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Tadpole community structure in lentic and lotic habitats: richness and diversity in the Atlantic Rainforest lowland

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The analysis of species richness and community composition provides basic information to understand the structure of species assemblages. Here, we compared species richness and composition, compositional similarity and species turnover of tadpole communities in 14 lentic and eight lotic habitats in the Atlantic Rainforest of southeastern Brazil. Because the occurrence in lotic habitats requires some degree of morphological or behavioural specialisations of tadpoles to fast flowing water, we expected to find low species richness and species turnover in lotic than in lentic habitats. We compared species richness using abundance and sample-based rarefaction and species composition by PERMANOVA. We analyzed the Species Abundance Distribution (SAD) in each habitat type using a Whittaker diagram. To assess the similarity in species composition, we used a hierarchical cluster analysis. We compared the beta diversity between lentic and lotic habitats using Whittaker index and the species richness was recorded in lentic habitats (20 species), whereas only seven species occurred in lotic habitats. The species composition also differed markedly between lotic and lentic habitats, with only one shared species (*Aplastodiscus eugenioi*). Both habitats had few dominant and rare species and a greater proportion of species with intermediate abundance, but different processes are underlying this distribution abundance pattern in each type of habitat. Our results indicate that species richness, abundance, and occurrence are associated to habitat type (lentic and lotic), indicating a possible effect of the environmental filtering process associated to different life history strategies.

Key words: Amphibians; Community ecology; Species composition; Species diversity; Species turnover.

INTRODUCTION

The parameters measured to describe ecological community structure are usually species richness, composition, and abundance distribution, which are the basic dataset for ecology (Gotelli & Colwell, 2001). In the last decades, many studies have evaluated the factors involved in amphibian community structure in tropical forests (Parris, 2004; Strauß et al., 2010; Provete et al., 2014; Almeida et al., 2015), which are home to the highest amphibian diversity in the world (Haddad et al., 2013). Anurans of tropical forests (e.g. Atlantic Rainforest) also have a high diversity of reproductive modes (Haddad & Prado, 2005).

The reproductive modes of anuran encompass direct and indirect development (Haddad & Prado, 2005; McDiarmid & Altig, 1999). Therefore, tadpoles are found in a wide variety of habitats, such as humid forest floor, ponds, streams, marshes, bromeliads, and water-filled cavities in trees (Inger et al., 1986; Alford, 1999; Haddad & Prado, 2005; McDiarmid & Altig, 1999). Of these, lentic habitats such as ponds and marshes, and lotic habitats such as fast-flowing and lowland streams are the most common used breeding habitats (Haddad & Prado, 2005; Strauß et al., 2013; Provete et al., 2014). Among the aquatic ecosystems, one of the main differentiations is found precisely between lentic and lotic habitats, which have distinct hydrological characteristics (Tundisi & Matsumura-Tundisi, 2011). Lotic habitats have unidirectional and oscillating flow (Tundisi & Matsumura-Tundisi, 2011), and are often connected to each other to form a dendritic structure (Altermatt, 2013). Lotic habitats are mainly influenced by marginal vegetation, which acts as a source and filter of organic material, affecting energy flow (Lecerf et al., 2005). On the other hand, lentic habitats are frequently isolated from other lentic habitats (Tundisi &

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Matsumura-Tundisi, 2011) and support greater richness and abundance of aquatic vegetation than lotic habitats (Tundisi & Matsumura-Tundisi, 2011). So, lentic and lotic habitats differ from each other in connectivity and environmental heterogeneity (Heino et al., 2015).

The differences in water flow, and consequently in the structure of aquatic habitats, may impose distinct selection pressures on both adult anurans and tadpoles. However, most studies evaluating the amphibian community structure were developed in either lentic (e.g., Both et al., 2009; Silva et al., 2012; Provete et al., 2014; Almeida et al., 2015) or lotic habitats (e.g., Inger et al., 1986; Parris, 2004; Afonso & Eterovick, 2007; Eterovick et al., 2010), with few studies involving both habitat types (e.g., Eterovick & Sazima, 2000; Vasconcelos et al., 2011). Tadpole occurrence is determined primarily by oviposition site choice of adults (Resetarits & Wilbur, 1989; Resetarits et al., 2005). Further, tadpole communities are influenced by species interactions (Kopp et al., 2006; Nomura et al., 2011) and environmental conditions (Semlitsch et al., 2015; Queiroz et al., 2015), which act as a filter (Strau β et al., 2010), selecting species that are able to establish and survive in the local community. Herein, we compared the structure of tadpole communities between lentic and lotic habitats with regards to species richness and turnover, which is a component of beta diversity describing changes in species composition among communities (Tuomisto, 2010). Additionally, we evaluated how much species turnover in lentic and lotic habitats contributes to the total species richness of each of these two habitat types. Anuran species that reproduce in flowing water show some adaptations to prevent eggs and tadpoles from drifting away (Haddad & Prado, 2005; McDiarmid & Altig, 1999). Thus, we expect to find lower species richness and lower turnover in lotic than lentic habitats, due to the restricted occurrence of anuran species adapted to fast water flow.

MATERIALS AND METHODS

Study area

The Brazilian Atlantic Rainforest is one of the 25 global biodiversity hotspots due to its high species richness and high rates of endemism and threat (Myers et al., 2000). This biome houses about 60% of the Brazilian anurans species, of which about 90% are endemic (Haddad et al., 2013). Our sampling sites are located in the State Park of Serra do Mar (23º21'36''S; 44º50'52''W, datum WSG84) in Ubatuba, north coast of the state of São Paulo, Brazil (Fig. 1). The Pinciguaba unit of the Park has approximately 47,500 ha and ranges from the sea level to 1,340 m a.s.l. The native vegetation comprises a mosaic of forest formations, including mostly lowland, submontane and montane ombrophilous dense forest, and pioneer formations with marine (dunes), fluvial (sandbank), and fluvial-marine influence (mangroves; Joly et al., 2012). The climate is Af (tropical moist, without dry season) according to the Köppen-Geiger system (Peel et al., 2007). The mean annual rainfall is greater than 2,200 mm, with a mean annual temperature of 24 °C (Joly et al., 2012).

Sampling design

We sampled tadpoles in 22 habitats (14 lentic and eight lotic) monthly from September 2011 to March 2012, covering an area of about 250 km² (Fig. 1). The habitats were selected to represent the variety of aquatic environments in the ombrophilous dense forest used by anurans, including ponds of different sizes and hydroperiods, and fast- and slow-flowing streams (Table 1). Also, we selected only water bodies without connection to others located in lowland area between 1 m and 150 m above sea level to reduce the influence of altitudinal effects and dispersal. We sampled habitats between 8 am and 6 pm using a hand dip-net (32 cm diameter) with a 3 mm² mesh passed throughout the whole lentic habitats (Rossa-Feres & Jim, 1996; Vasconcelos et al., 2011), and along a 100 m transect in lotic habitats. In the latter, some samples were also made using small dip nets to sample narrow spaces between rocks. All habitats were sampled for one hour.

To characterise habitat structure, we measured the following variables (Table 1): (i) percentage of canopy cover, which was estimated with a concave spherical densiometer (Forest densitometer model C; Lemmom, 1956), at four points in each quarter of habitat to compute the mean for each habitat, (ii) maximum depth (cm), (iii) greater width, measured using a tape, (iv) percentage of substrate types (boulders, cobbles, gravel and sand, clay and mud, and leaf litter), and (v) percentage of floating aquatic vegetation. The substrate types and amount of aquatic vegetation were visually estimated by the same observer, as six categories: 0 for 0%, 0.1 for 1% to 20%, 0.3 for 21% to 40%, 0.5 for 41% to 60%, 0.7 for 61% to 80%, and 0.9 for 81% to 100%. For lotic habitats, we divided the 100 m transect sampled in four squares (25 m each one). We measured all the environmental variables in each square, and then we used the average of all squares to characterise the habitat.

All tadpoles collected were anesthetised with benzocaine solution and fixed in a 1:1 solution of 70% ethanol: 15% formalin. All voucher specimens were deposited in the collection DZSJRP - Amphibia - Tadpoles of the Department of Zoology and Botany from the Universidade Estadual Paulista (UNESP), São José do Rio Preto, São Paulo, Brazil.

Data analysis

Species Abundance Distribution (SAD) in each habitat type was analysed using Whittaker diagram (Magurran & McGill, 2011). This is an intuitive method for understanding community structure that incorporates species richness, composition, and abundance (Magurran & McGill, 2011).

The different number of lentic and lotic habitats reflects the availability of habitat types in the study area. Thus, to take into account the different replicates of each habitat type, we used individual- and samplebased rarefaction curves to compare the species richness in lentic and lotic habitats (Gotelli & Colwell, 2001). For both, individual- and sample-based rarefaction, we used the log Gama algorithm separately to lentic and lotic habitats, employing 999 randomisations of species total



Figure 1. Study area and spatial distribution of sampling sites in the Serra do Mar State Park - Picinguaba, state of São Paulo, Brazil. Abbreviations according to Table 1.

abundance (Krebs, 1999). The 95% confidence intervals of this metric is given by the standard error calculated by the square root of the variance between samples (Hammer, 2001). Additionally, the mean log-transformed species richness and abundance in lentic and lotic habitats were compared using a t-test. Analysis were conducted in Past v. 2.16 (Hammer et al., 2001).

To test for spatial autocorrelation in species composition, we performed a Mantel correlogram in which the compositional similarity (calculated using Bray-Curtis) is plotted against the geographic distance between communities (Legendre & Legendre, 2012). Analysis was conducted in the R v. 3.3.1 (R Core Team, 2016) using the packages vegan (Oksanen et al., 2016) and fields (Nychka et al., 2015).

We calculated the species turnover between pairs

of habitats using the Jaccard similarity index (Cj) for presence-absence data (Magurran & McGill, 2011). We chose a binary index to remove the influence of highly abundant species, since tadpole abundance mostly reflects the aggregative behaviour (Hoff et al., 1999) and number of eggs per clutch (Hartmann et al., 2010). We used the Jaccard similarity matrix to build dendrograms using Ward, single linkage, and unweighted pairwise mean (UPGMA) methods and chose that with the highest cophenetic correlation coefficient (r; Romesburg, 1984). Values of r > 0.9 indicates a very good fit, 0.9-0.81 represents a good fit, 0.8-0.7 represents a poor fit, and r < 0.7 represents a very poor fit (Rohlf, 2000). The UPGMA method had the highest r. To perform a Permutational Multivariate Analysis of Variance (PERMANOVA) we applied the Jaccard similarity index in the presence-



Figure 2. Species abundance distribution for tadpoles sampled from September 2011 to March 2012 in the Serra do Mar State Park - Picinguaba, state of São Paulo, Brazil. A) Lentic habitats; abbreviations: Llat = *L. latrans*; Rorn = *R. ornata*; Halb = *H. albomarginatus*; Hfab = *H. faber*; Aeug = *A. eugenioi*; Patl = *Physalaemus atlanticus*; Stym = *S. tymbamirim*; Shay = *S. hayii*; Stra = *S. trapicheiroi*; Sarg = *S. argyreornatus*; Dele = *D. elegans*; Dmin = *D. minutus*; Sper = *S. perereca*; Eova = *E.* aff. *ovalis*; Dber = *D. berthalutzae*; Ccar = *C. carvalhoi*; Tmes = *Trachycephalus mesophaeus*; Bhyl = *Bokermannohyla* cf. *hylax*; Slit = *S. littoralis*; Sperp = *S. perpusillus*. B) Lotic habitats; abbreviations: Sang = *S. cf. angrensis*; Hphy = *H. phyllodes*; Hasp = *H. asper*; Aeug = *Aplastodiscus eugenioi*; Ttao = *Thoropa taophora*; Cbor = *Cycloramphus boraceiensis*; Vura = *Vitreorana uranoscopa*.



Figure 3. A) Sample rarefaction curve and B) individual rarefaction curve of tadpole communities in 14 lentic and 8 lotic habitats sampled from September 2011 to March 2012 in the Serra do Mar State Park- Picinguaba, state of São Paulo, Brazil. Dashed lines represent 95% confidence intervals.



Figure 4. Mantel correlogram with species composition dissimilarity plotted against distance classes (in km) in A) lentic, and B) lotic habitats. Empty and black squares represent non-significant and significant autocorrelations, respectively.



Figure 5. Similarity in species composition of lentic and lotic habitats sampled from September 2011 to March 2012 in the Serra do Mar State Park - Picinguaba, São Paulo State, Brazil. Dendrogram obtained using Jaccard index and UPGMA. Cophenetic coefficient (r) = 0.95. Abbreviations: PP = permanent pond; TP = temporary pond; TM = temporary marsh; FS = fast-flowing stream; LS = low-land stream.

absence matrix to test for a difference in species composition between lentic and lotic habitats (Anderson, 2001). The statistical significance of PERMANOVA was evaluated with 10,000 randomisations. To evaluate how much the species turnover in lentic and lotic habitats contributed to the total species richness of each one of these two habitat types, we calculated the multiplicative beta diversity index (βw: Whittaker, 1960) separately for lentic and lotic habitats. Whittaker's beta diversity is an index that performs the multiplicative partitioning of total diversity, reflecting the influence of beta diversity on gamma diversity of each data set. Low values of βw indicate low contribution of beta diversity to gamma diversity, whereas high values indicate little or no overlap in species composition and high contribution of beta diversity to gamma diversity (Magurran & McGill, 2011). Data were analysed using Past v. 2.16.

RESULTS

We found tadpoles of 20 species in lentic and seven in lotic habitats. Only *A. eugenioi* occurred in both habitats (Table 2). In lentic habitats, *L. latrans* (n = 6,138) was dominant, accounting for 53.5% of total abundance and occurred in two lentic habitats, specifically in one temporary pond and one temporary marsh (Fig. 2a). In lotic habitats, *S.* cf. *angrensis* was widely distributed and abundant, accounting for 48.7% of total abundance and occurring in five of the eight sampled lotic habitats (Fig. 2b).

As we expected, lentic habitats had four times more species than lotic habitats (Table 2). Even controlling for the different sample size in each habitat type, lentic habitats showed higher species richness, as shown by sample (Fig. 3a) and individual-based rarefaction (Fig. 3b). The total abundance of tadpoles was also higher in lentic than lotic habitats (11,477 and 1,045 individuals, respectively). However, the mean values of species richness and abundance per sample unit did not differ between habitats (richness: t=0.61, DF=19; P=0.546; abundance: t=0.48, DF=19; P=0.635).

Species composition in lentic habitats showed positive but non-significant spatial autocorrelation in the first (between 0 and 500 m) and fourth distance class (between 1,500 m and 2,000 m), and non-significant negative autocorrelation in the second and third distance classes (between 500 m and 1,500 m; Fig. 4a). Species composition in lotic habitats showed significant, positive spatial autocorrelation in the first distance class (between 0 and 1,000 m), and non-significant positive spatial autocorrelation in the second distance class (between 2,000 m to 2,500 m), and a non-significant negative spatial autocorrelation in the last class (between 3,000 m to 3,500 m; Fig. 4b).

Species composition differed between lentic and lotic habitats (F1,16 = 5.062; P = 0.0002). Lentic habitats (β w = 3.48) contributed more to total diversity than lotic habitats (β w = 1.45). The cluster analysis showed four habitat groups: three of them had only species that occurred in lentic habitats, and one group species occurring in lotic habitats (Fig. 5). Three subgroups had higher similarity **Table 1.** Environmental variables of sampling sites in the State Park of Serra do Mar – Picinguaba, state of São Paulo,Brazil. Abbreviations: PP = permanent pond; TP = temporary pond; TM = temporary marsh; FS = fast-flowing stream; LS= lowland stream. The sequence of substrate type indicates their predominance in descending order.

Habitat	Width (m)	Depth (m)	Canopy cover (%)	Substrate type	Water flow (m/s)	
PP1	6.41	0.29	78.4	mud > litter > sand = boulders	0	
PP2	48	0.46	8.4	mud > litter > sand	0	
PP3	12	0.69	64.9	mud > litter > cobbles = sand	0	
PP4	0.94	0.18	NA	clay = litter = mud	0	
TP1	5.32	0.3	74.15	mud = litter > sand	0	
TP2	11.3	0.2	80.7	mud = litter > sand	0	
TP3	0.78	0.8	93.6	mud > litter = sand > clay	0	
TM1	4.2	0.6	95.8	mud > litter	0	
TM2	3.2	0.56	95.3	mud > litter = sand = gravel	0	
TM3	6.92	0.14	86.1	mud > litter	0	
TM4	3.8	0.86	91.9	mud > litter > sand	0	
TM5	2.4	0.22	97.5	mud = litter > sand	0	
TM6	3	0.75	96.1	mud = litter > clay	0	
TM7	7.1	0.4	0	mud = litter > sand	0	
FS1	7.47	0.82	84.9	boulders > cobbles = gravel > sand > litter	0.23	
FS2	2.56	0.2	92.1	boulders > cobbles = litter > gravel = sand	0.16	
FS3	5.64	0.77	91.7	boulders = gravel > cobbles > sand = litter	0.53	
FS4	2.04	0.19	91.7	boulders = gravel > cobbles = sand = litter	0.31	
FS5	7.89	0.89	90.5	boulders > gravel = cobbles > sand = litter	0.33	
LS1	5.89	0.5	91.2	gravel = sand > boulders = cobbles = litter	0.37	
LS2	7.1	0.4	95.9	boulders > cobbles > gravel = sand = litter	0.32	
LS3	4.9	0.46	71.9	gravel = sand > boulders = gravel = litter	0.25	

in species composition within than among groups: (1) temporary marshes (TM1, TM3, and TM4) had exactly the same species composition: only *A. eugenioi*; (2) one permanent (PP4) and one temporary pond (TP3), which shared *Physalaemus atlanticus, Chiasmocleis carvalhoi*, and *Scinax argyreornatus*; (3) lotic habitats (FS1 and FS3) that shared tadpoles *Cycloramphus boraceiensis, S.* cf. *angrensis, Hylodes asper*, and *H. phyllodes*.

DISCUSSION

Lentic habitats harbored almost 80% of the species. Despite the commonness of this pattern of more species occurring in lentic than lotic habitats in Brazilian Atlantic Rainforest (e.g., Conte & Rossa-Feres, 2006; Garey & Hartmann, 2012; Garey et al., 2014), an opposite pattern of high richness in lotic habitats has been reported in other tropical rainforest, such as Borneo (Inger et al., 1986) and Madagascar (Strauß et al., 2013). These different patterns of habitat use can be explained by the occurrence of different phylogenetic lineages in the regional species pool and by differences in geomorphologic characteristics. The tropical forests of Madagascar and Borneo are associated with mountain topography, and the slope of the relief limits the formation of ponds, restricting the available habitats to streams (Inger et al., 1986; Strauβ et al., 2013). However, the low altitude (0 to 150 m) and low slope in the studied area do not restrict the formation of lentic habitats, which could favour the high species richness in different lentic habitats. Thus, besides the evolutionary influence, geomorphological processes could also explain these opposite patterns.

Despite lentic habitats harboured the majority of species and more than 10 times the total abundance of lotic habitats, the abundance pattern was similar in both habitat types. Both had few dominant and rare species and a greater proportion of species with intermediate abundance, which is expected in heterogeneous environments, like the Atlantic Rainforest (Bastazini et al., 2007; Van Sluys et al., 2007; Magurran & McGill, 2011). In lotic habitats, where tadpoles are typically less abundant (Eterovick & Barros, 2003; Vasconcelos et al., 2011; this study), the dominance of S. cf. angrensiss seems to be related to the greater number of eggs per clutch in comparison to other stream-dwelling species (Hartmann et al., 2010). In lentic habitats, the dominant species (L. latrans) has clutch with great number of eggs (more than 4,000 eggs per clutch) and exhibit parental care (Vaz-Ferreira & Gerhau, 1975; Hartmann et al., 2010), which increase individual fitness.

Despite lentic habitats harbouring almost 80% of the species in our study area, the mean species number per water body did not differ between lentic and lotic. Thus, the greater species richness in lentic habitat is explained mostly by the greater species turnover in comparison to the lotic habitats. The greater dissimilarity in species composition among lentic habitats may be related to different structural characteristics among these habitats (ponds, marshes, swamps), which creates different possibilities for habitat selection by adults (Wellborn et al., 1996; Van Buskirk, 2005). The structural differences among lotic habitats were subtler than among lentic habitats. Marshes and ponds differed mostly in relation to depth and presence of vegetation, both characteristics have a recognised influence on species composition (e.g., Kopp & Eterovick, 2006; Queiroz et al., 2015).

The species in the studied area may have been filtered to different habitat types according to the evolutionary history of reproductive modes in anurans (Gomez-Mestre et al., 2012). The process of environmental filtering acts on a given species pool, selecting species with morphological, physiological, or behavioural traits which allow their survival and persistence in local communities (Weiher et al., 2011). The stream-dwelling tadpoles need specific morphological and behavioural adaptations to survive in these environments (e.g., Altig & McDiarmid, 1999a,b; Wells, 2010). For example, the rheophilic tadpoles of V. uranoscopa, T. taophora, H. asper and C. boraceiensis have a specialised morphology to live in fast-flowing streams (Villa & Valerio-Gutiérrez, 1982; Wassersug & Heyer, 1983), such as elongated or flattened bodies, muscular tails, and reduced tail fins (Altig & McDiarmid, 1999a,b; Wells, 2010). These specialisations of stream-dwelling species limit their occurrence in other habitat types (Ribeira & Vogler, 2000; Strau β et al., 2010). Nonetheless tadpoles of *S. angrensis* and *A. eugenioi*, found in the sampled lotic habitats, had generalised morphology. Despite in the sampled area we found tadpoles of *S. angrensis* only in stream backwaters, this species is known to reproduce also in lentic habitats (Haddad et al., 2013). Tadpoles of *A. eugenioi* occur in both lentic and lotic habitats (Haddad et al., 2013). The generalised morphology seems to allow their occurrence in both types of habitat.

In short, we found a difference in total species richness and composition between lentic and lotic habitats, and a high species turnover among ponds. Lentic habitats had the majority of species and higher species turnover than lotic habitats. Despite the low species richness and turnover, streams harbour exclusive lineages with specialised reproductive modes. This result indicates that habitat type may be an environmental filter determining patterns of species richness and composition in tadpole communities in the Brazilian Atlantic Rainforest, due to their specific dynamics and environmental characteristics.

Family	Species		Types of habitats				
		РР	ТР	тм	LS	FS	
Bufonidae	Rhinella ornata (Spix, 1824)	Х	Х	-	-	-	
Centrolenidae	Vitreorana uranoscopa (Müller, 1924)	-	-	-	х	-	
Cycloramphidae	Cycloramphus boraceiensis (Heyer, 1983)	-	-	-	-	Х	
	Thoropa taophora (Miranda-Ribeiro, 1923)	-	-	-	х	-	
Hylidae	Aplastodiscus eugenioi (Carvalho-e-Silva & Carvalho-e-Silva, 2005)	х	-	Х	х	Х	
	Bokermannohyla cf. hylax	Х	-	Х	-	-	
	Dendropsophus berthalutzae (Bokermann, 1962)	-	Х	Х	-	-	
	D. elegans (Wied - Neuwied, 1824)	х	-	х	-	-	
	D. minutus (Peters, 1872)	х	-	Х	-	-	
	Hypsiboas albomarginatus (Spix, 1824)	х	Х	Х	-	-	
	H. faber (Wied - Neuwied, 1821)	х	Х	Х	-	-	
	Scinax cf. angrensis	-	-	-	х	Х	
	S. argyreornatus (Miranda-Ribeiro, 1926)	х	Х	Х	-	-	
	S. hayii (Barbour, 1909)	х	-	Х	-	-	
	<i>S. littoralis</i> (Pombal & Gordo, 1991)	х	-	-	-	-	
	S. perereca (Pombal, Haddad & Kasahara, 1995)	х	-	Х	-	-	
	S. trapicheiroi (Lutz, 1954)	х	Х	Х	-	-	
	S. perpusillus (Lutz & Lutz, 1939)	Х	-	-	-	-	
	S. tymbamirim (Nunes et al., 2012)	Х	-	Х	-	-	
	Trachycephalus mesophaeus (Hensel, 1867)	-	-	Х	-	-	
Hylodidae	Hylodes asper (Müller, 1924)	-	-	-	-	-	
	H. phyllodes (Heyer & Cocroft, 1986)	-	-	-	х	Х	
Leptodactylidae	Leptodactylus latrans (Steffen, 1815)	Х	-	Х	-	Х	
	Physalaemus atlanticus (Haddad & Sazima, 2004)	х	х	Х	-	-	
Microhylidae	Chiasmocleis carvalhoi (Cruz, Caramaschi & Izecksohn 1997)	х	х	-	-	-	
	Elachistocleis aff. ovalis	Х	Х	Х	-	-	

Table 2. Tadpoles recorded in different habitats in the State Park of Serra do Mar – Picinguaba, state of São Paulo, Brazil. Abbreviations: PP = permanent pond; TP = temporary pond; TM = temporary marsh; FS = fast-flowing streams; LS = lowland stream.

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