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The Role of Environmental Heterogeneity in Maintenance of Anuran Amphibian Diversity of the Brazilian Mesophytic Semideciduous Forest

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1. Introduction

Since the 1950s, most ecologists have assumed that animal communities are not simply random assemblages of species (Wells, 2007). Therefore, deterministic factors were pointed out as being responsible for the variation in species diversity and composition along environmental and/or spatio-temporal gradients (Chase & Leibold, 2003). However, according to the recent Hubbell's Neutral Theory, the structure of assemblages (such as diversity and species composition) results from stochastic processes (i.e. ecological drift) that are not influenced by species traits and/or environmental conditions (see details in Tilman, 2004 and Chase, 2007). Therefore the Neutral Theory predicts that species abundance results solely from structured random walks, leaving unexplained the correlations between species traits and their abundances within habitats and/or along environmental gradients (see references in Tilman, 2004).

Some studies highlighted that Neotropical assemblages show little or no structure (Eterovick & Barros, 2003, Afonso & Eterovick, 2007 for anurans and França & Araújo, 2007 for snakes), corroborating the Neutral Theory. On the other hand, partitioning of resources has been historically stressed in terms of both space and time for anuran assemblages (Crump, 1971), where a temporal axis has been considered the first dimension partitioned in the larval phase, and space in adult phase (Toft, 1985). Several studies showed that similar habitats within relatively close distance often have slightly different amphibian assemblages since some species live in a variety of habitats, while others can have more specialized habitat requirements (Snodgrass et al., 2000; Wells, 2007). Therefore, most anuran assemblages appear to be structured since differences in environmental conditions from site to site have explained differences in assemblage features such as richness and abundance of species (Toft, 1982). In addition, other factors such as biological interactions (e.g., predation and competition) and phylogenetic constraints are also considered important to explain structural patterns of assemblages (Zimmerman & Simberlof, 1996; Eterovick & Sazima, 2000; Eason Jr. & Fauth, 2001; Werner et al., 2007).

According to Paton & Crouch (2002) and Bosch & Martínez-Solano (2003), local studies on breeding site preferences of amphibians can provide more accurate information for management purposes than studies on a wider scale, which can be affected by regional variations. In fact, spatial segregation in breeding site occupancy has been recorded for adult and/or larval assemblages of anurans on a local scale (Collins & Wilbur, 1979; Gascon, 1991; Santos et al., 2007; Both et al., 2009) but unfortunately, few studies have applied specific approaches to confirm assemblage structures (see Both et al., 2010; Vasconcelos et al., 2011 for recent examples). Thus, studies on the spatial pattern of assemblages are urgently required to delineate conservation strategies for anurans in ecosystems under strong anthropogenic pressure such as the Mesophytic Semideciduous Forest (MSF), the most fragmented and threatened ecosystem of the Brazilian Atlantic Domain (Viana & Tabanez, 1996). This kind of forest was almost totally devastated because of their soil fertility, smooth relief and high availability of valuable hardwood and because of unscrupulous political interests (Murphy & Lugo, 1986; Prado & Gibbs, 1993; Dean, 1998). Besides, the Semideciduous Forests have been historically neglected as areas for conservation unit creation because of their low level of endemism when compared with the humid forests (Jansen, 1997; Prado, 2000; Pennington et al., 2006).

In the present study, we employed tests of null hypotheses to assess whether patterns of spatial distribution of anuran assemblages differ from a random distribution among aquatic breeding sites monitored at Morro do Diabo State Park (MDSP), one of the four largest remnants of MSF in Brazil (Durigan & Franco, 2006). We also verified the existence of indicator anuran species of environmental heterogeneity on a local scale.

2. Material and methods

2.1 Study area and sampling procedures

We carried out this study in MDSP, a remnant of seasonally dry tropical forest with approximately 33,845 ha in area, located in southeastern Brazil (22°27'--22°40'S, 52°10'--52°22'W), where the altitude ranges from 260 to 599.50 m a.s.l.) (Fig. 1). MDSP is covered by a mosaic of Mesophytic Semideciduous Forest in different stages of regeneration, some small patches of Cerrado *sensu stricto* (savanna-like vegetation), and transitional forests (Durigan & Franco, 2006). The climate is characterized as subtropical with dry winters and wet summers (Cwa type of Köppen's classification) (Leite, 1998), and historical records indicate a mean annual temperature of 22 °C and annual rainfall ranging from 1,100 to 1,300 mm (Faria, 2006).

We monthly monitored (from September 2005 to March 2007) six anuran breeding sites in MDSP: two permanent streams (PS1 and PS2; sections of 500 m in length), two permanent dams (PD1 and PD2), and two temporary ponds (TP1 and TP2; see a complete characterization in Table 1). Physicochemical water measurements were collected and based on a mean of three samples, using a Hach 2100P Turbidimeter (for turbidity) and an YSI 556 Handheld Multiparameter (for the remaining variables).

Permanent dams were located within the borders of forests and presented great depth, low canopy cover, and a bed composed of clay and organic deposits. Dam waters showed low electric conductivity, intermediate oxygenation, and high richness in potential aquatic predators (insects, crustaceans, and fish) (Table 1).

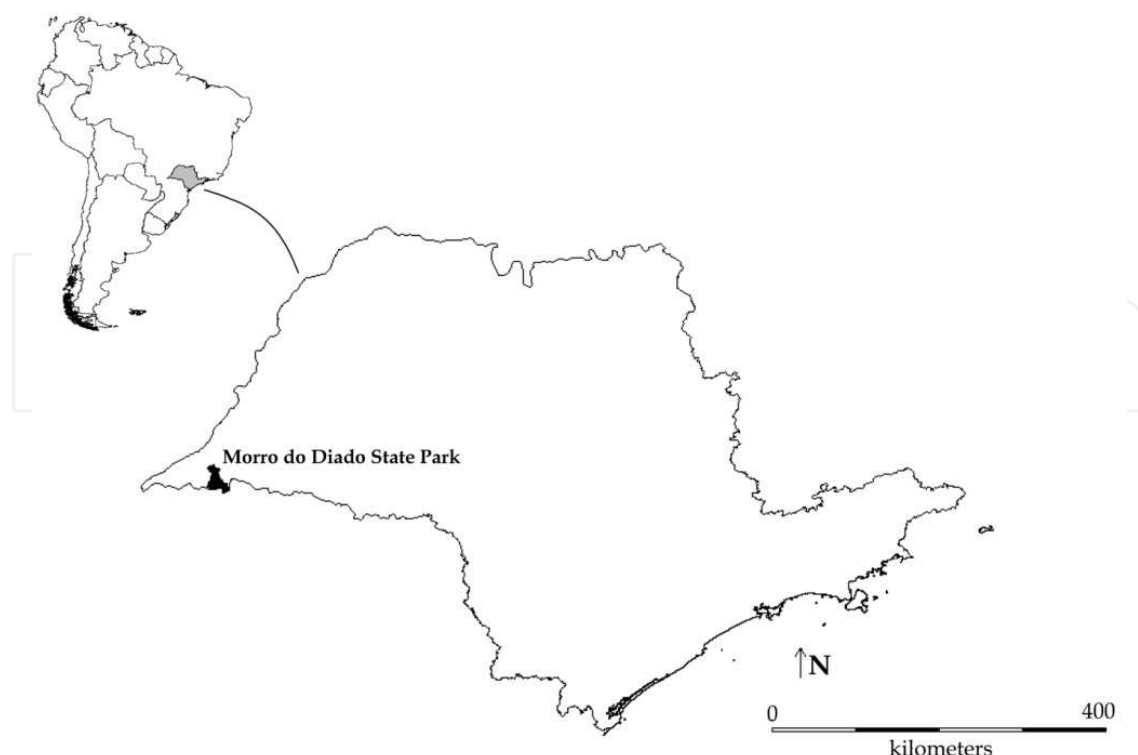


Fig. 1. Geographical localization of the studied area (Morro do Diabo State Park: MDSP), located in the westernmost region of the state of São Paulo, southeastern Brazil.

Permanent streams were located inside the forests and presented a bed mainly composed of sand (PS2) and gravel (PS1), and backwaters with deposits of mud and organic matter. Stream waters were well oxygenated with intermediate conductivity, had a lower temperature than permanent dams and temporary ponds, and high richness of potential aquatic predators (Table 1).

Temporary ponds were shallow and presented a bed covered by leaf litter and other detritus of terrestrial vegetation (such as decaying grasses in TP2) that grows in dry pond basins. Temporary pond water presented high conductivity, low dissolved oxygen, and low richness in potential aquatic predators (Table 1). In addition, temporary waters presented brownish coloration and high salinity, probably due to humic substances and evaporation respectively (Williams, 2006). However, the two temporary ponds differed regarding their canopy cover, since water surface of TP1 was covered by trees whereas TP2 was scarcely shadowed.

We recorded the monthly abundance of anuran species in each breeding site by performing the “surveys at breeding sites” methodology (Scott & Woodward, 1994) during the nocturnal period (from sunset to midnight, when most species had already reduced their calling activities). The search for anurans was made along the perimeters of breeding sites, by recording males engaged in calling activities. Habitat inspections were carried out using artificial light (head lamps), a methodology widely performed and recommend in protocols of inventory and monitoring of amphibians (Heyer et al., 1994), since males of anurans call even if under artificial light. The amount of time spent in each breeding site varied according to its size and complexity (Scott & Woodward, 1994). Additional information regarding MDSP characterization and sampling schedule is available in Santos et al. (2009) and Vasconcelos et al. (2009).

Environmental describers	Breeding sites					
	PD1	PD2	PS1	PS2	TP1	TP2
Geographic coordinates	22°27'03.7"S 52°20'43.3" W	22°37'00.4"S 52°10'09.5" W	22°36'16.2"S 52°18'00.8" W	22°28'30.8"S 52°20'30.9" W	22°37'10.5"S 52°09'55.8" W	22°37'07.8"S 52°10'01.9" W
Altitude (m)	261	264	299	299	263	259
Water features						
Electric conductivity (μ S/cm)	18.33	14.67	24.33	21	49.33	33.67
Dissolved O ₂ [mg/L (%)]	5.74 (72.3)	3.39 (41.1)	7.88 (90.4)	8.04 (92.8)	1.24 (15.43)	1.25 (15.3)
pH	5.8	4.67	6.61	5.68	5.8	5.52
Salinity (ppt)	0.01	0.01	0.01	0.01	0.02	0.01
Temperature (°C)	27.08	25.12	22.1	22.51	26.52	25.27
Turbidity (ntu)	5.61	26.57	18.03	5.12	10.75	46.74
Movement	io	s	r	r	s	s
Size (m)						
Length	200	25	500	500	70	26
Width	50	5	2.13	2.7	50	27
Depth	>2	>2	0.14	0.26	0.4	0.48
Hydroperiod (months)	18	18	18	18	10	8
Origin	m	m	n	n	n	n
Canopy cover (%)	<5	<5	80	70	90	<5
Edge type	fl, st	st	fl, st	fl, st	fl	fl, st
Bed substrate type	yc, om	yc, om	sa, om, co, gr	sa, om, af	om, yc	om, yc
Vegetation type						
Aquatic	he	he	he	he	he, sh, ar	he, sh
Edges	he, sh, ar	he, sh, ar	he, sh, ar	he, sh, ar	he, sh, ar	he, sh, ar
Matrix	fm, oa	oa, rf, fp	mf	fm	oa, rf	oa, rf
Richness of aquatic predators						
Fish	4	3	4	3	1	1
Insects and crustaceans	10	6	12	12	5	4

Table 1. Localization and environmental characterization of six breeding sites monitored in Morro do Diabo State Park, São Paulo state, southeastern Brazil. Breeding sites: Permanent dams (PD), permanent streams (PS), and temporary ponds (TP); Water movement: running

(r), inlet and outlet flow (io), and standing (s); Hydroperiod: number of months with water from September 2005 to March 2007; Origin: man-made (m), and natural (n); Edge type: flat (fl), and steep (st); Bed substrate type: sand (sa), yellow clay (yc), gravel (gr), arenitic flagstone (af), accumulation of organic matter and mud (om), and cobble (co); Vegetation type: herbaceous (he), shrubby (sh), and arboreal (ar); Matrix vegetation type: disturbed open area (oa), Forest of Myrtaceae (fm), Forest of *Pinus* (fp), regeneration of Mesophytic Semideciduous Forest (rf), mature Mesophytic Semideciduous Forest (mf); Aquatic predator richness: numbers of families of insects and crustaceans, and number of species of fish collected with dip nets through monthly sampling.

2.2 Statistical analyses

We carried out an environmental representation of the monitored breeding sites in MDSP by calculating the Euclidean Distance index (Krebs, 1999) on abiotic and biotic quantitative measurements (i.e. physicochemical water features, size, canopy cover, and richness in potential aquatic predators). We based Euclidean Distances on transformed (square root) and normalized (by standard deviation) environmental variables, due to deviations of normality of original data and no comparable measurement scales (Clarke & Gorley, 2006). In addition, we tested the existence of spatial patterns in the distribution of anuran assemblages among the six breeding sites monitored by computing similarity analysis (Bray-Curtis index) (Krebs, 1999). We based the similarity matrix on the total abundance of anuran species in each breeding site. Abundance of each species in each breeding site was considered as the highest number of calling males recorded during the monitored period. We adopted this procedure to avoid overestimation of species due to recounting individuals in a serial sampling schedule (Gottsberger & Gruber, 2004; Vasconcelos & Rossa-Feres, 2005; Santos et al., 2007).

We represented dissimilarity and similarity matrices by cluster analysis (UPGMA) (Krebs, 1999), and assessed statistical significance of genuine clusters performing the SIMPROF similarity profile test (Clarke & Gorley, 2006). SIMPROF is a series of permutation tests of the null hypothesis that assumes that the samples are a priori unstructured (i.e. that the breeding sites are unstructured regarding environmental characteristics and/or anuran assemblages). This test is based on an expected profile shape of similarity/dissimilarity obtained by permuting the entries for each variable 1,000 times (i.e. species and/or environmental variables) across that subset of samples; this produces a null condition in which samples have no group structure. The 1,000 permuted values are averaged to produce a mean profile which is statically compared (999 times) with the real similarity profile by absolute distances (Phi) (Clarke & Gorley, 2006). According to Clarke & Gorley (2006), whether environmental variables are responsible for structuring assemblages, it is expected that a plot, based on environmental information, groups the breeding sites in the same way as for a species composition plot. Therefore, we looked for concordance among cluster plots of environmental characteristics and anuran assemblages, in order to explain the spatial patterns of breeding sites used by anurans in MDSP.

We also computed Principal Components Analysis (PCA) (Legendre & Legendre, 1998) to represent together the monthly samples of breeding sites and the species. The purpose of this analysis was to capture as much as possible the variability of the original dataset in a

low-dimensional solution, represented by orthogonal axes. Thus, most of the variance is accounted for on the first two or three axes (Clarke & Warwick, 2001; Manly, 2008). We based PCA on a variance/covariance matrix, since we measured all variables in the same unit (i.e. abundance of anurans). Because our data set was composed of temporally serial samples (*sensu* Legendre & Legendre, 1998) and because we were more interested in spatial rather than temporal structures, we used a covariable matrix in PCA, representing time of sampling (i.e. sampling months as dummy variables) to minimize temporal effects in PCA solution.

Finally, we performed the Indicator Species Analysis (ISA) (Dufrêne & Legendre, 1997) to test for the existence of indicator species of environmental heterogeneity. This method is based on a data matrix where there are data groups (a priori established) that can be indicated by some species. According to McCune & Mefford (1999), each species receives an indicator value (IV) of each group, which varies from zero (no indication) to 100 (perfect indication). The null hypothesis in ISA considers that the maximum IV is not greater than that expected by chance. The indicator value is calculated using relative abundance and relative frequency of species across the sample units (considered herein as the monthly records of species abundance in each breeding site). Thus, a good indicator species of a determined group must be frequent and abundant across the samples in this group (Dufrêne & Legendre, 1997). Established groups for ISA were considered based on the clusters indicated by SIMPROF and PCA analyses. Statistical significances of the maximum value indicated for each group were performed using the Monte Carlo permutation test (Manly, 1998) (5,000 times). We based all analyses on log-transformed ($\log x+1$) abundance of anuran species in order to down-weight the contributions of quantitatively dominant species in the similarity analysis, and to linearize relationships in PCA analysis. SIMPROF and ISA analyses were performed using Primer-E 6.1 (Clarke & Gorley, 2006) and PC-ORD 4.0 (McCune & Mefford, 1999) software respectively. PCA was performed using CANOCO 4.0 for Windows software (ter Braak & Smilauer, 1998).

3. Results

We recorded a total of 23 anuran species in the six monitored breeding sites in MDSP and the number of anuran species in the breeding sites ranged from three (PS2) to 17 species (TP1) (Table 2). Anuran abundance ranged from 22 (PS2) to 316 individuals (TP1) (Table 2).

The SIMPROF similarity profile test showed three consistent groups of breeding sites in relation to environmental characteristics: permanent dams, permanent streams, and temporary ponds (Fig. 2A). The first node separated temporary ponds from permanent dams and permanent streams (Fig. 2A). The second node separated permanent streams from permanent dams (Fig. 2A). In addition, the SIMPROF test also showed that anuran species differed from a spatial distribution expected by chance and clustered three consistent groups of breeding sites in MDSP (Fig. 2B). These groups correspond to the same groups previously evidenced by the environmental features (Fig. 2A). The first node separated lotic (permanent streams) from lentic environments (permanent dams and temporary ponds), whilst the second node separated lentic environments in permanent dams and temporary ponds (Fig. 2B). The multivariate structure within the genuine clusters did not differ statistically (Fig. 2).

Species	PD1	PD2	PS1	PS2	TP1	TP2
<i>Chiasmocleis albopunctata</i>	0	0	0	0	7	15
<i>Dendropsophus minutus</i>	0	0	0	0	5	1
<i>Dendropsophus nanus</i>	50	20	0	0	45	25
<i>Elaschistocleis bicolor</i>	0	0	0	0	30	25
<i>Hypsiboas albopunctatus</i>	1	5	5	18	0	0
<i>Hypsiboas lundii</i>	0	0	0	1	0	0
<i>Hypsiboas punctatus</i>	0	12	0	0	0	0
<i>Hypsiboas raniceps</i>	6	0	0	0	20	8
<i>Leptodactylus chaquensis</i>	0	0	0	0	7	1
<i>Leptodactylus fuscus</i>	0	0	0	0	2	4
<i>Leptodactylus labyrinthicus</i>	0	0	0	0	1	0
<i>Leptodactylus mystaceus</i>	0	0	3	0	1	0
<i>Leptodactylus mystacinus</i>	0	0	0	0	20	8
<i>Leptodactylus podicipinus</i>	10	2	6	3	100	30
<i>Physalaemus cuvieri</i>	8	0	7	0	32	15
<i>Pseudis platensis</i>	0	0	0	0	1	0
<i>Rhinella ornata</i>	0	0	13	0	0	0
<i>Rhinella schneideri</i>	3	0	0	0	0	0
<i>Scinax berthae</i>	0	5	0	0	17	11
<i>Scinax fuscomarginatus</i>	60	12	0	0	0	0
<i>Scinax fuscovarius</i>	0	0	0	0	8	3
<i>Scinax similis</i>	0	0	0	0	2	30
<i>Trachycephalus typhonius</i>	0	0	1	0	18	5
Species abundance	138	56	35	22	316	181
Species richness	7	6	6	3	17	14

Table 2. Spatial distribution of anuran species among the six breeding sites, monitored monthly from October 2005 to March 2007 in Morro do Diabo State Park, São Paulo state, southeastern Brazil: permanent dams (PD), permanent streams (PS), and temporary ponds (TP).

PCA analysis showed congruent results with SIMPROF analysis whereas the two-dimensional solution of PCA accounted for 61.4% of the total explained variance (Fig. 3). Third and fourth axes account for few of the total explained variance (only 8.6% and 6%, respectively). PCA 1 (42.3%) showed a tendency to segregate among samples of streams (mainly related to *Hypsiboas albopunctatus*), and samples of permanent dams and temporary ponds (mainly related to *Dendropsophus nanus*, *Hypsiboas raniceps*, *Leptodactylus podicipinus*, *Physalaemus cuvieri*, and *Scinax fuscomarginatus*). On the other hand, PCA 2 (19.1%) showed a tendency to segregate among samples of permanent dams (mainly related to *Dendropsophus nanus* and *Scinax fuscomarginatus*) and samples of temporary ponds (mainly related to *Chiasmocleis albopunctata*, *Elaschistocleis bicolor*, *Leptodactylus chaquensis*, *L. mystacinus*, *L. podicipinus*, *Physalaemus cuvieri*, *Scinax similis*, and *Trachycephalus typhonius*).

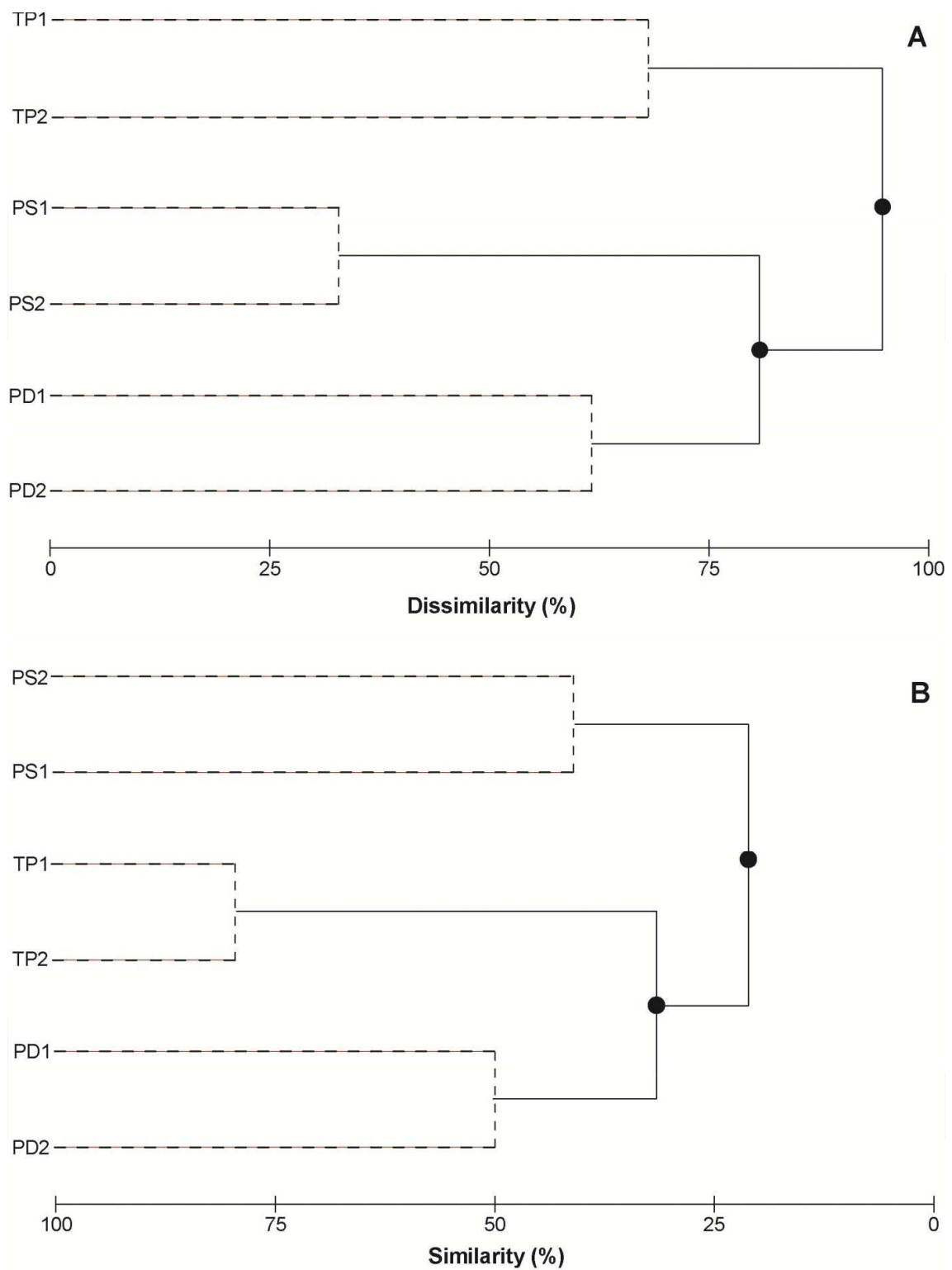


Fig. 2. SIMPROF similarity profile test for environmental characteristics (Euclidian Distance index) (A) and anuran species composition (Bray-Curtis index) (B) recorded in the six breeding sites, monitored monthly from October 2005 to March 2007 in Morro do Diabo State Park, São Paulo state, southeastern Brazil: permanent dams (PD), permanent streams (PS), and temporary ponds (TP). Continuous lines indicate statistically consistent groups ($P < 0.05$), whereas dotted lines indicate no statistical evidence for any structural pattern ($P > 0.05$).

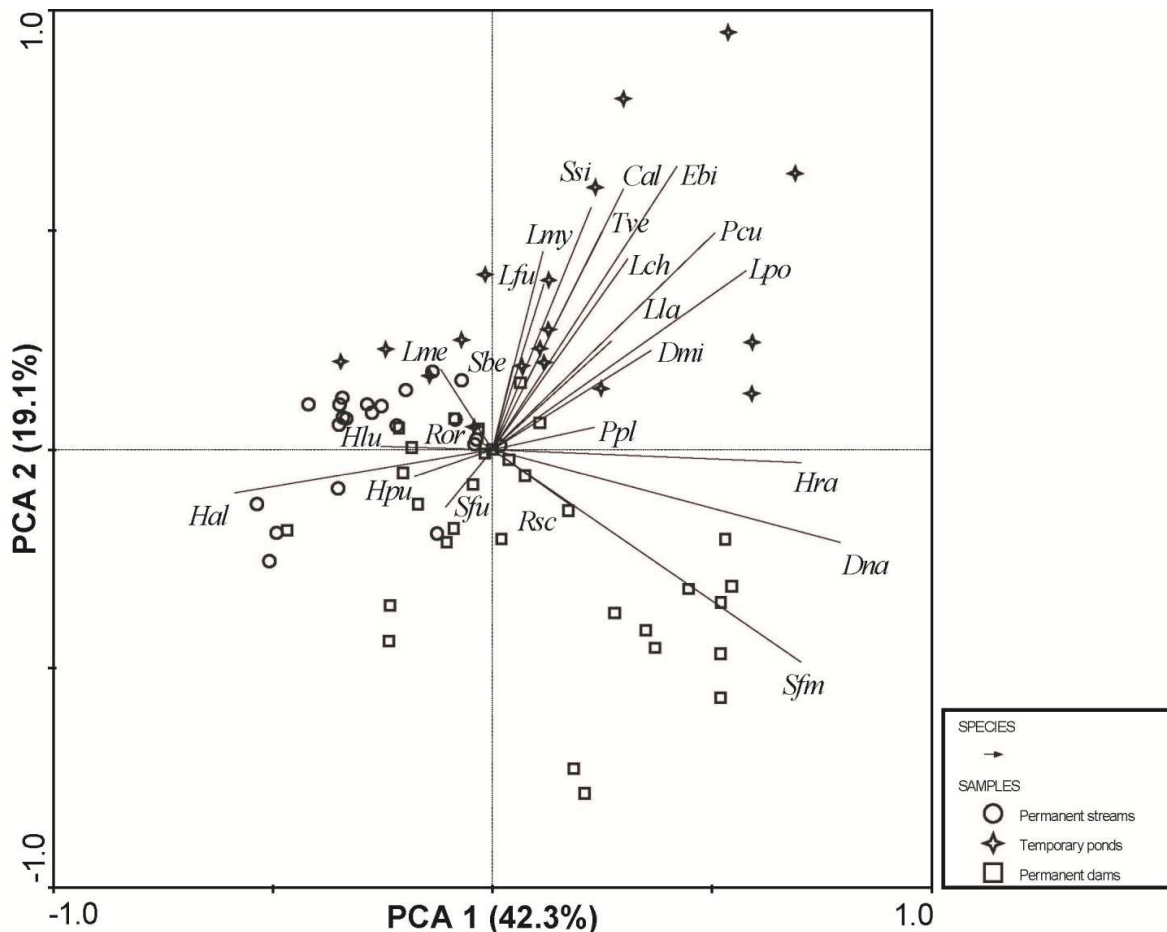


Fig. 3. PCA ordination for 23 anuran species recorded in the six breeding sites, monitored monthly from October 2005 to March 2007 in Morro do Diabo State Park, São Paulo state, southeastern Brazil. Species: *Chiasmocleis albopunctata* (Cal), *Dendropsophus minutus* (Dmi), *D. nanus* (Dna), *Elachistocleis bicolor* (Ebi), *Hypsiboas albopunctatus* (Hal), *H. lundii* (Hlu), *H. punctatus* (Hpu), *H. raniceps* (Hra), *Leptodactylus chaquensis* (Lch), *L. fuscus* (Lfu), *L. labyrinthicus* (Lla), *L. mystaceus* (Lme), *L. mystacinus* (Lmy), *L. podicipinus* (Lpo), *Physalaemus cuvieri* (Pcu), *Pseudis platensis* (Ppl), *Rhinella ornata* (Ror), *R. schneideri* (Rsc), *Scinax berthae* (Sbe), *S. fuscomarginatus* (Sfm), *S. fuscovarius* (Sfu), *S. similis* (Ssi), and *Trachycephalus typhoni* (Tve).

Congruent to the results recorded above, ISA results showed that the frequency of occurrence and abundance of 19 anuran species (about 83% of the total species) is not random when we adopted permanent dams, permanent streams, and temporary ponds as a priori groups in analysis (Table 3, Fig. 4):

Hypsiboas albopunctatus, *H. lundii*, and *Rhinella ornata* were indicator species of permanent streams.

Dendropsophus nanus, *Hypsiboas punctatus*, *Scinax fuscomarginatus*, and *S. fuscovarius* indicated permanent dams.

Chiasmocleis albopunctata, *Dendropsophus minutus*, *Elachistocleis bicolor*, *Hypsiboas raniceps*, *Leptodactylus chaquensis*, *L. fuscus*, *L. mystacinus*, *L. podicipinus*, *Physalaemus cuvieri*, *Scinax berthae*, *S. similis*, and *Trachycephalus typhoni* indicated temporary ponds.

Four anuran species were not indicators of environmental heterogeneity: *Leptodactylus labyrinthicus*, *L. mystaceus*, *Pseudis platensis*, and *Rhinella schneideri* (Table 3).

Species	Group	IV	P
<i>Chiasmocleis albopunctata</i>	3	27.8	0.00
<i>Dendropsophus minutus</i>	3	27.8	0.00
<i>Dendropsophus nanus</i>	2	36.2	0.03
<i>Elaschistocleis bicolor</i>	3	44.4	0.00
<i>Hypsiboas albopunctatus</i>	1	52.9	0.00
<i>Hypsiboas lundii</i>	1	13.6	0.04
<i>Hypsiboas punctatus</i>	2	21.9	0.01
<i>Hypsiboas raniceps</i>	3	33.9	0.01
<i>Leptodactylus chaquensis</i>	3	16.7	0.02
<i>Leptodactylus fuscus</i>	3	16.7	0.02
<i>Leptodactylus labyrinthicus</i>	3	5.6	ns
<i>Leptodactylus mystaceus</i>	1	11.3	ns
<i>Leptodactylus mystacinus</i>	3	38.9	0.00
<i>Leptodactylus podicipinus</i>	3	65.1	0.00
<i>Physalaemus cuvieri</i>	3	53.2	0.00
<i>Pseudis platensis</i>	3	5.6	ns
<i>Rhinella ornata</i>	1	13.6	0.04
<i>Rhinella schneideri</i>	2	3.1	ns
<i>Scinax berthae</i>	3	22	0.02
<i>Scinax fuscomarginatus</i>	2	38.7	0.00
<i>Scinax fuscovarius</i>	2	18	0.02
<i>Scinax similis</i>	3	27.8	0.00
<i>Trachycephalus typhonius</i>	3	21.2	0.01

Table 3. Species Indicator Analysis (ISA) for spatial distribution of anuran species in the six breeding sites, monitored monthly from October 2005 to March 2007 in Morro do Diabo State Park, São Paulo state, southeastern Brazil. Groups: 1) permanent streams; 2) permanent dams; and 3) temporary ponds. Indicator values (IV) and statistical significance (P). ns = $P > 0.05$.



Fig. 4. Some anuran species indicators of environmental heterogeneity at Morro do Diabo State Park, São Paulo State, Brazil: *Dendropsophus nanus* (A) and *Scinax fuscomarginatus* (B), typical of permanent dams; *Hypsiboas lundii* (C) and *Rhinella ornata* (D), recorded only in permanent streams; and *Chiasmocleis albopunctata* (E) and *Scinax similis* (F), typical of temporary ponds.

4. Discussion

Our results indicated that anuran assemblages of MDSP were structured and related to the environmental heterogeneity of breeding sites, disagreeing with Hubbell's neutral model of communities (Hubbell, 2001). Werner et al. (2007) also reported that amphibian assemblages of wetlands in Michigan USA, deviated from the neutral model because spatial distribution of species across breeding sites differed from an expected random distribution, and that assemblage structure was also related to the environmental heterogeneity of ponds (i.e. mainly related to gradients of disturbance, productivity, and pond area). In fact, several studies around the world have shown that adult anurans can actively choose breeding sites according to habitat characteristics (Collins & Wilbur, 1979; Eason & Fauth, 2001; Bosch & Martínez-Solano, 2003; Werner et al., 2007).

We expected a spatial structure of the anuran assemblages, since the groups of monitored breeding sites in MDSP (permanent dams, permanent streams, and temporary ponds) differed widely in relation to environmental characteristics. For Neotropical anuran assemblages, studies have also pointed out differential utilization of breeding sites by adults and/or larvae of anurans (Basso, 1990; Hero, 1990; Eterovick & Sazima, 2000; Bertoluci & Rodrigues, 2002; Both et al., 2010; Vasconcelos et al., 2011), although few had effectively used statistical approaches for confirming spatial structure. In the present study, the remarkable degree of concordance between anuran assemblage and environmental plots (i.e. both groups with very similar topology) indicated that the suite of environmental variables has explained spatial patterns of anuran distribution among breeding sites (*sensu* Clarke & Gorley, 2006).

We recorded by SIMPROF and PCA analyses, a primary segregation of stream anuran assemblages in MDSP. In fact, few anuran species ($n = 7$) occurred in permanent streams (PS1 and PS2) and all of those occurred only in backwaters, except *Rhinella ornata* which was also recorded in riffles and running waters. The low anuran species richness recorded in streams was also reported in other localities of southern and southeastern Brazil (e.g. Bernarde & Anjos, 1999; Bernarde & Machado, 2001; Brasileiro et al., 2005), which may result from four non exclusive hypotheses: i) phylogenetic constraints related to the historic process of colonization in South America (Zimmerman & Simberlof, 1996); ii) pressure of aquatic predators (mainly fish) considered strong in this type of environment (e.g. Gascon, 1991; Magnusson & Hero, 1991); iii) runoff spawns; and iv) morphological limitations in the larval phase (Gascon, 1991). The anuran segregation of streams from the remaining breeding sites (permanent and temporary lentic habitats) differed from the pattern observed in the environmental context, where the external group was composed by temporary ponds, and streams were closely related to the dams. High structural similarity between streams and dams was naturally expected, since dams are originated from dammed streams. However, for anuran assemblages, temporary ponds and dams are more closely related, since both of them are lentic waters, while streams are lotic environments usually unsuitable to colonization.

We recorded through ISA analysis three anuran species as stream indicators: *Hypsiboas albopunctatus*, *H. lundii*, and *Rhinella ornata*. *H. albopunctatus* occurred in backwaters of streams, very similar to swamps (i.e. in wide stream sections with a mud bed, slow-flowing water, and under natural clearings). According to Cei (1980), *H. albopunctatus* lives in open

spaces of forests at the edges of standing waters. However, in most studies this species has been reported as being associated with streams (Haddad et al., 1988; Kwet et al., 2002) and swamps (Brasileiro et al., 2005; Santos et al., 2007) with little water flow. *H. albopunctatus* has a generalized reproductive mode (mode 1; Haddad & Prado, 2005) and can be found in human settlements and in disturbed environments (Vasconcelos & Rossa-Feres, 2005; Santos et al., 2007).

Hypsiboas lundii is an anuran species typical from the Brazilian Cerrado (Frost, 2011), totally dependent on gallery forests (Brasileiro et al., 2005). Reproduction of this species is associated with permanent streams of primary and secondary forests (International Union for Conservation of Nature, 2011). Males usually construct basins in banks of streams where eggs are deposited and tadpoles are carried from the basins after flooding caused by heavy rains (mode 4; Haddad & Prado, 2005, Eterovick & Sazima, 2004).

Rhinella ornata is distributed within the Atlantic forest (Frost, 2011). It is a toad that deposits eggs in streams, with exotrophic tadpoles developing in stream backwaters (mode 2; Haddad & Prado, 2005). Our observations indicate that males of this species call in still backwaters and running waters of MDSP streams, highlighting that this toad species is dependent on forest habitats. In fact, a recent study has demonstrated that populations of *R. ornata* undergo genetic erosion due to habitat fragmentation of the Atlantic Coastal Forest (Dixo et al., 2009).

In the current study, we recorded segregation between assemblages of permanent dams and temporary ponds in MDSP. Anuran species richness in permanent dams (PD1 and PD2) was intermediate in relation to permanent streams and temporary ponds (i.e. higher than permanent streams but lower than temporary ponds). In fact, dams have intermediate features between lotic and lentic environments and these are harmful to the reproduction of many species due to changes in physical and chemical features of the water (Esteves, 1998). These statements were corroborated by Both et al. (2008), since they recorded low diversity and high species dominance in the dam environment monitored in southern Brazil. In the present study, dams were dominated by two anuran species (*Dendropsophus nanus* and *Scinax fuscomarginatus*) that have wide distribution in South American biomes and are typically well adapted to anthropogenic disturbances (Duellman, 1999; Frost, 2011; IUCN, 2011). These anuran species have the generalized reproductive mode (mode 1; Haddad & Prado, 2005).

In addition to *Dendropsophus nanus* and *Scinax fuscomarginatus*, two other anuran species were indicators of dams: *Hypsiboas punctatus* and *Scinax fuscovarius*. The former has a wide distribution comprising South and Central America (Duellman, 1999; Vasconcelos et al., 2006), whilst *S. fuscovarius* present more southern distribution in South America (Frost, 2011). Both species have the generalized reproductive mode (mode 1; Haddad & Prado, 2005) and occur in either preserved or disturbed areas (Santos et al., 2007, 2008).

On the other hand, we recorded that temporary ponds (TP1 and TP2) supported high anuran species richness and were spatially structured, disagreeing with the stochastic pattern expected for habitats with low predictability (such as temporary water bodies) (Bonner et al., 1997). The pattern of high anuran species richness that we recorded in temporary ponds can be explained by the high productivity usually reported in temporary environments (Williams & Feltmate, 1992; Brönmark & Hansson, 2005; Williams, 2006), as

well as the absence or low abundance of aquatic predators (fish and insects respectively) in comparison with permanent ponds (Heyer et al., 1975; Smith, 1983; Woodward, 1983; Skelly, 1997), and the intermediate-disturbance hypothesis (see Both et al., 2009 for review).

In fact, comparisons of community composition between permanent and temporary waterbodies reveal relatively little overlap regarding the biota (review in Williams, 2006). High species richness has been reported in previous studies on Neotropical anuran assemblages of temporary ponds (e.g. Basso, 1990; Zimmerman & Simberloff, 1996; Santos et al., 2007; Both et al., 2009) and seems to be related to specific features of these environments that make the colonization by several exclusive anuran species advantageous, mainly by those which are more opportunistic. In the present study, we reported many anuran species as indicators of temporary ponds, and our ecological data indicate that most of them (e.g., *Chiasmocleis albopunctata*, *Elachistocleis bicolor*, *Leptodactylus chaquensis*, *Physalaemus cuvieri*, *Scinax similis*, and *Trachycephalus typhonius*) are opportunistic breeders with calling males starting activity after heavy rains (Santos et al., unpubl. data).

Amphibians that use different types of ponds along the permanence gradient tend to have different life-history characteristics (Semlitsch et al., 1996), such as adaptations to deal with drying ponds. Therefore, anuran species that lay eggs in foam nests (e.g. leiuperids and leptodactylids) have an advantage to explore temporary environments due to protection by the foam against desiccation of eggs and/or embryos (Heyer, 1969; Downie, 1988), and probably against wide fluctuations in water levels, typical of temporary breeding sites (Vasconcelos & Rossa-Feres, 2005; Santos et al., 2007). In addition, anuran species with a generalized reproductive mode have high reproductive investments (large clutches), faster larval development, and can also show an evolutive response to explore unpredictable environments such as temporary ponds (Basso, 1990). In our study, 42% of anuran species that were considered as indicators of temporary ponds deposited eggs in foam nests (mode 11: *Physalaemus cuvieri* and *Leptodactylus chaquensis*, mode 13: *L. podicipinus*, and mode 30: *L. fuscus* and *L. mystacinus*), while the remaining 58% presented the generalized reproductive mode (mode 1: *Chiasmocleis albopunctata*, *Elachistocleis bicolor*, *Dendropsophus minutus*, *Hypsiboas raniceps*, *Scinax berthae*, *S. similis*, and *Trachycephalus typhonius*), highlighting that life-history characteristics of these species allow them to explore temporary sites.

The abundance and frequency of occurrence of four anuran species recorded in MDSP did not differ from the randomly expected distribution (*Leptodactylus labyrinthicus*, *L. mystaceus*, *Pseudis platensis*, and *Rhinella schneideri*), and consequently did not indicate association with any breeding site. Three of these were rare at the monitored water bodies (*Leptodactylus labyrinthicus*, *Pseudis platensis*, and *Rhinella schneideri*), which makes interpretations on spatial pattern distribution of these species unfeasible. On the other hand, *Leptodactylus mystaceus* was a ubiquitous anuran species in MDSP. We recorded males of this species calling within mud basins of stream banks and in temporary ponds, as previously reported by Toledo et al. (2003). Reproduction of *L. mystaceus* takes place in sites seasonally flooded by heavy rains (Duellman, 1978) and tadpoles are able to generate foam, probably as an adaptation to survive in places with unpredictable rainfall (Caldwell & Lopez, 1989). Therefore, we believe that the reproductive requirements of *L. mystaceus* seem to be more related to short hydroperiods of breeding sites (such as seasonally flooded banks of permanent streams in MDSP), than to other environmental characteristics, such as lentic or lotic waters.

5. Conclusion

We recorded that anuran assemblages in MDSP were not a random set of species since they were structured according to distinct groups of breeding sites (permanent dams, permanent streams, and temporary ponds). In addition, we also pointed out the existence of species indicators of environmental heterogeneity, i.e. anuran species typical of each group of breeding sites. Regarding indicator species analysis (ISA), we observed lower ISA values associated with anuran indicators of temporary ponds than for those of permanent dams and streams. This result seems to be related to the reproductive patterns of anuran species, since ISA is based on relative abundance and relative frequency of species in the samples (Dufrêne & Legendre, 1997). Therefore, explosive breeding species that occupied temporary ponds for short periods contributed for few samples (i.e. low frequency of occurrence) in ISA analysis, decreasing the final indicator values. On the other hand, anuran species typical of permanent sites remained in streams and dams for longer periods, increasing indicator values. Despite this possible bias in indicator values, we believed in the robustness of ISA results since we recorded a higher number of anuran species as indicators of temporary ponds than of permanent dams and streams. Ecological consistence of ISA can also be supported by other studies showing the same association of anuran species here indicated by ISA with temporary ponds or permanent breeding sites (Brasileiro et al., 2005; Prado et al., 2005; Santos et al., 2007), although direct comparisons are limited due to the lack of similar statistical approaches.

Our results are relevant to conservation proposals since Mesophytic Semideciduous Forests are the most fragmented and threatened ecosystem of the Atlantic Domain and only 2% of this forest type remains in the state of São Paulo as “islands of biodiversity” in an agricultural landscape (Viana & Tabanez, 1996). Therefore, strategies of biodiversity conservation are urgently required for this forest type, and our results have significant implications for anuran conservation actions in remnants of Mesophytic Semideciduous Forest because the importance of heterogeneous breeding sites in the maintenance of high diversity in assemblages of anurans was highlighted. Therefore, the choice of areas for anuran conservation in this forest type must consider the presence of distinct breeding sites such as lotic and lentic environments, as well as sites with different hydroperiods. In this context, the Brazilian Forest Act revision, which hopes to expand agricultural frontiers by clear-cutting the vegetation in riparian zones and legal reserves of private lands, is a recent threat to anuran conservation (Silva et al., 2011). This law proposal, which was approved in the Brazilian Chamber of Deputies, will endanger the water quality and availability, modifying also the hydroperiod of waterbodies used to anuran breeding activity. Besides, the reduction and fragmentation of native vegetation can disconnect areas of shelters and/or foraging from their breeding sites (Becker et al., 2007), as well as promote genetic erosion of anuran species (Dixo et al., 2009).

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7. References

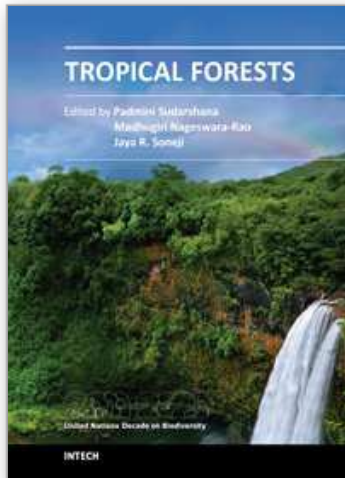
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The astounding richness and biodiversity of tropical forests is rapidly dwindling. This has severely altered the vital biogeochemical cycles of carbon, phosphorus, nitrogen etc. and has led to the change in global climate and pristine natural ecosystems. In this elegant book, we have defined "Tropical Forests" broadly, into five different themes: (1) tropical forest structure, synergy, synthesis, (2) tropical forest fragmentation, (3) impact of anthropogenic pressure, (4) Geographic Information System and remote sensing, and (5) tropical forest protection and process. The cutting-edge synthesis, detailed current reviews, several original data-rich case studies, recent experiments/experiences from leading scientists across the world are presented as unique chapters. Though, the chapters differ noticeably in the geographic focus, diverse ecosystems, time and approach, they share these five important themes and help in understanding, educating, and creating awareness on the role of "Tropical Forests" for the very survival of mankind, climate change, and the diversity of biota across the globe. This book will be of great use to the students, scientists, ecologists, population and conservation biologists, and forest managers across the globe.

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