ZOOLOGIA 28 (5): 610–618, October, 2011
doi: 10.1590/S1984-46702011000500009

Environmental heterogeneity: Anuran diversity in homogeneous environments

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ABSTRACT. The northwestern region of São Paulo was extensively deforested during the agricultural expansion in the last century and only small fragments of the original vegetation cover remained. In this study, we investigated how habitat features influence the composition, richness, and diversity of anurans in environments homogenized by agricultural activities. We sampled monthly six breeding ponds located in pasture areas during twelve months. We recorded ten environmental descriptors for each breeding pond. We found 18 anuran species. The breeding ponds were structurally similar, but species composition differed among them. The environmental descriptors influence varies for each species, as demonstrated by the different associations between species and environmental descriptors shown in the Canonical Correspondence Analysis (CCA). Seven of the ten environmental descriptors explained 67% of the species richness, showing that environmental characteristics influenced the occurrence of the different species. There is no such data set for the region and also for most Brazilian regions, despite its importance in guiding species-oriented conservation actions.

KEY WORDS. Amphibia; community ecology; environmental indicators; habitat use, beta diversity.

A fundamental area of community ecology is the characterization and explanation of how a set of species manages to coexist in certain environmental situations (Lewinsohn 1990). This in turn may shed light on which forces are involved in the assembly of biological communities (Brooks & McLennan 1993). Environmental heterogeneity has been recognized as one of the explanations for variation in species diversity (Huston 1994, Fraser 1998, Moreno-Rueda & Pizarro 2007, Vasconcelos & Rossa-Feres 2008, Vasconcelos *et al.* 2009).

Amphibians are highly dependent on environmental quality (Duellman & Trueb 1994, Marco 1993) and also strongly influenced by abiotic factors, such as rainfall, temperature, and vegetation (Gascon 1991, Eterovick 2003, Parris 2004, Werner *et al.* 2007). Furthermore, several studies have shown that complex environments that provide more microhabitats harbor a higher number of species than homogeneous environments (e.g., Brandão & Araújo 1998, Haddad 1998, Bernarde & Kokubum 1999, Cunha & Rego 2005, Haddad & Prado 2005, Afonso & Eterovick 2007, Bastazini *et al.* 2007, Vasconcelos *et al.* 2009).

In addition to environmental heterogeneity (Rossa-Feres & Jim 1996, Pombal Jr 1997, Bernarde & Kokubum 1999, Vasconcelos & Rossa-Feres 2005, Vasconcelos *et al.* 2009), the behavioral plasticity of some species (Cardoso *et al.* 1989, Vasconcelos & Rossa-Feres 2008) is also an important parameter in the diversity and coexistence of anurans. However, different studies have found varying degrees of segregation between anuran species in the same community, ranging from complete segregation to complete overlap (Heyer *et al.* 1990, Rossa-Feres & Jim 1996, 2001, Bertoluci 1998, Bertoluci & Rodrigues 2002, Vasconcelos & Rossa-Feres 2005). To understand this ecological issue, studies should be conducted at several spatial scales, ranging from geographical scales (Vasconcelos *et al.* 2009) until the recognition of which attributes at a local scale, restricted to the characteristics of water bodies, could be good predictors of species richness and of the presence of a particular species (Hazell *et al.* 2001).

In this paper, we evaluated the influence of environmental heterogeneity of breeding ponds on anuran richness and composition in a landscape homogenized by agricultural activities and also which environmental descriptors favor the occurrence of individual anuran species.

MATERIAL AND METHODS

This study was conducted in Icém (20°20'31"S, 49°11' 42"W, 449 m a.s.l.), in the northwest of the São Paulo State, Brazil. According to the Regional Agricultural Division (Divisão Regional Agrícola, DIRA) of São José do Rio Preto, the climate of the region is hot, with humid summers and dry winters. The rainy season's start (September-March) varies from year to year (Rossa-Feres & Jim 2001), and it concentrates 85% of the annual rainfall; the cold, dry season (April-August) receives only 15% of the annual rainfall, which range from 1,100 to 1,250 mm (± 250 mm) (Barcha & Arid 1971). The native vegetation consists of Semi-deciduous Forest and Cerrado patches (Ab'Saber 2003) heavily devastated by agriculture, due to its fertile soil. Currently, only small, scattered fragments of this fertile land remain (São Paulo 2000).

We sampled six breeding ponds in pasture areas with different physiognomic and structural characteristics: four permanent dams (PD1-PD4), one permanent (PM) and one temporary marsh (TM), apart 25-4000 m from each other, resulting in a total sampled area of 7.5 km^2 (Fig. 1). We determined the environmental descriptors for each breeding pond during the rainy season, in which more than 99% of regional anuran fauna are found (Vasconcelos & Rossa-Feres 2005, Santos *et al.* 2007). Specifically, we recorded the following environmental descriptors as categorical variables: a) Size of the pond: 1 = small (up to 300 m^2), 2 = medium (301-600 m^2), and 3 = large (over 601 m^2); b) Number of margin slopes: flat, slope and gully – 1 = only one type of margin, 2 = two types of margins, 3 = three types of margins; c) Number of margin types: dry with vegetation, dry without vegetation, wetland with vegetation, wetland without vegetation – 1 = only one type of margin, 2 = two types of margins, 3 = three types of margins, and 4 = four types of margins; d) Predominant height of the marginal vegetation: 1 = 00-30 cm, 2 = 31-60 cm, 3 = 61-90 cm, and 4 = 91-120 cm; e) Percentage of pond surface covered with vegetation: 1 = 0%, 2 = 25%, 3 = 50%, 4 = 75%, or 5 = 100%; f) Number of plant clusters inside the pond: 1 = one cluster, 2 = 2-4 clusters, and 3 = 5-7 clusters; g) Number of vegetation types inside the pond: (ShV) shrubby vegetation, (ArV) arboreal vegetation, (M) macrophytes, (UHV) upright herbaceous vegetation, (SHV) small herbaceous vegetation, (NS) nude soil – 1 = 1 or 2 types of vegetation, 2 = 3 or 4 different vegetation, 3 = 4 to 6 types of vegetation; h) Number of marginal vegetation types: (ShV) shrubby vegetation, (ArV) arboreal vegetation, (M) macrophytes, (UHV) upright herbaceous vegetation, (SHV) small herbaceous vegetation, (NS) nude soil – 1 = 1 or 2 types of vegetation, 2 = 3 or 4 different vegetation, 3 = 4 or 6 types of vegetation; i) Depth: 1 = shallow (30 cm), 2 = medium (31-60 cm), and 3 = deep (over 61 cm); j) Hydroperiod: 1 = permanent and 2 = temporary.

These environmental descriptors were considered in several ways, depending upon the type and purpose of the analysis applied. We applied the Shannon-Wiener index to the two data sets: quantitative data to verify the influence of pond heterogeneity on species composition and categories of environmental descriptors to verify the influence of pond heterogeneity on richness and diversity of communities (Tab. I, Fig. 1).

We sampled each breeding pond every two weeks during the rainy season (between September 2004 and May 2005) and monthly during the dry season (between June and August 2005), between 5 pm and 12 am. We randomized the sequence of sampling for each breeding pond. We estimated the abundance of each species using the technique of surveys at breeding sites (Scott & Woodward 1994), by counting all males in calling activity around the perimeter of each pond (see Silva *et al.* 2010).

We estimated species richness using species accumulation curve and two richness estimators: Bootstrap and ACE (Abundance-based Coverage Estimator), with 500 randomizations. Calculations were performed in EstimateS v.7.0 (Colwell 2004). The Bootstrap is an incidence-based estimator, whereas the ACE is a quantitative method based on the proportion of rare species in the sample (Cullen Jr *et al.* 2003, Krebs 1999).

We used the Shannon-Wiener index (Krebs 1999) to determine species diversity in each breeding pond and the Pielou index to quantify abundance evenness (Zar 1999, Morin 1999) using BioDiversity Pro 2.0 (McAlecee *et al.* 1997). For these analyses, we considered species abundance as the maximum abundance of males of each species in all habitats (Vasconcelos & Rossa-Feres 2005). This procedure was adopted to avoid an overestimation of species abundance due to repeated counting of individuals, which occurs when one considers the total abundance of species as the sum of the abundance of repeated sampling over a season, and also to avoid under-estimation from using the average abundance of successive samples (Vasconcelos & Rossa-Feres 2005).

To test if species composition and pond heterogeneity corresponded, we applied a hierarchical cluster analysis with UPGMA as clustering method to the similarity matrix obtained by the Bray-Curtis index for the matrix containing the quantitative data of the environmental descriptors (Krebs 1999). Group stability was assessed by bootstrap analysis with 1,000 replicates (Akins *et al.* 2005). The dendrogram was considered representative of the original data matrix when the cophenetic correlation coefficient (r) was equal to or greater than 0.8.

We used the inverse of the Jaccard similarity index (1-Cj; Krebs 1999) to evaluate differences in species composition among ponds. We considered values of 1-Cj $\geqslant$ 0.50 as indicative of high species turnover (Tuomisto 2010) between environments, i.e., high β diversity. We used a partial Mantel test (Smouse *et al.* 1986) to evaluate the influence of structural heterogeneity of ponds on species composition after removing the effect of geographic distance (km) between ponds. For this analysis the environmental heterogeneity was obtained by applying Shannon-Wiener index to quantitative data of the environmental descriptors of each pond. The method consists of comparing two matrices (A and B), after removing the effect of a third (C), using a correlation of C on A and B, and obtaining a residual matrix that represents the variation of matrices A and B, not explained by matrix C (Smouse *et al.* 1986). In this way, the two residual matrices can be compared normally. The partial Mantel test was performed in NTSYS 2.10S software

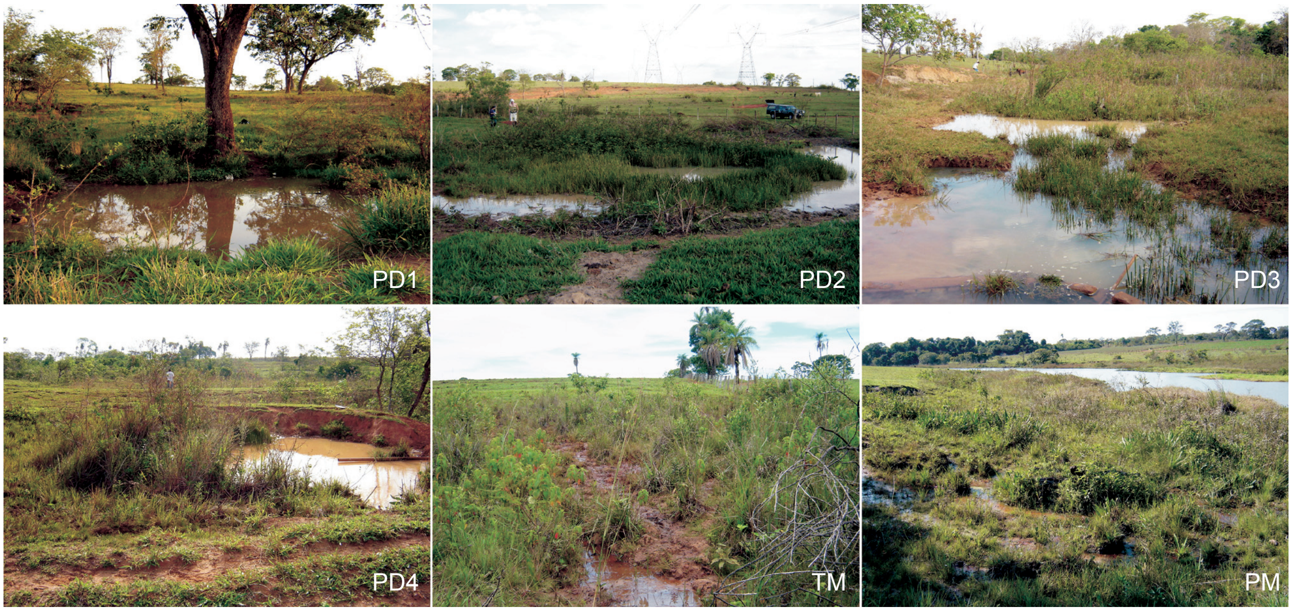

Figure 1. Breeding ponds sampled in Icém, São Paulo. (PD) Permanent dams, (TM) temporary marsh, (PM) permanent marsh.

Table I. Environmental descriptors of breeding ponds studied: (PD) permanent dams, (TM) temporary marsh, and (PM) permanent marsh. (BD) Breeding pond hydroperiod, (TM) type of margin, (MP) margin slope, (PC) percentage of vegetation on water surface, (NC) number of plant clusters, (PH) predominant height of the vegetation, (VI) vegetation, (MV) marginal vegetation, SB) size, and DB) depth. Types of margins: (DNV) dry without vegetation, (DWV) dry with vegetation, (FNV) flooded without vegetation, (FWV) flooded with vegetation. Type of margin slope: (Fl) flat, (Sl) slope, (Gu) gully. Vegetation: (ShV) shrubby vegetation, (ArV) arboreal vegetation, (M) macrophytes, (UHV) upright herbaceous vegetation, (SHV) small herbaceous vegetation, (NS) nude soil. Number of vegetation clusters within the breeding pond: group 1 = 1 cluster, 2 = 2-4 clusters, 3 = more than five clusters.

Breeding ponds	Size (m^2)	TM	MP	DB (cm)	VI	MV	PC	PH (cm)	NC
PD1	124	DNV, DWV, FNV,	Fl, Sl, Gu	0.9	SHV, ShV, M, UHV	SHV, ShV, UHV, ArV	50	31 a 60	2
PD2	324	DNV, DWV, FNV, FWV	Fl, Sl, Gu	0.9	UHV, ShV, M	UHV, SHV, ShV	75	31 a 60	1
PD3	2850	DNV, DWV, FWV,	Fl, Gu	0.9	UHV, M, ShV	SHV, UHV, ShV	75	61 a 90	2
PD4	130	DNV, DWV, FNV, FWV	Fl, Gu	0.8	ShV, UHV	SHV, ArV	50	1 a 30	1
PM	288	DWV, FWV	Fl, Sl, Gu	0.3	SHV, UHV	SHV, ArV	100	1 a 30	3
TM	210	DWV, FWV	Fl, Gu	0.2	UHV, SHV, NS	ArV, SHV, UHV	50	1 a 30	2

(Rohlf 2000). Statistical significance was determined using Monte Carlo randomization (Smouse *et al.* 1986) with 5,000 permutations. Additionally, we used the Spearman correlation (r_S, Zar 1999) to test for the influence of the environmental heterogeneity on species richness, diversity, and evenness.

We used Canonical Correspondence Analysis (CCA) to test the influence of environmental descriptors on the occurrence and spatial distribution of species. CCA allows us to simultaneously represent the spatial ordering of samples, species and environmental variables, which indicates how the set of species optima varies with environment (Ter Braak & Smilauer 2002). To produce a CCA, a matrix containing the environmental descriptors and the abundance of species in each breeding pond was built. The partial Mantel test, similarity, cluster analyses, and CCA were performed with PAST v.2.0 (Hammer *et al.* 2001).

RESULTS

We recorded 18 anuran species belonging to nine genera and five families (Tab. II). The species accumulation curve, built on the basis of species abundance, tended to reach an asymptote (Fig. 2). However, the two richness estimators indicated that two more species could be found in the sampled area (bootstrap = 20.15 ± 0 species; ACE = 18 ± 2 species).

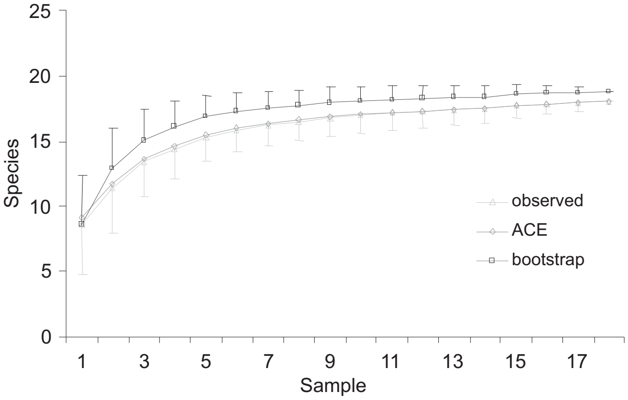

Figure 2. Bootstrap and ACE estimators for 18 sampling periods between September 2004 and August 2005 in Icém, São Paulo. Curves were generated with 500 randomizations. Bars represent the standard deviation.

We recorded the highest species richness at PD2 (13 species), and the highest total abundance in PD3 (106 individuals), but the PD2 and PD1 had the highest values of species diversity (H' = 2.34) and evenness (Pielou's e = 0.96), respectively (Tab. II). *Leptodactylus furnarius* Sazima & Bokermann, 1978, *Physalaemus centralis* Bokermann, 1962, *Scinax fuscovarius* (Lutz, 1925), *Scinax similis* (Cochran, 1952), *Scinax fuscomarginatus* (Lutz, 1925), and *Rhinella schneideri* (Werner, 1894) (33% of the total recorded species) occurred in only one breeding pond. Only *Pseudopaludicola* aff. *falcipes* and *Hypsiboas albopunctatus* (Spix, 1824), which represent 11% of the total species recorded, occurred in all ponds sampled (Tab. II).

With the exception of the permanent marsh (PM), the remaining ponds are similar in structure (minimum similarity = 76%, bootstrap = 28%, Fig. 3). However, β diversity was high (1-Cj > 0.5) for 53% of the 15 combinations of sites (Tab. III). In order to identify the causes of this variation in species composition, we tested for the influence of environmental descriptors of each pond on species composition and abundance. Environmental heterogeneity influenced the composition and abundance of species ($r_M = -0.56$, $p = 0.04$), as well as the richness ($r_S = 0.96$, $p = 0.002$) and diversity of species in ponds ($r_S = 0.97$, $p = 0.01$). Only species evenness was not correlated with environmental heterogeneity ($r_S = 0.48$, $p = 0.34$).

We found some patterns in species association to environmental variables. *Leptodactylus podicipinus* (Cope, 1862), *Leptodactylus fuscus* (Schneider, 1799), *Leptodactylus labyrinthicus*

Table II. Abundance, richness, evenness, diversity, and niche width (Levins index) of species recorded in the six breeding ponds sampled between September 2004 and August 2005 in Icém, São Paulo.

Species	PD1	PD2	PD3	PD4	PM	TM	Niche width
Leptodactylus fuscus (Schneider, 1799)	5	7	1	0	2	0	0.37
L. labyrinthicus (Spix, 1824)	5	2	0	0	0	0	0.14
L. podicipinus (Cope, 1862)	4	5	5	2	5	0	0.73
L. furnarius Sazima & Bokermann, 1978	0	0	0	0	0	7	0
Pseudopaludicola mystacalis (Cope, 1887)	0	2	0	3	0	6	0.29
P. aff. *falcipes* (Hensel, 1867)	6	10	15	4	10	8	0.84
Physalaemus cuvieri Fitzinger, 1826	3	8	15	8	4	0	0.56
P. centralis Bokermann, 1962	0	9	0	0	0	0	0
Eupemphix nattereri Steindachner, 1863	6	0	2	0	3	0	0.29
Scinax fuscovarius (Lutz, 1925)	4	0	0	0	0	0	0
S. similis (Cochran, 1952)	0	4	0	0	0	0	0
S. fuscomarginatus (Lutz, 1925)	0	15	0	0	0	0	0
Dendropsophus nanus (Boulenger, 1889)	1	20	40	0	10	0	0.27
D. elianeae (Napoli and Caramaschi, 2000)	5	12	7	2	0	4	0.56
D. minutus (Peters, 1872)	0	0	10	40	0	2	0.12
Hypsiboas albopunctatus (Spix, 1824)	2	2	10	5	4	2	0.62
Elachistocleis bicolor (Guérin-Méneville, 1838)	0	4	1	0	7	2	0.36
Rhinella schneideri (Werner, 1894)	3	0	0	0	0	0	0
Abundance	44	100	106	64	45	31	–
Richness	11	13	10	7	8	7	–
Eveness	0.96	0.91	0.80	0.66	0.94	0.92	–
Diversity	2.31	2.34	1.85	1.29	1.95	1.80	–

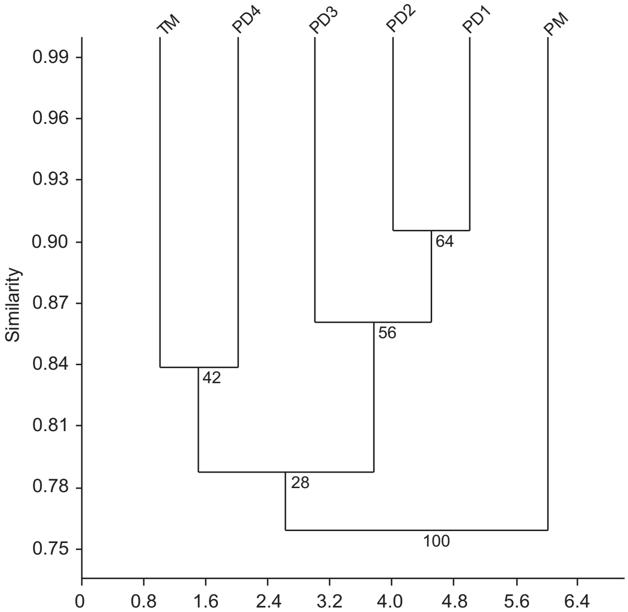

Figure 3. Similarity between breeding ponds in relation to environmental descriptors (Bray-Curtis index) determined between September 2004 and August 2005 in Icém, São Paulo.

Table III. Beta diversity between the six breeding ponds sampled in Icém, São Paulo, Brazil, between September 2004 and August 2005. The highest beta diversity values recorded are indicated in bold.

	PD1	PD2	PD3	PD4	TM	PM
PD1	1	0.47	0.33	**0.58**	**0.78**	0.36
PD2	+	1	0.47	**0.57**	**0.67**	**0.50**
PD3	–	+	1	0.45	**0.58**	0.20
PD4	–	–	+	1	0.44	**0.64**
TM	–	–	–	+	1	**0.75**
PM	–	–	–	–	+	1

(Spix, 1824), *Eupemphix nattereri* Steindachner, 1863, *S. fuscovarius*, and *R. schneideri* were associated with ponds with a great variety of margin slopes, whereas *Elachistocleis bicolor* (Guérin-Méneville, 1838) was associated with great number of vegetation clusters inside ponds. *Pseudopaludicola* aff. *falcipes* was associated with a large amount of marginal herbaceous vegetation. *Leptodactylus furnarius* occurred only in temporary ponds, and *Physalaemus cuvieri* Fitzinger, 1826 was more abundant in large ponds; *Dendropsophus nanus* (Boulenger, 1889) was associated with pond depth, and *H. albopunctatus* was associated with high vegetation bulk and height within ponds (Fig. 4). Thus, 70% of the quantified environmental descriptors explained the occurrence of 67% of species.

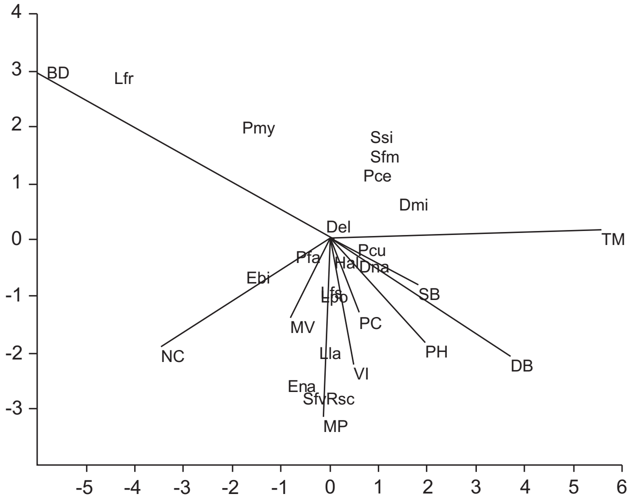

Figure 4. Canonical Correspondence Analysis (CCA) for species composition in the six breeding ponds sampled from September 2004 to August 2005 in Icém, São Paulo. Arrows represent the environmental descriptors: (WD) pond hydroperiod, (TM) type of margin, (MP) margin slope, (PC) percentage of vegetation on water surface, (NC) number of plant clusters, (PH) predominant height of the vegetation, (VI) vegetation, MV) marginal vegetation, (SW) size, and (DW) depth. The species are represented by abbreviations: (Lfs) *Leptodactylus fuscus*, (Lla) *L. labyrinthicus*, (Lpo) *L. podicipinus*, (Lfr) *L. furnarius*, (Pmy) *Pseudopaludicola mystacalis*, (Pfa) *P.* aff. *falcipes*, (Pcu) *Physalaemus cuvieri*, (Pce) *P. centralis*, (Ena) *Eupemphix nattereri*, (Sfv) *Scinax fuscovarius*, (Ssi) *S. similis*, (Sfm) *S. fuscomarginatus*, (Dna) *Dendropsophus nanus*, Del) *D. elianeae*, (Dmi) *D. minutus*, (Hal) *Hypsiboas albopunctatus*, (Ebi) *Elachistocleis bicolor*, and (Rsc) *Rhinella schneideri*.

DISCUSSION

We cannot rule out the possibility of an increase in the number of species in the sampled area, because we recorded only 47% of the 38 species known to inhabit the northwestern region of São Paulo (Rossa-Feres & Jim 2001, Vasconcelos & Rossa-Feres 2005, Prado *et al.* 2008, Silva 2009, Silva *et al.* 2010, Provete *et al.* 2011). Although the great majority of these species are generalists with broad areas of occurrence (Santos *et al.* 2007), some are explosive breeders (Nomura 2005, Santos *et al.* 2007) and were found during short periods of the year. Species with this reproductive pattern may not be recorded when the samplings are made once a month. Hylids was the most speciose group. This pattern is, consistent with different Brazilian biomes, such as the Atlantic and the Semi-deciduous Forests (e.g., Haddad & Sazima 1992, Brandão & Araújo 1998, Bernarde & Machado 2001, Pombal Jr & Gordo 2004, Conte & Machado 2005).

We found more terrestrial (12 species from the families Leiuperidae, Leptodactylidae, Bufonidae, and Microhylidae) than arboreal species (six species of Hylidae). Besides biogeographic processes, the higher richness of terrestrial species may be related to the low environmental heterogeneity of the ponds sampled, which are located in a pasture matrix with grasses as the main marginal vegetation type (Cardoso *et al.* 1989, Rossa-Feres & Jim 2001, Santos & Rossa-Feres 2007, Vasconcelos & Rossa-Feres 2008, Vasconcelos *et al.* 2009).

Species diversity has been measured by various indices (Magurran 1988) that integrate species richness and evenness (Krebs 1999). Comparative studies are scarce, complicating the interpretation of results obtained with the application of these indices. Therefore, the two components of diversity have been considered independently instead of using diversity indices (Jost 2007). However, in this study, the diversity index reflected the environmental heterogeneity. The species richness and diversity were directly proportional to the environmental heterogeneity of the ponds sampled. This relationship probably reflects the decrease in the number of microhabitats, which reduces the possibility of spatial partitioning (McArthur & Levins 1967, Cardoso *et al.* 1989). The evenness was not affected by the environmental heterogeneity of breeding ponds. Because evenness is a measure of the degree of homogeneity in the distribution of species abundance in a community, a high value of evenness can be found in samples with either high or low species abundance. The low carrying capacity of a habitat may limit both the number of species that occupy an environment as well as species abundance (Cardoso *et al.* 1989, Gascon 1991, Huston 1994, Pombal Jr 1997, Brandão & Araújo 1998, Eterovick 2003, Vasconcelos & Rossa-Feres 2008, Vasconcelos *et al.* 2009). This explains how one homogeneous pond had similar evenness values to heterogeneous ponds, since the few species that occurred in that breeding pond presented low abundance.

The relationship between pond characteristics and their use by amphibians has a long history of research (e.g., Cooke & Frazer 1976, de Fonseca & Jocqué 1982). The high species richness recorded in several Brazilian regions has commonly been attributed to high habitat heterogeneity (Cardoso *et al.* 1989, Pombal Jr 1997, Arzabe *et al.* 1998, Arzabe 1999, Bernarde & Kokubum 1999). Species segregation in communities can occur as a result of vegetation structure (Parris & McCarthy 1999, Hazell *et al.* 2001, Parris 2004, Afonso & Eterovick 2007, Bastazini *et al.* 2007, Vasconcelos & Rossa-Feres 2008, Vasconcelos *et al.* 2009), hydroperiod (Parris & McCarthy 1999, Babbitt 2005, Burne & Griffin 2005, Werner *et al.* 2007, Vasconcelos *et al.* 2009), and pond size (Ricklefs & Lovette 1999, Babbitt 2005, Burne & Griffin 2005, Werner *et al.* 2007, Santos *et al.* 2007, Pardini *et al.* 2010), among other factors, such as environmental heterogeneity and human population influence (Rossa-Feres & Jim 2001, Moreno-Rueda & Pizarro 2007). More recent approaches can detect which environmental descriptors have greater influence on species composition (e.g., Parris 2004, Afonso & Eterovick 2007, Bastazini *et al.* 2007, Keller *et al.* 2009, Vasconcelos *et al.* 2009). However, there is no consensus regarding the influence of different descriptors. In this study, habitat use was evaluated in breeding ponds with the same general structure (lentic ponds in pasture areas). But despite this condition, species composition differed among them, having been influenced by the degree of pond heterogeneity. This result is corroborated by CCA analysis, which allowed the detection of different associations between species and environmental descriptors, indicating that the influence of each descriptor was different for each species of the communities studied. The margin slope types influenced the occurrence of most species (33% of recorded species). However, seven out of the 13 species associated with some environmental descriptor were unique associations. This result is consistent with the conclusions of Vasconcelos *et al.* (2009), who suggested that the influence of a single environmental descriptor might differ in different anuran communities.

Ernst & Rödel (2006) also observed responses to certain habitat characteristics, such as the presence or absence of specific breeding sites and tree size classes in forest environments. Other studies also indicate that specific differences for each species should not be neglected and could dramatically alter the analysis of anuran species composition in primary and secondary forests (Ernst & Rödel 2008).

Our results suggest that evaluating the importance of habitat type only by species richness does not provide all the necessary information to support species management and conservation plans, because the occurrence of a particular species or guild of species may vary due to small differences in certain habitat features (Hazell *et al.* 2001, 2004).

In the sampled area, heterogeneous ponds supported a higher species richness and diversity, showing that environmental heterogeneity analyses provide valuable information about processes that regulate species richness and composition. Furthermore, the detection of environmental descriptors that favor the occurrence of each one of the species in a community is an important step for understanding the reproductive biology of species, to detect processes involved in community assembly, and to support species-oriented conservation and management.

ACKNOWLEDGMENTS

The authors thank Fausto Nomura, Fernando R. Silva, Michel Varajão Garey, Carolina P. Candeira, and Natacha Y. N. Dias for help in the fieldwork. We also thank Mr. Toninho Viana and Mr. Eduardo Torres Viana for allowing access to the study area and for their hospitality. Diogo B. Provete reviewed the English language. DCRF is a CNPq fellow.

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Submitted: 09.IX.2010; Accepted: 29.VI.2011.
Editorial responsibility: Mauricio O. Moura