

# An experimental assessment of landscape configuration effects on frog and toad abundance and diversity in tropical agro-savannah landscapes of southeastern Brazil

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**Abstract** Amphibians are an imperiled group of vertebrate animals that typically have biphasic life histories involving a shift from aquatic larval habitats to terrestrial adult habitats. Habitat loss is the greatest threat to amphibians and the importance of the spatial configuration of terrestrial and breeding habitats upon the landscape in determining amphibian persistence is poorly known. The information gap is particularly acute in tropical landscapes that simultaneously host the greatest and most imperiled amphibian fauna on Earth. We installed 125 artificial ponds at different distances from forest fragments embedded in an agricultural

matrix in southeastern Brazil. Constructed ponds attracted 13 anuran species; ponds at the forest fragment-matrix transition hosted a greater abundance and higher species richness of frogs and toads than those installed either far from or well within forest fragments. Forest fragments larger than 70 ha in agricultural areas harbored more individuals than smaller fragments. Our results indicate that landscape configuration has an important influence on frog and toad distribution and abundance in tropical agricultural landscapes and we suggest guidelines for maintaining favorable configurations of aquatic and terrestrial habitats for conserving this rich and imperiled species suite.

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## Introduction

Globally there are approximately 6,835 known amphibian species (AmphibiaWeb 2011), with the Neotropics sheltering the highest number of frog and toad species (Duellman 1999, Young et al. 2004). Over recent decades, widespread species declines and extirpations of populations have been reported (e.g., Alford and Richards 1999; Houlahan et al. 2000). Neotropical amphibians are the most threatened (Stuart et al. 2004), including Brazilian species of frogs and toads (Silvano and Segalla 2005), that

together represent the greatest component of frog and toad diversity in the world (AmphibiaWeb 2011).

The causes for recent amphibian declines are many, but emerging disease (chytridiomycosis) along with habitat loss and fragmentation are considered the greatest threats to amphibian populations, affecting 89% of all threatened species (Alford and Richards 1999; Blaustein and Kiesecker 2002; Young et al. 2004; Cushman 2006). A primary reason is that most amphibians have biphasic life histories that involve migrating to aquatic breeding areas and returning to terrestrial habitats (Duellman and Trueb 1986; Sinsch 1990; Blaustein et al. 1994), which provide places of foraging, aestivation, migration, hibernation and dispersal (Stebbins and Cohen 1995; Marsh and Trenham 2001). Forest fragments have been identified as important habitats that enhance landscape connectivity (Laan and Verboom 1990), and reduction of connectivity through habitat loss may reduce anuran diversity (Lehtinen et al. 1999; Becker et al. 2010). Forest fragments provide refuge for many species that spend part or all of the time in trees, bushes or in leaf litter when not breeding (Knutson et al. 1999; Hazell et al. 2001). Because discontinuity between suitable aquatic and terrestrial habitats forces many species with aquatic larvae to perform risky breeding migrations through disturbed environments (Becker et al. 2007; Becker et al. 2010), the spatial configuration of aquatic and terrestrial habitats could be an important influence on amphibian diversity and distribution by influencing population viability (Laan and Verboom 1990; Marsh et al. 2000; Marsh and Trenham 2001; Gibbons 2003).

The complex patterns of habitat use by amphibians pose challenges for conserving them in part because we know relatively little about the details of habitat connectivity. For example, high temperatures and low humidity in open areas can be limiting for amphibians, which have high risk of desiccation (Rothermel and Semlitsch 2002). Although commonly assumed to be extremely limited, the dispersal ability of amphibians is difficult to study and usually underestimated by conventional, mark–recapture studies (Porter and Dooley 1993); indeed amphibians migrating to distances of 2–15 km have been reported (Alford and Richards 1999; Marsh and Trenham 2001; Funk et al. 2005). Moreover, little is known about the factors that influence the dispersal ability of amphibians in different types of landscapes (Rothermel 2004).

Few studies have provided clear insights into relationship between the configuration of aquatic and terrestrial habitats and population persistence in any tropical amphibian and thus it is difficult to design habitat plans to conserve this highly diverse and simultaneously threatened group of vertebrates. For this reason, we installed 135 artificial ponds at different distances from forest fragments to evaluate the interaction between forest fragment size and distance between breeding and terrestrial habitats. We hypothesized that breeding areas near forest fragments would have greater species richness and greater abundance than breeding areas farther from forest fragments because proximity decreases risks associated with dehydration and predation during breeding migrations. Furthermore, because most species recorded in this region breed in ponds located in open areas (“pasture matrix”) but rely on forest fragments for shelter and foraging during the extended non-reproductive period in the dry season (Silva and Rossa-Feres 2007, 2011b), we expected to find more use of artificial ponds in larger forest fragments.

## Materials and methods

### Study area

Experimental ponds were constructed in watersheds of Turvo-Grande, São José dos Dourados, Baixo Tietê and Tietê-Batalha in the State of São Paulo, Brazil. The region is one of most altered watersheds in South America (Castro et al. 2005) given that the original vegetation of the region—mesophytic semideciduous forest and patches of cerrado (Ab’Saber 2003)—has been devastated by agricultural activities such that the remaining forest is distributed among a few, small and highly scattered fragments (SMA/IF 2005). The region’s hot and humid climate is characterized by two well-defined climatic seasons (IBGE 2009): a rainy season between October and March and a pronounced dry season between April and September during which only 15% of the total annual rainfall of 1,100–1,250 mm falls.

### Experimental design

Several studies have demonstrated that combinations of environmental variables measured at local and

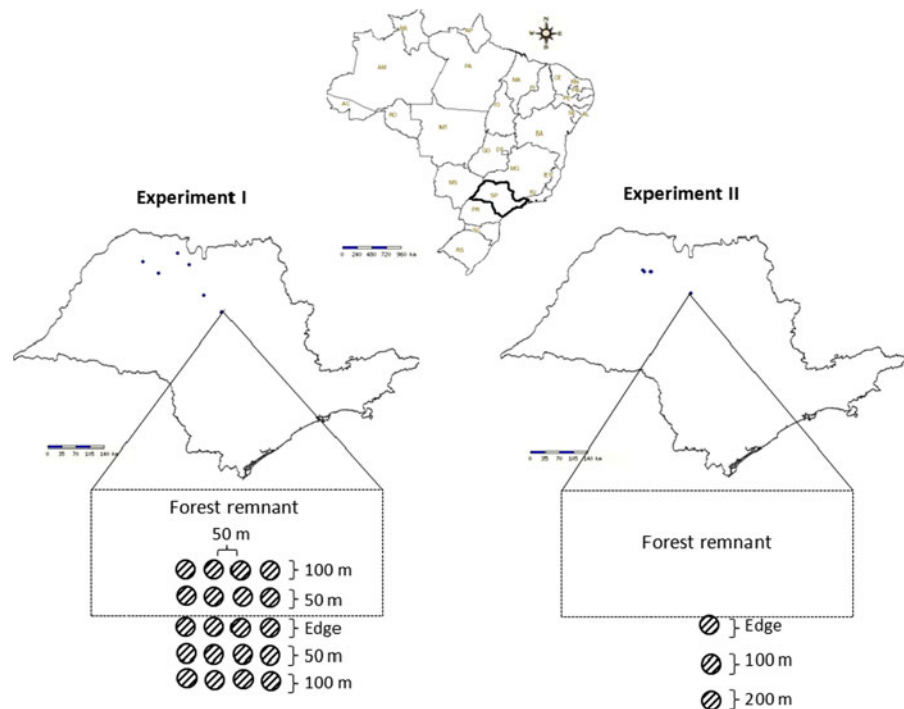
regional scales are important drivers of the structure of frog and toad communities (Werner et al. 2009; Shulse et al. 2010; Hamer and Parris 2011). Natural ponds differ greatly in structure and heterogeneity (Metzger 2003; Cushman 2006) so we used artificial ponds which can permit better controlled experiments at local scale making it easier to discern the influence of larger scale factors on the drivers of amphibian distribution (e.g., Marsh et al. 1999). We conducted experiments with artificial ponds during two rainy seasons (between 2007 and 2009) when most anuran species in the region breed (e.g., Rossa-Feres and Jim 2001; Vasconcelos and Rossa-Feres 2005; Santos et al. 2007). Ponds were constructed in association with particular forest fragments that: (1) had pasture area along at least one edge and (2) were separated from other forest fragments by a distance at least twice that to artificial ponds installed away from the focal forest fragment's edge.

#### *Experiment I: forest fragment proximity effects*

We selected six forest fragments well separated from each other (by 40–215 km) and in two size categories (Fig. 1): (1) three “medium” forest fragments (67, 95 and 108 ha) and (2) three “large” forest fragments

(1,360; 1,656 and 2,189 ha). Associated with each forest fragment we installed a set of 20 artificial ponds, totaling 120 ponds. Ponds were created along four transects 50 m apart and 200 m in length extending perpendicular to a particular fragment's edge, from the fragment's interior into the surrounding matrix of pasturelands (Fig. 1). Each transect consisted of five treatments: ponds installed at the forest edge, in the matrix 50 and 100 m from the forest edge, and in the forest fragment's interior 50 and 100 m from the fragment's edge (Fig. 1). The ponds were hand dug, 1.5 m long, 1.0 m wide and 0.3 m deep. Each pond's bottom was covered with plastic sheeting to provide an impervious substrate on which was placed a small soil layer and leaf litter and then allowed to fill with rainfall. Frog and toad community surveys were conducted between 1,900 and 2,400 h to characterize the number of individuals counted within 2 m of each pond's border and the presence of tadpoles sampled with hand net (3 mm<sup>2</sup> mesh) every time the ponds had water accumulated. Visual and acoustic surveys involved walking the perimeter of each pond upon arrival and recording the number of each species observed or heard calling. When the ponds had no water, their interiors were inspected for hidden individuals. Pool communities were sampled three

**Fig. 1** Location of study area in Brazil. São Paulo State is highlighted showing the locations of the forest fragments (blue circle). Offset: Experimental design (without scale) showing the spatial arrangement of artificial ponds. Experiment I: artificial ponds installed in the edge, 50 and 100 m from the edge toward the matrix and –50 and –100 m from the edge toward the interior of the forest fragments in the rainy season of 2007/2008. Experiment II: artificial ponds installed at the edge, 100 and 200 m of forest fragments in the rainy season 2008/2009



times for five consecutive days each (December 2007–February 2008), totaling 15 days of sampling in each forest remnant.

### Experiment II: fragment size effects

To better evaluate the influence of forest tract size within the range of fragment sizes typical of the region (90% of forest fragments in São Paulo State have areas smaller than 40 ha, Nalon et al. 2008) we performed further sampling in five forest fragments (5, 11, 17.5, 67 and 108 ha). In each forest remnant we installed a set of three artificial ponds, totaling 15 ponds, of dimensions identical to those in “Experiment I” section. The ponds were installed at a given forest’s edge and at 100 and 200 m away within the agricultural matrix (Fig. 1). Each group of ponds was sampled five times for five consecutive days each, during December 2008–March 2009, totaling 25 days of sampling in each forest remnant, using the methods described in “Experiment I” section, except that to verify if frogs and toads were in resident ponds throughout the reproductive season each individual was marked with a cotton string (which would eventually rot off) tied in the inguinal region; capture histories were recorded by individual variation in the number of knots tied in the string.

### Data analyses

To investigate which variables explain the distribution of abundance (number of individuals) and species richness of frogs and toads, we fitted generalized linear mixed models (GLMMs) to the data using the lmer function implemented in the lme4 package (Bates and Maechler 2009) in R 2.12.2 (R Development Core Team 2011); forest fragments (blocks) were considered as random effects and treatment and size of fragments (categorical variables) as fixed effects. For each response variable (number of species and abundance), we used sequential removal of parameters to evaluate the two fixed effects: (1) response variable – distance + size + distance:size + (1|block); (2) response variable – distance + size + (1|block); (3) response variable – distance + (1|block); (4) response variable – size + (1|block) and; (5) response variable – 1(only intercept) + (1|block).

Because the response variables (abundance and species richness) were count data, we started with a

Poisson error distribution and log link function (Zuur et al. 2009). When we detected overdispersion, we corrected the standard errors using a quasi-GLMM model where the variance is given by  $\varphi \times \mu$ , where  $\mu$  is the mean and  $\varphi$  the dispersion parameter (Zuur et al. 2009). Akaike’s information criterion, corrected for small sample sizes ( $AIC_c$ , Burnham and Anderson 1998), was used as the model selection criterion. When overdispersion was detected, quasi-likelihood method (QAICc) was used. Akaike weights ( $wAIC_c$ ) were used to evaluate model-selection uncertainty, which express the weight of evidence favoring that model as the best of all models in the model set (Burnham and Anderson 1998). We also used likelihood ratio tests to evaluate the contribution of each parameter to the model.

## Results

### Experiment I

We recorded 52 individuals of 11 frog and toad species using the artificial ponds (Table 1). *Chiasmocleis albopunctata* was the only species recorded in the larval stage, with tadpoles found in an artificial pond installed 100 m within one of the forest fragments. Two individuals of *Pseudopaludicola* aff. *falcipes* and one of *Leptodactylus labyrinthicus* were recaptured in the same artificial pond installed 50 m far from the edge toward the matrix. Species richness (likelihood ratio test,  $\chi^2 = 13.25$ ,  $df = 4$ ,  $P = 0.01$ ) and abundance ( $\chi^2 = 34.69$ ,  $df = 4$ ,  $P < 0.000$ ) differed among distance treatments, but not in relation to fragment size (species richness,  $\chi^2 = 1.26$ ,  $df = 1$ ,  $P > 0.26$  and abundance,  $\chi^2 = 2.45$ ,  $df = 1$ ,  $P > 0.11$ ). Higher species richness was estimated in ponds installed at (1) the forest edge and 50 m into the pasture than those (2) 50 and 100 m within forest fragments and at 100 m into pasture (Fig. 2). The models explaining the number of species and abundance that included only the distance treatment were best supported (Table 2; Fig. 2).

### Experiment II

We recorded 35 individuals of eight anuran species using the artificial ponds (Table 1). Only *Leptodactylus* gr. *latrans* and *Leptodactylus fuscus* were not

**Table 1** Number of species and abundance of frogs and toads recorded in artificial ponds installed at different distances from forest fragments in the northwestern São Paulo State

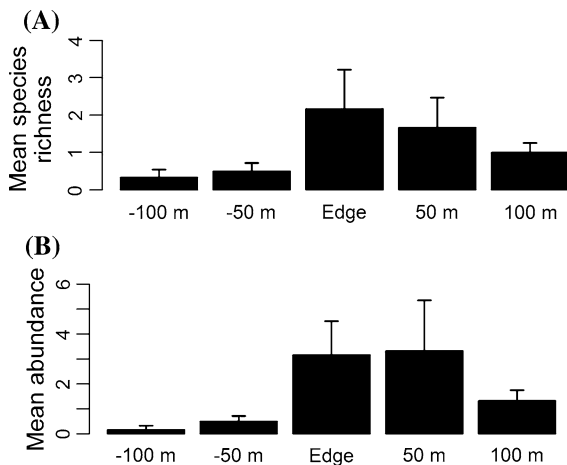
	Experiment I					Experiment II		
	–50	–100	Edge	50	100	Edge	100	200
<i>Chiasmocleis albopunctata</i>		1 <sup>b</sup>	1 <sup>a</sup>			5 <sup>a</sup>		
<i>Dendropsophus nanus</i>				1 <sup>a</sup>				
<i>Dendropsophus minutus</i>						1 <sup>a</sup>		
<i>Eupemphix nattereri</i>			3			3	1	1
<i>Leptodactylus gr. latrans</i>							1	
<i>Leptodactylus fuscus</i>			8	10	5		1	2
<i>Leptodactylus mystacinus</i>	1		1 <sup>a</sup>					
<i>Leptodactylus mystaceus</i>	1		1					
<i>Leptodactylus labyrinthicus</i>				2				
<i>Pseudopaludicola aff. falcipes</i>				4 <sup>a</sup>	1			
<i>Physalaemus cuvieri</i>	1	1	1	1	2	6		
<i>Scinax fuscovarius</i>			1	1		4 <sup>a,c</sup>		
<i>Rhinella schneideri</i>			3		1	10		
Number of species	3	1	8	6	4	6	3	2
Total abundance	3	2	19	19	9	29	3	3

In Experiment I artificial ponds were placed at the forest edge, –50 and –100 m from the edge toward the interior of the forest fragments and 50 and 100 m from the edge toward the matrix. In Experiment II artificial ponds were installed at the edge, 100 and 200 m into the matrix

<sup>a</sup> Recorded based on vocalization

<sup>b</sup> Recorded in the larval stage

<sup>c</sup> Pair recorded mating in the artificial pond



**Fig. 2** **a** Mean abundance of frogs and toads ( $\pm 1$  SE) and **b** mean species richness ( $\pm 1$  SE) recorded in the artificial ponds installed at different distance from six forest fragments (Experiment I). Distances: edge, 50–100 m from the edge toward the matrix (pasture) and –50 and –100 m from the edge toward the interior of the forest fragments

recorded in artificial ponds located at the edge of the forest fragments, whereas at ponds installed at 100 and 200 m of the forest fragments we recorded three and two species, respectively (Table 1). The model containing only the distance treatment was the best supported in explaining species richness (Table 2; Fig. 3), with distance treatments ( $\chi^2 = 8.55$ ,  $df = 2$ ,  $P = 0.01$ ) showing difference among treatments, but not the size of forest fragments ( $\chi^2 = 2.62$ ,  $df = 1$ ,  $P = 0.1$ ). Ponds installed at the forest fragment edge hosted a higher species richness and abundance of frogs and toads than those located 100 and 200 m into pasture (Figs. 3, 4). The model explaining frog and toad abundance that included both distance treatment and size of forest fragments was best supported (Table 2; Fig. 4), with both distance treatments ( $\chi^2 = 36.51$ ,  $df = 2$ ,  $P < 0.000$ ) and size of forest fragments ( $\chi^2 = 8.01$ ,  $df = 1$ ,  $P < 0.004$ ) contributing.

**Table 2** The a priori model set used to examine the relationship within tropical agro-savannah landscapes in southeastern Brazil between abundance and species richness of frogs and toads (response variables) in relation to distance treatment and forest remnant size (explanatory variables) based on generalized linear mixed-effects in two experiments with artificial ponds

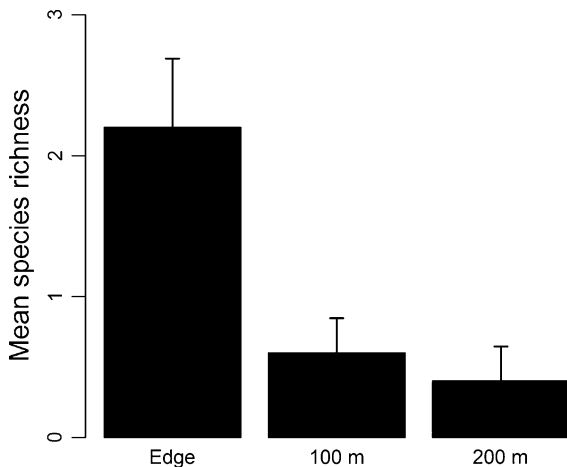
Experiment I	<i>k</i>	$\Delta AIC_c$	$wAIC_c$	LL	Deviance	%DE
Response variable: abundance						
Abundance – distance	7	0	0.74	–27.16	54.33	38.97
Abundance – distance + size	8	2.1	0.26	–25.94	51.88	41.72
Abundance – 1 (only intercept)	3	11.44	0.000	–44.51	89.02	0
Abundance – size	4	12.45	0.000	–43.29	86.57	2.75
Abundance – distance + size + distance $\times$ size	12	13.88	0.000	–20.27	40.53	54.46
Response variable: species richness						
Richness – distance	6	0	0.53	–18.27	36.54	26.61
Richness – 1 (only intercept)	2	1.84	0.21	–24.9	49.8	0
Richness – distance + size	7	2.43	0.16	–17.64	35.28	29.15
Richness – size	3	3.18	0.11	–24.27	48.54	2.53
Richness – distance + size + distance $\times$ size	11	11.41	0.000	–12.66	25.33	49.13
Experiment II	<i>k</i>	$\Delta AIC_c$	$wAIC_c$	LL	Deviance	%DE
Response variable: abundance						
Abundance – distance + size	5	0	0.841	–4.58	9.168	82.92
Abundance – distance	4	3.4	0.157	–8.59	17.19	67.99
Abundance – distance + size + distance $\times$ size	7	13.1	0.001	–4.48	8.973	83.29
Abundance – size	3	28	<0.001	–22.84	45.68	14.93
Abundance – 1 (only intercept)	2	32.9	<0.001	–26.85	53.7	0
Response variable: species richness						
Richness – distance	4	0	0.461	–4.39	8.79	49.3
Richness – 1 (only intercept)	2	1.6	0.212	–8.67	17.34	0
Richness – distance + size	5	2.0	0.166	–3.08	6.16	64.45
Richness – size	3	2.1	0.161	–7.35	14.71	15.15
Richness – distance + size + distance $\times$ size	7	15.3	<0.001	–3.04	6.08	64.89

*k* number of parameters,  $\Delta AIC_c$  difference in Akaike's Information Criterion,  $\Delta QAIc_c$  difference in Quasi-Akaike's Information Criterion,  $wAIC_c$  AICc weight,  $wQAIc_c$  QAICc weight, *LL* negative log-likelihood, and %DE percent deviance explained in the response variable by the model under consideration

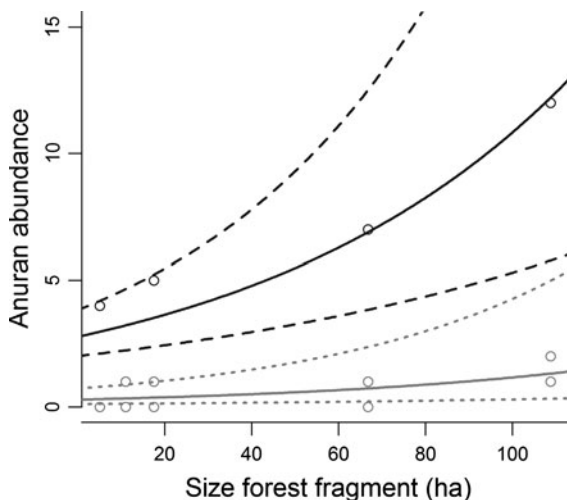
## Discussion

Our results show that breeding areas 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 areas located 100 and 200 m far from forest fragments in our southeastern Brazil study area. Similarly, many temperate-zone focused studies have reported an increase in abundance and species richness of amphibians in breeding areas near forest fragments (e.g., Loman 1988; Laan and Verboom 1990; Findlay and Houlihan 1997; Herrmann et al. 2005). Among the only tropical-

based studies ever conducted on this topic, Gascon et al. (1999) recorded that species richness of frogs and toads in central Amazonia increased after forest fragmentation with some frogs mainly associated with matrix habitats occasionally invaded fragments, which contributed to the general increase in species richness. Similarly, Dixo and Martins (2008) in a study in Brazilian Atlantic Forest recorded two generalist and non-forest species, *Physalaemus cuvieri* and *Leptodactylus ocellatus* (also recorded in the present study) at forest edges. Silva and Rossa-Feres (2011a) in a study in the same region verified that anuran abundance was greater in breeding pools near forest



**Fig. 3** Mean frog and toad species richness ( $\pm 1$  SE) recorded in artificial ponds installed at different distance from five forest fragments (Experiment II). Distances: edge versus 100–200 m from the edge toward the matrix (pasture)



**Fig. 4** Frog and toad abundance recorded by generalized linear mixed model (GLMM) in artificial ponds installed at different distance from five forest fragments (Experiment II). The lines represent the GLMM fit to the data with 95% confidence interval. Black circles = abundance recorded in artificial ponds installed at edge of forest fragments; Gray circle = abundance recorded in artificial ponds installed at 100 and 200 m from the edge toward the matrix (pasture)

fragments (far as 50 m) than breeding pools farther from forest fragments.

Most frog and toad species recorded in the artificial ponds are generalist species associated with more than one biome in Brazil (IUCN et al. 2006). According to Santos et al. (2009), the climate of the region, which

has a pronounced dry season, favors species with flexible reproductive modes adapted to desiccation resistance (Santos et al. 2009). Despite our focal species suite being generalists, our results nevertheless showed that greater abundance and species richness of frogs and toads at the forest edge is not a simple consequence of augmenting species associated with matrix habitat with those from the forest interior, as in most studies. These results stress that the proximity between forest fragments (shelter and foraging areas) and breeding habitats in this seasonal dry region is the factor responsible for this pattern.

Becker et al. (2010) demonstrated that even species that usually avoid open habitats are forced to cross inhospitable matrix habitats when breeding sites are not present within forest fragments. Accordingly “habitat split” is a widespread phenomenon in fragmented landscapes increasing the chance of extinction for species with aquatic larvae. However, in contrast to the frog and toad species recorded in Brazilian Atlantic Forest by Becker et al. (2010), those recorded in this study do not avoid matrix habitats. The generalist species in this study used both pasture and the forest habitat and are obligated to cross open habitats because pasture, despite its inherent risks when traversing it, provide high quality habitat for anuran reproduction in the form of artificial water bodies created by agriculturalists for a variety of reasons including as a water source for cattle (Urbina-Cardona et al. 2006). Thus, proximity to forest fragments that can provide refuges from heat and water stress likely is the main driver influencing the ability of frogs and toads to establish and sustain breeding populations in open land ponds. These results stress that forest fragments despite their greatly reduced occurrence in tropical landscapes heavily transformed by agriculture nevertheless play an important role in sustaining frogs and toads in southeast Brazil.

Forest size was an important factor in this study affecting frog and toad abundance but not overall species richness. It is widely recognized that large fragments are essential to some anurans dependent on certain microclimate conditions to their reproduction or physiology (Pearman 1997; Vallan 2000; Haddad and Prado 2005; Cushman 2006). So-called “edge effects” in small fragments are more severe for air temperature, air moisture, soil moisture and light intensity showing higher variation when compared

with large forest fragments (Laurence 1991; Murcia 1995). Therefore, because frog and toad species associated with open lands likely use the forest fragments for shelter and foraging (Silva and Rossa-Feres 2007) we emphasize the importance of conservation of forest fragments of adequate size in agricultural areas. Notably, in fragments of Brazilian Atlantic Rainforest, Dixo et al. (2009) reported that genetic diversity in *Rhinella ornata* populations, a species with relatively high dispersal capacities, was lowest in the smallest fragments (1–5.5 ha), likely due to decreases in population sizes. These studies together suggest that preservation of forest fragments larger than 70 ha in agricultural areas will harbor a higher number of individuals than smaller ones and consequently contribute to maintenance of more viable frog and toad populations.

Although, artificial ponds permitted better-controlled experiments, they had two limitations. The first is that artificial ponds did not differ in vertical heterogeneity. Therefore, some hylid species that vocalize perched in the vegetation could not be recorded in these ponds because of the absence of their calling and/or oviposition sites. Second, the small size of the ponds did not allow the ponds to retain water for a long period of time. The record of calling activity of some species in the artificial ponds occurred only in rainy days or just after the rains, suggesting that the unpredictability of the water retained in the artificial ponds was a limiting factor for occupancy and reproduction by anurans. From the 13 anuran species recorded in the artificial ponds six were recorded calling and one species (*Scinax fuscovarius*) was recorded in amplexus. We suspect the general lack of tadpoles was consequence of short time that artificial ponds retained water. Despite these limitations, we believe that artificial ponds are comparable with constructed temporary ponds (used by livestock as a drinking water source) which are used as breeding habitats by most anuran species of the region because our results were similar to those reported by Silva and Rossa-Feres (2011a) that focused on natural water bodies in the same region.

## Conclusion

Our results emphasize the value of conserving forest fragments to protect amphibian diversity and

abundance in tropical agro-savannah landscapes, even for species typically identified primarily as breeders in ponds of open environments. More specifically, our results identify the importance of proximity between aquatic and terrestrial habitats in determining local patterns of abundance and species richness. Preservation of forest fragments larger than 70 ha in agricultural areas will also generally enhance local population sizes and thereby overall population viability. Furthermore, artificial ponds can be a useful despite their mentioned limitations for determining how spatial factors affect the distribution pattern of frogs and toads.

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