species richness. We used Akaike weights to evaluate model-selection uncertainty. We calculated the percentage deviance explained (%DE) as a measure of model goodness-of-fit.

The relative importance of local and landscape variables to the abundance of each anuran species was examined using hierarchical partitioning (Mac Nally 2000, 2002). Because the data for species abundance were overdispersed, the analysis used a quasi-Poisson distribution. Hierarchical partitioning compares all possible models for a multiple regression and determines the independent capacities of the predictive variables to explain the patterns of variability in the corresponding response variable (Chevan and Sutherland 1991). For each predictor, the independent explanatory power on the dependent variable is characterized with an index "I", which reflects the independent contribution of the predictor to the variance explained by the model. A second parameter, "J", measures the interaction between each predictor and the others. Variables that independently explained a larger proportion of variance than expected by chance alone were identified using randomization tests (Mac Nally 2002). For each predictor, the observed contribution of I was compared to the distribution of a population of I's from 1000 randomizations of the data matrix. Significance was accepted at the upper 95% confidence limit (z-score=1.65)

(Mac Nally 2002). For this analysis, the species abundance was considered the greatest abundance sampled among the 12 collections from each pool. This approach was adopted because, according to Vasconcelos and Rossa-Feres (2005), it avoids both sub-estimates of population abundance (due to the use of sample averages) and super-estimates, due to the recounting of individuals in successive samples. Moreover, only species that occurred in at least six of the 18 temporary pools studied were considered in this analysis to diminish noise caused by the presence of rare species. All statistical analyses were conducted using R Ver. 2.13.1 (R Development Core Team 2011), with $\alpha=0.05$.

Results

Frog and Toad Surveys

We recorded 27 anuran species distributed among five families (Frost 2010): Bufonidae (1), Hylidae (12), Leiuperidae (5), Leptodactylidae (6), and Microhylidae (3) (Online Table S1). *Physalaemus cuvieri* Fitzinger and *Leptodactylus fuscus* (Schneider) were recorded in all the pools whereas *Dendropsophus melanargyreus* (Cope), *Hypsiboas faber* (Wied-Neuwied), *Pseudopaludicola mystacalis* (Cope), *Trachycephalus venulosus* (Linnaeus), and *Elachistocleis cesarii* (Miranda-Ribeiro) were in only one pool. The richness estimators produced stable estimates, close to the observed richness (Online Table S2), indicating that pools were adequately sampled.

Relationships Between Species Richness and Environmental Variables

Pools with a longer hydroperiod and pools with higher percentage of vegetation in the interior (PVI) supported higher species richness than habitats with a short hydroperiod and lower PVI (Fig. 1). The model with hydroperiod and PVI was chosen as the most parsimonious (AICc=91.81) with 61.1% of variation in species richness explained (Fig. 1; Table 2).

Species-Specific Relationships with Environmental Variables

Of the 27 anuran species recorded in the pools, only 11 species were recorded from at least six pools and thus used in the hierarchical partitioning analysis (Online Table S3). Abundance of *L. fuscus*, *Scinax fuscovarius* (Lutz), *P. cuvieri*, and *P. centralis* (Bokermann) were not influenced by any explanatory variable (Online Table S3) but among remaining species five environmental descriptors were important variables explaining their patterns of abundance.

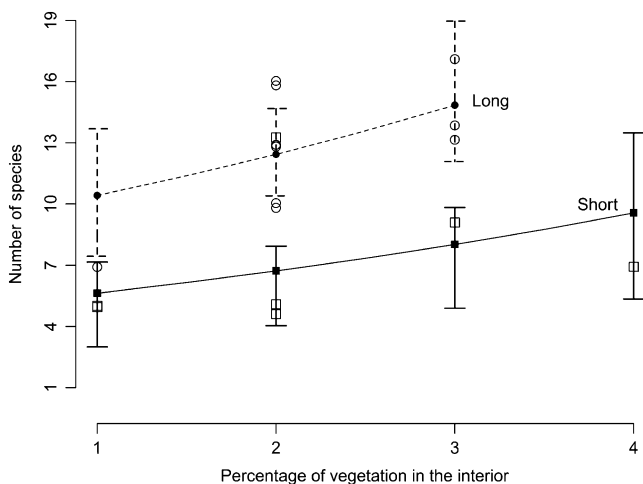


Fig. 1 Predicted number of anuran species in 18 breeding pools of different hydroperiod and percentage of vegetation in the interior (PVI), sampled in northwestern São Paulo State, Brazil in the rainy season 2008–2009. The lines represent the GLM fit to the data, with 95% confidence intervals. ○: observed species richness in long hydroperiods; □: observed species richness in short hydroperiods; ●: estimated species richness in long hydroperiods; ■: estimated species richness in short hydroperiods. Number of species = 0.9354 + 0.6158 * hydroperiod + 0.1768 * PVI

Heterogeneity of vegetation in the interior was the most important variable explaining the abundance distribution for *Dendropsophus nanus* (Boulenger) ($R^2=0.355$) and *Scinax fuscomarginatus* (Lutz) ($R^2=0.330$) (Fig. 2). Distance from the pool to the nearest forest remnant was the most important variable explaining the abundance distribution for *Elachistocleis bicolor* (Guérin-Méneville) ($R^2=0.390$), while distance from the pool to the nearest forest remnants and hydroperiod were important variables for *Eupemphix nattereri* Steindachner ($R^2=0.237$ and $R^2=0.227$, respectively) (Fig. 2). Distance from pool to the

nearest road was the most important variable explaining the abundance distribution for *D. minutus* (Peters) ($R^2=0.460$), while distance to road and pool area were important variables for *Leptodactylus podicipinus* (Cope) ($R^2=0.262$ and $R^2=0.241$, respectively) (Online Table S3, Fig. 2).

Discussion

Our results showed that both local- and region-scale variables influenced the structure of open-area anuran communities in a tropical agricultural landscape of southeastern Brazil. Species richness was directly related to the hydroperiod and percentage of vegetation in the interior of the temporary pools. Significant species-specific abundances were associated with percentage of vegetation in the interior of the temporary pools, distance from the pool to the nearest forest fragment, distance to the nearest paved road, and hydroperiod. Our studies emphasize that species diversity cannot be fully explained by considering only local or only regional scales, but requires simultaneous consideration of both (see also Burne and Griffin 2005; Van Buskirk 2005; Karraker and Gibbs 2009; Bickford et al. 2010; Shulse et al. 2010; Wassens et al. 2010; Hamer and Parris 2011).

Our results are consistent with many past studies on amphibian communities in indicating that species richness of amphibians was greatest in temporary pools with intermediate to long hydroperiods (Semlitsch and Bodie 1998; Snodgrass et al. 2000; Egan and Paton 2004; Lichtenberg et al. 2006; Otto et al. 2007; Karraker and Gibbs 2009). In our study area, climate severity (long and intense dry seasons, unpredictable and variable rainfall in the beginning of the wet season) and predator pressure are probably important factors promoting the use of long-term

Table 2 The *a priori* model set used to examine relationships between anuran species richness (response variables) environmental variables in 18 temporary breeding pools in the northwestern São Paulo State, Brazil, in the rainy season 2008–2009. ΔAIC_c = difference in Akaike’s Information Criterion for each model from the most parsimonious model; k = number of parameters; $wAIC_c$ = AIC_c weight; and %DE = percent deviance explained in the response variable by the model

Models	ΔAIC_c	k	weight	%DE
HDP + PVI	0	3	0.31	61.14
HDP	0.1	2	0.29	50.72
HDP + PVI + PVM	0.2	4	0.28	71.94
HDP + PVI + PVM + DFR	2.6	5	0.08	77.06
HDP + PVI + PVM + DFR + DBA	6.3	6	0.01	80.41
HDP + PVI + PVM + DFR + DBA + HVI	11.5	7	0.001	81.47
HDP + PVI + PVM + DFR + DBA + HVI + AREA	18.2	8	<0.001	82.02
HDP + PVI + PVM + DFR + DBA + HVI + AREA + DR	26.6	9	<0.001	82.11

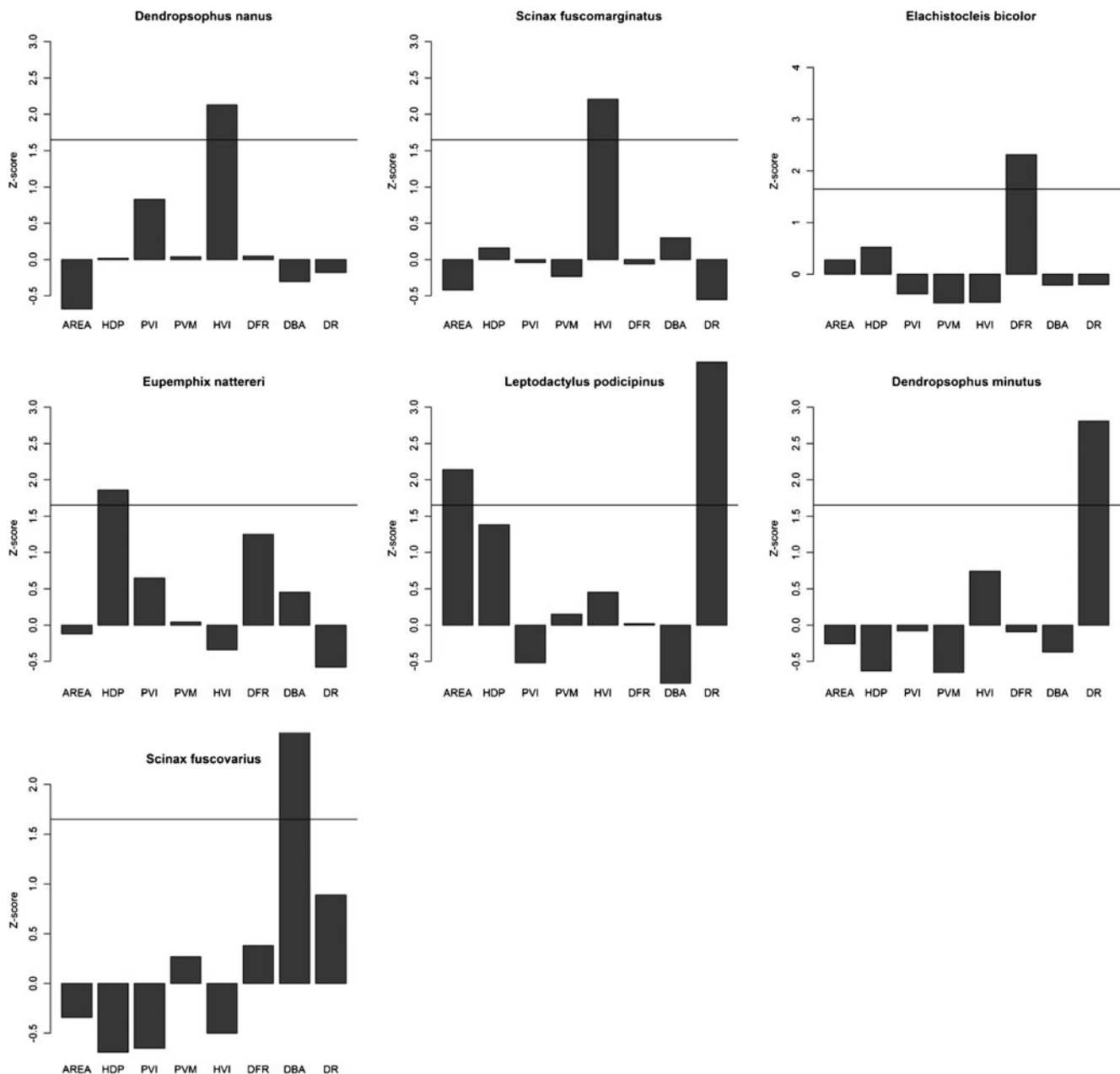


Fig. 2 Independent contributions of environmental drivers to abundance of 11 anurans species sampled in northwestern São Paulo State Brazil in the rainy season 2008–2009. Plots are Z-scores for independent contributions, I , from randomizations of data matrices for potential explanatory predictor variables for abundance of each species. The horizontal line represents upper 95% confidence value for

the Z-scores. AREA = breeding pool size; HDP = hydroperiod; PVI = percentage vegetation in the interior; PVM = percentage of vegetation in the margin; HVI = heterogeneity of vegetation in the interior; DFR = distance from the nearest forest fragment; DBA = distance from the nearest breeding pool, DR = distant from the nearest road

temporary habitats for amphibian reproduction. For example, a study of Santa Fé do Sul municipality in northwestern São Paulo State reported that short-term temporary breeding pools dried more than once during the rainy season, causing mass mortality of tadpoles (Santos et al. 2007). For the majority of the species observed, reproduction is concentrated during the rainy season (October to March) so it is probably most advantageous to occupy long-hydroperiod temporary breed-

ing pools, where there are few predators, than to occupy either short-hydroperiod sites breeding pools that may be free from predators yet have high risk of desiccation or permanent-water sites with elevated numbers of predators (Wellborn et al. 1996).

High heterogeneity of vegetation in the interior pools was important for some species. *Scinax fuscomarginatus*, and *D. nanus*, two small hyloid species that vocalize mainly

perched in the vegetation, are examples. Pools with high structural complexity may be more conducive to anuran reproduction because they offer more and varied sites for vocalization, amplexus, and oviposition, as well as shelter for recently metamorphosed tadpoles and adults from predators (Egan and Paton 2004; Burne and Griffin 2005; Shulse et al. 2010; Wassens et al. 2010). Notably, the highest abundances of *D. minutus* and *L. podicipinus* were recorded in pools distant from roads. Many studies suggest that roads negatively impact many amphibians (Fahrig et al. 1995; Gibbs 1998; Cushman 2006; Eigenbrod et al. 2008; Sutherland et al. 2010). Habitat fragmentation by roads or other barriers diminishes dispersal (Gibbs 1998), increases mortality (Fahrig et al. 1995; Sutherland et al. 2010), and reduces genetic diversity (Reh and Seitz 1990). Distance from forests was also an important variable for some species. More specifically, pools near forest fragments supported the greatest abundance of *E. bicolor* and *E. nattereri*, two small burrowing frogs that probably have low capacity of dispersal, corroborating results of other studies (e.g., Laan and Verboom 1990; Findlay and Houlihan 1997; Herrmann et al. 2005; Otto et al. 2007; Silva and Rossa-Feres 2011). The vulnerability of many amphibians due to physiological limitations (Duellman and Trueb 1994), low mobility (Gibbs 1998), and high mortality during dispersal through roads or inhospitable areas (Fahrig et al. 1995; Becker et al. 2007) are likely factors that limit the colonization and favor the extinction of species in highly isolated pools (Silva and Rossa-Feres 2011).

The fact that *L. fuscus*, *P. cuvieri*, and *P. centralis* did not exhibit any relationships with the environmental variables measured might be explained by the spatial distribution of these species. *Leptodactylus fuscus* and *P. cuvieri* occurred in 18 and 17 of 18 temporary pools, respectively, with similar abundances among pools (Online Table S1). On the other hand, *P. centralis* was detected in only six pools, and in five involved detections of just one individual (Online Table S1). We probably failed to associate the distribution of the abundance of these species with any environmental variable because two were generalist species capable of persisting in diverse conditions and the third a rare species with low abundances that comprise understanding its habitat relationships.

Conclusion

Our study presents the first science-based guidelines for preservation and conservation of created temporary pools for anurans in northwestern São Paulo State, a vast and biologically-diverse region. Constructed temporary ponds of southeastern Brazil provide breeding habitat for many anuran species (Santos et al. 2007), but are under threat

from sugarcane expansion (Rodrigues et al. 2008). There is no conservation strategy currently employed by the Brazilian government to protect temporary or permanent pools from human development. However, the Brazilian government requires that a legal reserve or forest area be created within every rural property, equivalent to at least 20% of the total area (laws nº 4.771/65; 7.803/89). We suggest that preservation of pools could occur through collaborative initiatives with farm owners. Cattle ranchers are motivated to maintain and even create pools as drinking water course for cattle and possibly would consider focusing on temporary pools that are heavily vegetated (emergent vegetation herbaceous, floating aquatic pteridophytes, shrub vegetation) and located near forest to benefit both cattle and native anurans.

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