



# Tadpole species richness within lentic and lotic microhabitats: an interactive influence of environmental and spatial factors

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Anurans inhabiting lentic and lotic water bodies show distinct responses to environmental and spatial variables due to dispersal by adults and microhabitat selection by tadpoles, which creates a hierarchical structure in these metacommunities. Aiming to understand the influence of tadpole microhabitat selection and adult dispersal on species richness distribution, we tested the influence of microhabitat environmental variables and habitat spatial variables on tadpole richness in lentic and lotic water bodies located in the Atlantic Rainforest. We sampled tadpoles in 99 lentic microhabitats and 288 lotic microhabitats for seven months. We performed a Hierarchical Partitioning Analysis to test the influence of environmental and spatial variables. The percentage of aquatic vegetation within microhabitats and the main spatial gradient (dbMEM1) affected species richness in lentic water bodies. Sand percentage, aquatic vegetation, and depth in the microhabitat and small-scale spatial gradient (dbMEM4) affected species richness in lotic water bodies. Spatial processes indicate an influence of adult dispersal limitation in search of reproductive habitats. The influence of microhabitat variables was mostly related to the amount of aquatic vegetation, indicating the influence of environmental processes on the larval phase of anuran life cycle. In conclusion, both environmental and spatial processes are driving the species richness in microhabitats inside lentic and lotic water bodies in the Atlantic Rainforest.

**Key words:** Amphibians; biodiversity hotspot; microhabitat; species number; Tropical Rainforest.

## INTRODUCTION

Understanding how environmental and spatial processes operate in community assembly of species with complex life cycles (CLC) is a challenge for ecologists. CLC species are those whose individuals undergo two distinct development phases (larval and adult) in an abrupt morphological, physiological, and behavioral change, usually associated with the use of different habitats such as aquatic and terrestrial (Wilbur, 1980; Duellman & Trueb 1994; Moran, 1994). Amphibians are the only tetrapods with CLC strategy (Wells, 2007); therefore, their different development phases are expected to respond differently to environmental and spatial processes. Adults colonise and choose breeding sites according to abiotic (Eterovick & Barata, 2006; Prado et al., 2009; Both et al., 2011; Vasconcelos et al., 2011) and biotic variables (Both et al., 2009, 2011). However,

the patchy distribution of aquatic habitats (Resetarits et al., 2005) together with reduced dispersal ability of some individual anuran species (Smith & Green, 2005) could impede new habitat colonisation by adults. Breeding site selection seems to determine the occurrence of tadpoles in each habitat (e.g., Provete et al., 2014). However, inside habitats (i.e., at the water body scale) tadpoles may select their occurrence sites according to environmental microhabitat characteristics (e.g., Kopp et al., 2006). Habitat and microhabitat selection strategies of anurans are linked to the relative influence of adults and tadpoles on anuran species distribution, and consequently, the relative influence of these different developmental phases on the species richness pattern of anurans.

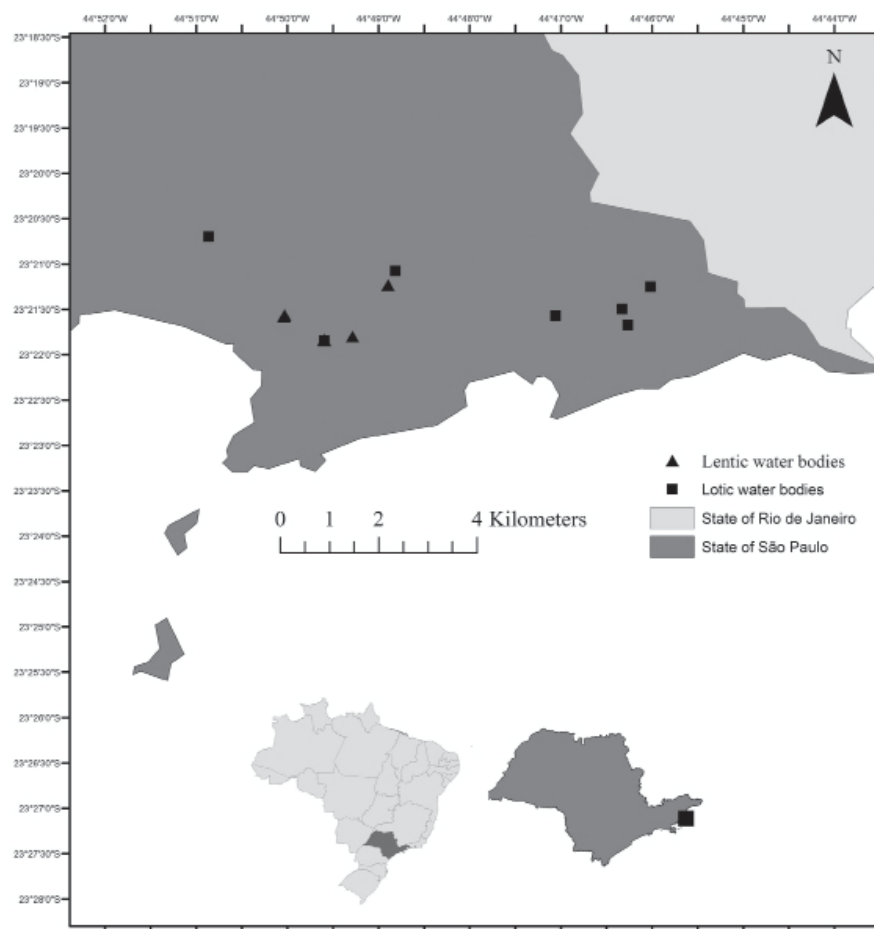
Previous studies have shown that microhabitat selection by tadpoles in ponds and streams is influenced by food availability (Warkentin, 1992; Govindarajulu & Anholt, 2006), predation risk (Wilbur & Fauth, 1990;

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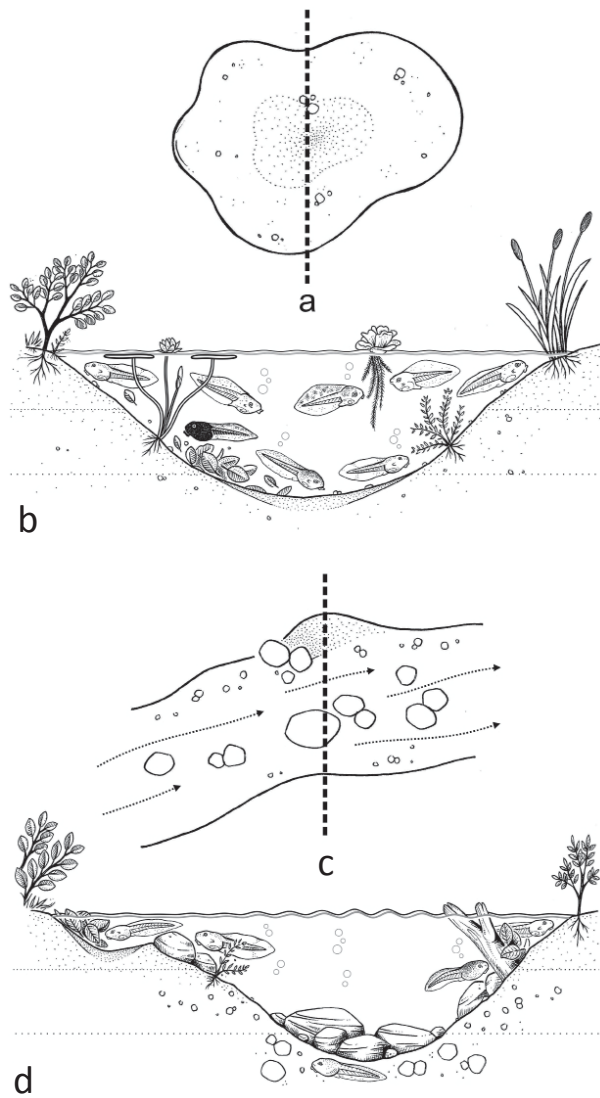
Hero et al., 2001; Teplitsky et al., 2003), and physical and chemical variables such as dissolved oxygen, pH, turbidity, and conductivity (Evans et al., 1996; de Oliveira & Eterovick, 2009). Specifically in ponds, depth and amount of aquatic vegetation increase microhabitat availability, favouring species occurrence and survival from predation, which thus increase tadpole species richness (Fairchild et al., 2003; Kopp & Eterovick, 2006; Prado et al., 2009). In tropical streams, water flow, number of potential predators, stream volume and depth, and type of substrate are microhabitat characteristics selected by tadpoles and other co-occurring organisms, such as fishes and macroinvertebrates (Power, 1984; Beisel et al., 1998; Brown, 1991; Zweimüller, 1995; Eterovick & Barata, 2006; Strauß et al., 2013). In addition, strategies for fixation in the substrate are of great importance in streams, preventing tadpoles from being carried away by the water current. Hence, substrate heterogeneity of streams could harbour species with different morphological adaptations to inhabit different substrate types (Hoff et al., 1999). For example, rheophilic tadpoles of *Vitreorana uranoscopa* bury themselves in the sand (Hoff et al., 1999), and tadpoles of genus *Thoropa* have a modified abdomen as an adherent ventral disk, for fixation on rocks covered only by a film of water (Rocha et al., 2002).

Several studies have already compared anuran communities at the habitat (e.g., Vasconcelos et al.,

2011; Provete et al., 2014) and microhabitat scales (e.g., Eterovick & Barata, 2006; Kopp & Eterovick, 2006). However, these studies focused only on one type of water body (lentic or lotic). Moreover, there is a lack of studies encompassing the microhabitat scale in pristine areas of Atlantic Rainforest. Therefore, we intend to detect the key factors driving microhabitat species richness within tadpole communities in ponds and streams of the Atlantic Rainforest. For this purpose, we investigated the influence of microhabitat environmental variables inside water bodies, which only influence tadpole distribution across the different types of microhabitats, and spatial location of ponds and streams, which influence adult tadpole occurrence in the habitat because of breeding site selection by adults. A higher influence of environmental variables on species richness variation might indicate that microhabitat selection by tadpoles plays a structuring role. On the other hand, a higher influence of the spatial location of water bodies might indicate that colonisation by adult dispersal is the most important process in determining species richness distribution of tadpole communities. As ponds and streams represent two distinct aquatic systems, we expect that the drivers of species richness in lentic and lotic microhabitat will be different. Thus, we expect that higher species richness may be associated to microhabitats in ponds with higher amount of aquatic vegetation, since they represent an important refuge from predators (Kopp et al., 2006).



**Figure 1.** Spatial distribution of the water bodies sampled in the Atlantic Rainforest, state of São Paulo, Brazil.



**Figure 2.** Illustration of environmental structure and species occurrence in lentic (a and b) and lotic (c and d) water bodies (WBs). (a) top view of lentic WB's and (b) the illustration of vegetation and substrate structure creating heterogeneity across the pond, (c) top view of lotic WB's and (d) the illustration of the stream and how the water current exerts a pressure and even tadpoles adapted to currents tend to stay in the backwaters, either attached to rocks or buried in sand at the bottom.

In streams, we expected to find a strong relationship between species richness and microhabitats with different types of substrate because of the high degree of tadpole specialisation required to deal with water flow (Hoff et al., 1999).

## MATERIALS AND METHODS

### Study area and sampling

We conducted this study at Parque Estadual da Serra do Mar Núcleo Picinguaba (PESM hereafter; 23°21'36"S, 44°50'52"W, datum WGS84), in the state of São Paulo, municipality of Ubatuba, south-eastern Brazil (Fig. 1). The total area (47,500 ha) of PESM is covered by Atlantic Rainforest (distributed from the sea level to 1,340 meters of altitude), and is legally protected by the Brazilian law.

The climate in this region is tropical humid with no dry season (Peel et al., 2007).

We sampled tadpoles in 288 microhabitats, 99 located in six lentic water bodies (WBs), three in open areas, and three inside the forest, and 189 microhabitats in seven lotic WBs (all inside the forest). We only sampled streams inside the forest because there are no streams in the open areas of this site. We carried out sampling once a month during the breeding period of most anuran species, from September 2011 to March 2012, between 8. a.m and 6 p.m with a randomised WB sampling sequence on each visit. We selected unconnected WBs with different environmental variables (different types of substrates, depths, and amount of vegetation in the WB), located in lowlands between 1m and 150m above sea level to reduce the influence of elevational effects. Microhabitats were sites inside WBs with different environmental variables (Figs 2a, 2b, 2c, and 2d). We sampled tadpoles in microhabitats distributed throughout the area of lentic WBs, whereas in lotic WBs, we sampled tadpoles along 100 meters. We sampled at least four microhabitats in each WB, except for the uncommon dry months (January to March 2012), when waters were very shallow. In this case, we sampled one to three microhabitats; this number varied according to the water volume available.

### Microhabitat

We quantified three environmental variables which generally affect tadpole distribution in each microhabitat (Kopp & Eterovick, 2006; Strauß et al., 2013) and these variables will be considered here as determinants of environmental processes. (i) percentage of vegetation in the microhabitat, (ii) percentage of substrate types (clay, rock, sand, gravel, organic matter, mud, or leaf litter), and (iii) maximum depth (in centimeters). Microhabitats selected were spaced at a minimum distance of two meters apart from each other, in order to include sites with different characteristics and represent the variation in environmental variables throughout the water body.

We sampled tadpoles using the Alford & Crump (1982) method in lentic WBs; according to this method, each sampled microhabitat is delimited by a metal cylinder (32 cm diameter and 70 cm length) open at both ends. We submerged the metal cylinder in the WB with a quick movement and buried its edge in the substrate, delimiting the selected sampling microhabitat. After this procedure, we checked for the existence of gaps between the cylinder and the substrate through which tadpoles could escape. If we found any space, we cancelled the sampling and selected a new microhabitat. We collected tadpoles contained in the cylinder with an 18cm x 10cm (length and width) rectangular-shaped net with wire mesh of 3mm<sup>2</sup>, moving it through the cylinder area 20 times. For each collected tadpole, we started counting the number of dipnet sweeps. Sampling ended after 20 dipnet sweeps without capturing any tadpoles.

Metal cylinder sampling was impracticable in lotic WBs due to their rocky substrate, which does not allow for burying the cylinder in the substrate in order to prevent tadpoles from escaping. Thereby, we visually defined the microhabitat. We collected tadpoles that could be

detected within three minutes in each microhabitat using the same wire net mesh described above. Due to water transparency, it was possible to visualise tadpoles on the stream substrate. When we could not capture tadpoles, we disregarded that sample and selected a new microhabitat.

In each type of WB, we performed microhabitat characterisation according to the following sequence. (i) determining percentage vegetation in the microhabitat; (ii) determining the types of substrates; and (iii) determining maximum depth with a measuring tape. To quantify the first two descriptors, we divided the space occupied by the microhabitat into four quadrants. We visually categorised the sum of vegetation and substrate types in each quadrant as follows. 1-20%, 21-40%, 41-60%, 61-80%, and 81-100%.

We anaesthetised tadpoles with benzocaine, and fixed them with a formalin (15%) and ethanol (70%) solution (1.1) in the field. We deposited all tadpoles in the DZSRP Amphibia-Tadpoles Scientific Collection at the "São Paulo State University, Campus of São José do Rio Preto, Brazil".

### Data analysis

We performed a Variance Inflation Factor (VIF) analysis to check and exclude collinear variables from the environmental data. In the VIF analysis, each variable is regressed with all the other variables in the system and a coefficient of determination is noted (Legendre & Legendre, 2012). Variables with high VIF coefficients must be investigated and might be dropped from the group of explanatory variables (Legendre & Legendre, 2012). Among the different values proposed to identify non-collinearity and to drop variables, we chose VIF > 3 for a more conservative choice of environmental variables (Zuur et al., 2010). All environmental variables showed collinearity (Online Appendix Table 1); thus, we performed further analyses including all the environmental variables in the system. Due to the different measure units and scales, we transformed the values of the environmental variables into unit variance so that they had a mean of zero and a standard deviation of one (Legendre & Legendre, 2012).

We used distance-based Moran's Eigenvector Maps (dbMEMs; Dray et al., 2012; Legendre & Legendre, 2012) to create spatial variables (eigenvectors) based on the Euclidean distance matrix of WB geographical coordinates. The dbMEM (formerly called Principal Coordinates of Neighbor Matrices, PCNMs) is an ordination method that produces orthogonal eigenvectors used to represent the spatial relationships among habitat samples; in our case, the WBs (Dray et al., 2012). This analysis first computes a pairwise Euclidean distance matrix between samples (waterbodies), and then, builds a truncated distance matrix based on a chosen threshold, and, finally, performs a principal coordinate analysis (PCoA) of the truncated distance matrix creating the orthogonal eigenvectors that are used as spatial predictors in multivariate analysis (Borcard & Legendre, 2002; Dray et al., 2006).

To evaluate how the spatial configuration and the distance among water bodies influence species richness,

we considered WB spatial eigenvectors as predictor variables. To select spatial explanatory variables we used forward selection (Blanchet et al., 2008). For lentic water bodies, we selected dbMEM 1 and dbMEM 4, and for lotic water bodies, we selected dbMEM 2 and dbMEM 4. We used a Hierarchical Partitioning Analysis (Chevan & Sutherland, 1991) to assess which set of variables (microhabitat environmental variables or water body spatial variables) influences species richness in lentic and lotic WBs. The output of Hierarchical Partitioning analysis is a list of predictor variables and their independent (I) and joint (J) influences on response variable Y (Mac Nally, 2002). In our analysis, we randomised the predictor database 1000 times to calculate the distribution of "I" for each predictor variable and "J" for all joint effects of each variable (Mac Nally, 2002). Results of Hierarchical Partitioning analyses are expressed as a Z-score with statistical significance based on 95% confidence limit and Z-score value higher than 1.65 (Mac Nally, 2002). To minimise the high effect of zeros and extreme values

**Table 1.** Percentage of each anuran family in the total tadpole abundance in lentic and lotic water bodies.

Waterbody type	Family	Abundance Percentage
Lentic	Leptodactylidae	81
	Bufonidae	12.5
	Hylidae	6.5
	Microhylidae	0.02
Lotic	Hylidae	58
	Hylodidae	33
	Cycloramphidae	9
	Centrolenidae	0.1

**Table 2.** Hierarchical Partitioning, Z-score values, I. independent contribution of predictors, J. interactions between each predictor and the others, and I (%) explanation percentage of each variable and significance value of environmental and spatial variables of species richness in lentic and lotic water bodies.

Variables		I	J	I (%)	Significance Z-score
Lentic	Leaf litter	0.009	0.017	3.30	-0.08
	Sand cover	0.002	-0.001	0.68	-0.62
	Clay cover	0.003	0.002	1.19	-0.50
	Mud	0.006	0.002	2.11	-0.25
	Organic matter	0.014	-0.004	5.44	0.34
	Aquatic vegetation	0.080	0.064	30.08	5.17*
	Depth	0.012	0.013	4.51	0.16
	dbMEM1	0.112	0.035	42.12	6.77*
	dbMEM4	0.028	0.006	10.57	1.28
Lotic	Rock cover	0.004	0.000	2.19	-0.20
	Sand cover	0.028	0.020	15.35	3.17*
	Leaf litter	0.002	-0.001	0.95	-0.47
	Mud	0.001	0.001	0.72	-0.50
	Aquatic vegetation	0.025	-0.010	13.75	2.60*
	Depth	0.064	0.037	35.28	8.43*
	dbMEM2	0.015	0.008	8.14	1.19
	dbMEM4	0.043	0.002	23.60	5.18*

\*Asterisks indicate significant values



in the original species composition matrix due to the high abundance of some tadpole species, we used the Hellinger transformation (Legendre & Gallagher, 2001). We also performed a Pearson correlation with significant environmental variables and species richness to find out whether influence among the dependent and independent variables was positive or negative, when Hierarchical Partitioning did not show the type of relationship. We did not correlate the spatial eigenvectors because they already represent spatial structure in species richness.

We adopted  $\alpha = 0.05$  and 1000 permutations in the tests of all analyses. We conducted all the analyses using R (version 3.0.2) software (R Development Core Team, 2013), with the following packages: *ade4* (Dray & Dufour, 2007), *hier.part* (Walsh & Mac Nally, 2012), *gtolls* (Warnes et al., 2013), *vegan* (Oksanen et al., 2012), *car* (Fox & Weisberg, 2011), *packfor* (Dray et al., 2011), *PCNM* (Legendre et al., 2013), and *spdep* (Bivand, 2014).

## RESULTS

We recorded 5,394 tadpoles of 21 anuran species (Online Appendix Table 2); 4,401 individuals of 15 species in ponds and 993 individuals of seven species in streams. Hylidae was the richest family in lentic WBs, represented by twelve species, and the most abundant family was Leptodactylidae, although it was represented by only one species (Table 1, Online Appendix Table 2). No families stood out in lotic water bodies regarding species richness; however, Hylidae was the most abundant family, followed by Hylodidae (Table 1, Online Appendix Table 2).

In lentic WBs, species richness was influenced by the percentage of aquatic vegetation inside the microhabitats and by dbMEM 1 (Table 2, Online Appendix Figure 1). Large amount of vegetation increased tadpole species richness (Pearson  $r = 0.380$ ). In lotic WBs, species richness was influenced by sand percentage in the substrate, aquatic vegetation and depth inside the microhabitats, and by dbMEM 4 (Table 2, Online Appendix Figure 1). Amount of sand (Pearson  $r = 0.22$ ), aquatic vegetation (Pearson  $r = 0.12$ ), and depth (Pearson  $r = 0.32$ ) positively affected species richness in stream microhabitats.

## DISCUSSION

Environmental and spatial processes affected species richness distribution of anuran larvae in both ponds and streams. Especially in ponds, spatial process had a higher influence on species richness than environmental process, emphasising that the oviposition site selected by adults is the main determinant of tadpole occurrence. Provete et al. (2014) had already found evidence of the influence of behavioural decisions of adults on tadpole distribution in a higher area of the Atlantic Forest. On the other hand, Almeida et al. (2015) found the opposite pattern in Central Amazonia, i.e., a lower influence of spatial variation on tadpole species richness than the number of ponds per plot, which was the major determinant. Almeida et al. (2015) assumed that the lower influence of spatial

variables was caused by the low dispersal limitation of anurans in the Amazon forest. Therefore, different processes probably drive species richness in the Atlantic Rainforest and in the Amazon rainforest. In streams, their natural spatial proximity seems to explain the higher influence of small-scale spatial gradient (dbMEM4) on the distribution of tadpole richness in lotic water bodies. Thus, the higher influence of spatial variables in ponds and of environmental variables in streams seems to be related to the scale at which each type of water body is inserted. Ponds encompassed a larger spatial scale than streams and this more likely increases the influence of longer distances (dbMEM1) on species richness.

Our results indicated that a high amount of vegetation inside microhabitats sheltered higher species richness in tadpole communities of both ponds and streams. Aquatic vegetation increases habitat complexity and suitability, which can increase food availability for tadpoles (Peltzer & Lajmanovich, 2004). It also provides a higher amount of shelter against predators (Baber & Babbitt, 2004; Kopp et al., 2006), which increases tadpole survival thus favouring species richness (Diaz-Paniagua, 1987; Baber & Babbitt, 2004). The positive effect of aquatic vegetation on tadpole species richness has been reported in lentic habitats (Kopp & Eterovick, 2006; Hamer & Parris, 2011; Peltzer & Lajmanovich, 2004). However, to our knowledge, this is the first study that shows that aquatic vegetation also positively affects tadpole species richness in lotic habitats (but see de Oliveira & Eterovick, 2009; for the influence of aquatic vegetation on variation in species composition in lotic habitats). The strong and positive influence of the amount of aquatic vegetation on microhabitats suggests that habitat complexity promotes the coexistence of species at the microhabitat scale.

Despite the favourable influence of aquatic vegetation on species richness, lotic water bodies generally have low amounts of aquatic vegetation. In these environments, the main sources of food for tadpoles are sediment and microalgae deposited in the substrate (Peterson & Boulton, 1999; Wells, 2007). Especially diatoms are deposited in sand substrates with a mild water current, because strong currents prevent the establishment of these algae (Grimm & Fisher, 1984; Atkinson et al., 2008). Accordingly, stream-dwelling tadpoles in Madagascar that feed on microalgae deposited in the sand were associated to less intense water currents (Strauß et al., 2013). Our results and those by Strauß et al. (2013) reinforce the hypothesis that sandbanks located in backwaters have higher tadpole richness. Thus, we suggest that higher tadpole richness in microhabitats of lotic water bodies could be influenced by a combination of deeper water column and lower water current, as a larger amount of sand can accumulate and diatom establishment might occur, increasing food availability. Accordingly, we only found a positive relationship between tadpole richness and microhabitat depth in streams.

In conclusion, we have demonstrated that species richness of tadpole communities in the Atlantic Rainforest of south-eastern Brazil is influenced by spatial and environmental processes. Spatial processes indicate

an influence of adult dispersal limitation in search of reproductive habitats. The influence of microhabitat variables was related mainly to the amount of aquatic vegetation, indicating influence of environmental processes (e.g. predation pressure, competition) in the larval phase of anurans life. Furthermore, our results bring new information about anuran species ecology in Atlantic Rainforest, one of the most threatened biomes of the world. In this way, this knowledge could ensure to help new theoretical insights and drive conservation efforts to conserve not just the forested area, but also keep the breeding habitats of anurans in good quality preserving its intrinsic environmental features.

## ACKNOWLEDGEMENTS

We thank Samuel Fernando Adami for the map of water bodies distribution. We sincerely thank all the people that helped us with the fieldwork, specially Mainara X. Jordani and Cássia de Souza Queiroz. We are grateful to Diogo B. Provete for some useful suggestions. We also thank the two anonymous reviewers who helped to improve this paper. ICMBio (26954-2) and COTEC (260108-004.450/2011). This paper is part of LSOM's master dissertation at the Post Graduate Program in Animal Biology, supported by fellowships from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 2012/09243-0; 2013/26101-8) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). DCRF is a researcher fellow of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 303522/2013-5) and thanks to the Sistema Nacional de Pesquisa em Biodiversidade. SISBIOTA Project on tadpoles ecology (FAPESP 2010/52321-7 and CNPq 563075/2010-4) for the financial support. MVG thanks to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq – Proc. 422537/2016-0).

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Accepted: 10 May 2017

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