Effects of environmental and spatial factors on the distribution of anuran species with aquatic reproduction in central Amazonia

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We evaluated the effect of environmental and spatial variables on the distribution of 11 species of anurans in 10,000 ha of non-flooded forest in central Amazonia. Diurnal and nocturnal frog assemblages were sampled in 72 plots using visual and auditory surveys. Distance from stream was the best predictor for species richness and abundance, with an increase in distance resulting in a decrease in number of species and individuals. Three species (*Osteocephalus oophagus*, *Trachycephalus resinifictrix* and *Vitreorana oyampiensis*) were not influenced by environmental predictors and occurred along all environmental gradients. The watersheds did not influence the abundance of the majority of species except *Allobates* sp., *Atelopus spumarius* and *Leptodactylus rhodomystax*. Our results indicate that most species studied occur along the margins of streams, which they also use as dispersal corridors. The removal of forests near streams could lead to local extinctions.

Key words: Anura, abundance, Brazil, community structure, distribution pattern, environmental factors

INTRODUCTION

Studies relating the distribution and diversity of anurans with environmental variables in tropical forests have often been based on litter communities on the forest floor (Fauth et al., 1989; Allmon, 1991; Giaretta et al., 1999). Topographic factors such as altitudinal variation (Giaretta et al., 1999) and edaphic factors such as pH (Wyman, 1988), humidity (Vonesh, 2001), type of soil (Hadden & Westbrooke, 1996), clay content (Menin et al., 2007) and leaf litter (Fauth et al., 1989) are the major factors influencing the distribution of many terrestrially breeding anurans. The composition of the assemblage of adults and tadpoles associated with riparian zones, on the other hand, is largely influenced by characteristics such as understory vegetation, stream size, slope and predation (Parris & McCarthy, 1999; Eterovick & Barata, 2006; Keller et al., 2009). The composition of such assemblages differs between areas, contributing to high overall anuran species richness and high species turnover between sites (Keller et al., 2009).

Studies conducted in central Amazonian forests that focused on riparian areas concluded that the distribution of anuran species is mainly affected by the presence of suitable breeding sites (Zimmerman & Bierregaard, 1986; Zimmerman & Simberloff, 1996). Terrestrially reproducing anurans are widely distributed along a range of environmental gradients, showing small beta diversity probably because of few constraints on dispersal (Menin et al., 2007). In a study in Atlantic forest in Brazil, species were dependent on the connectivity between forests and the presence of aquatic sites for reproduction, suggesting a differential distribution of adults during non-reproductive periods (Becker et al., 2007).

In the Amazon forest, the development of eggs and tadpoles of aquatically breeding species takes place mainly in temporary ponds near streams, isolated ponds on plateaux far from streams, in accumulated water in tree holes, bromeliads, palm leafs or bamboo internodes, or directly in streams (Hödl, 1990; Summers & McKeon, 2004; Lima et al., 2006). Aquatic-reproducing anurans use rather specific breeding sites, because the presence of their larvae depends on predator densities, hydroperiod of the water body, reproductive modes and the susceptibility of eggs to desiccation (Duellman & Trueb, 1994; Pearman, 1997; Hero et al., 1998; Both et al., 2010; Rodrigues et al., 2010).

Riparian zones are defined as the area around the margins of water bodies susceptible to flooding (Gregory et al., 1991), and can show differential composition in taxonomic groups such as terrestrial herbs. Plant composition along the margins of large rivers contributes to variation in beta-diversity between habitats (Ferreira, 2000; Sabo et al., 2005). Riparian environments are complex, because flooding patterns, water and litter accumulation and light availability in the understory can change rapidly in space and time (Drucker et al., 2008). In a *terra firme* forest in central Amazonia, 42 species of anurans have been reported, of which 28 deposit their eggs in aquatic sites in riparian zones or have an aquatic larval stage (Zimmerman & Simberloff, 1996; Lima et al., 2006). We studied the distribution of aquatic-reproducing anurans in 72 plots systematically distributed in an area of 64 km², involving locations near and distant from water bodies. We considered the species using three breeding sites: 1) streams, 2) ponds and 3) phytotelmata. We determined first, the role of biotic and abiotic factors in the abundance and occurrence of anuran species, and second, the pattern of

occurrence and abundance of species between two distinct watersheds.

MATERIALS AND METHODS

Study area

Our study was carried out at Reserva Florestal Adolpho Ducke (RFAD, 02°55'–03°01'S, 59°53'–59°59'W), adjacent to the city of Manaus, in the state of Amazonas, Brazil. The reserve covers 10,000 ha of *terra firme* (non-flooded) rainforest, a well-drained forest not subject to seasonal inundation. The forest is characterized by a 30–37 m tall closed canopy, with emergents growing to 40–45 m (Ribeiro et al., 1999). The understory contains abundant sessile palms (*Astrocaryum* spp. and *Attalea* spp.; Ribeiro et al., 1999). The climate is characterized by a rainy season from November to May and a dry season during the rest of the year (Marques Filho et al., 1981). Mean annual temperature is approximately 26 °C (Marques Filho et al., 1981) and mean annual rainfall was 2489 mm between 1985 and 2004. A north–south central plateau separates two main watersheds in the RFAD, which differ in their physical-chemical characteristics; see Costa et al. (2005) and Mendonça et al. (2005) for more details.

Data collection

The surveys were undertaken in the rainy season (November to May) between 2002 and 2004. Data were collected during five nocturnal and three diurnal samples in 72 plots systematically distributed over a 64 km² grid formed by trails 8 km long (see Fig. 1 in Menin et al., 2008). Each plot was at least 1 km away from an adjacent plot. Plots were 250 m long and positioned to follow the altitudinal contour lines to minimize altitudinal and soil variation within each plot (Magnusson et al., 2005). All plots were at least 1 km from the edge of the reserve.

Diurnal anuran assemblage surveys (*Atelopus spumarius*, *Dendrophryniscus minutus*, *Allobates* sp. and *Allobates femoralis*) lasted about two hours per plot, and were conducted between 0800 and 1600 by two people walking along a 250 m × 1 m (0.025 ha) plot. Observers visually scanned the leaf-litter. We sampled the nocturnal anuran assemblage by simultaneous visual encounter surveys and auditory sampling (Heyer et al., 1994). We sampled each plot for about one hour between 1830 and 2200. Every 5 m, the two observers stopped and recorded the number of vocalizing individuals of each species and searched the litter and vegetation for anurans. All individuals located visually or by their call within 20 m of the central line of the plot were recorded, so that 1 ha was searched per plot. We pooled the number of individuals recorded by the two methods of analyses.

Voucher specimens were deposited in the Amphibians and Reptiles Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA-H) in Manaus, Amazonas, Brazil. The nomenclature in this study is in accordance with Amphibian Species of the World (Frost, 2011).

Environmental parameters

The topographic parameters used were altitude and slope of each study plot. A professional surveyor meas-ured altitude at the beginning of each plot's trail. Slope measurements were taken with a clinometer every 50 m, perpendicular to the main axis of the plot, and summarized as plot averages (range 0.67–27.80º). Soil texture (clay content) was measured at the same points by collecting six samples to a depth of 5 cm. Samples were combined for each plot and analysed at the Soil Laboratory of the Agronomy Department at INPA, following EMBRAPA (1997). Soil clay content varied from 1.6% near streams to 87.7% on ridges.

The distance of the centre of each plot to the nearest stream margin was measured on a topographic map of RFAD (scale 1:50,000). The distance from the stream varied from 4 to 555 m. A previous study determined the number of trees per plot for three different diameter at breast height (DBH) classes. Individuals with 1 cm ≤ DBH <10 cm were counted in 250 m × 4 m plots; individuals with 10 cm ≤ DBH <30 cm were counted in 250 m × 20 m plots, and individuals with DBH ≥ 30 cm were counted in 250 m × 40 m plots (Castilho et al., 2006).

We measured litter volume twice during the study, at five points spaced every 50 m along each plot trail. At each point, the litter in a 60 × 60 cm area was collected and compressed in a bucket (24 cm high by 24 cm diameter), graduated in litres. We used a circular board with the same diameter as the bucket to compress the litter three times. We then removed the board and measured the volume. We use mean litter volume for each plot. Litter volume varied from 2.35 to 4.40 litres. The occurrence of each plot in the eastern and western watersheds was determined by the localization of each plot on a topographic map.

Data analysis

We used multiple regressions to investigate the effects of independent variables (slope, distance from stream, number of trees and volume of litter) on the abundance of each species, and on the number of species (Nsp) per plot. The mean abundance of each species per plot based on the five nocturnal samples or on the three diurnal samples was used in the analyses (the data are available at http://ppbio.inpa.gov.br/Eng/inventarios/ducke/anuros). Abundance data were *log* [*x*+1] transformed to reduce the effects of outliers. We did not include altitude and clay content in regression models because these were correlated with distance from stream (Pearson correlation $r=0.62$ and $r=0.68$, respectively). We used models containing only the significant variables ($P<0.05$) for graphical representations.

For species found in <36 plots, we analysed presence/absence data using logistic regression (model: presence/absence = a + slope + distance of stream + number of trees + litter volume). We recorded *Allobates* sp. and *D. minutus* mainly in diurnal samples; the individuals found in nocturnal samples (one *Allobates* sp. and eight *D. minutus*) were not considered in the analyses.

For arboreal species, only distance from stream, slope and number of trees were used in both multiple or logistic regression because we considered leaf litter not to be important to this group. For *T. resinifictrix* we considered only the number of trees with DBH > 30 cm because only such trees are used for vocalisation and egg deposition.

Table 1. Number of plots by watershed where each species was recorded at Reserva Florestal Adolpho Ducke, Manaus, Brazil. The visual and auditory samplings indicate the total number of individuals reported in all samples. The total number of individuals includes the visual and auditory samplings. Breeding site (sites of tadpole development or egg deposition and tadpole development): 1) temporary or permanent ponds near or distant from streams, 2) streams, and 3) arboreal sites (tree holes, bromeliads) (details in Menin et al., 2008).

Family/species	Breeding site	Number of plots by watershed Eastern	Western	Visual sampling	Auditory sampling	Total number of individuals
Aromobatidae						
Allobates femoralis (Boulenger, 1884)	1	1	1	2	-	2
Allobates sp.	1	-	15	43	-	43
Bufonidae						
Atelopus spumarius Cope, 1871	2	12	-	21	-	21
Dendrophryniscus minutus (Melin, 1941)	1,2	4	20	132	-	132
Rhinella marina (Linnaeus, 1758)	1	8	4	16	-	16
Rhinella proboscidea (Spix, 1824)	1	27	25	369	-	369
Centrolenidae						
Vitreorana oyampiensis (Lescure, 1975)	2	3	10	1	143	144
Hylidae						
Hypsiboas cinerascens (Spix, 1824)	2	6	16	-	136	136
Hypsiboas geographicus (Spix, 1824)	1	-	5	6	-	6
Hypsiboas lanciformis Cope, 1871	1	1	1	1	1	2
Osteocephalus oophagus Jungfer & Schiesari, 1995	3	33	39	255	2967	3222
Osteocephalus taurinus Steindachner, 1862	2	17	25	63	31	94
Phyllomedusa bicolor (Boddaert, 1772)	2	1	1	-	2	2
Phyllomedusa tarsius (Cope, 1868)	2	1	-	1	-	1
Phyllomedusa tomopterna (Cope, 1868)	2	2	1	1	3	4
Trachycephalus resinifictrix (Goeldi, 1907)	3	12	8	-	30	30
Leptodactylidae						
Leptodactylus knudseni Heyer, 1972	1	23	27	11	80	91
Leptodactylus lineatus (Schneider, 1799)	1	-	1	2	-	2
Leptodactylus mystaceus (Spix, 1824)	1	-	3	4	-	4
Leptodactylus rhodomystax Boulenger, 1884	1	-	12	7	8	15

We used SYSTAT 8.0 (Wilkinson, 1990) for all regression analyses.

A previous study (Menin et al., 2007) tested for spatial auto-correlation of independent variables using a Mantel test. There was no correlation between geographic distances among plots and the variables slope, clay content, distance from stream or number of trees (Mantel tests: $P>0.18$ in all tests). The significant correlation detected between the geographical distances between plots and litter volume ($P<0.01$) was not considered due to the small variance explained ($r^2=0.10$).

RESULTS

We detected twenty species of anurans with aquatic reproduction: nine species of Hylidae, four Leptodactylidae, four Bufonidae, two Aromobatidae and one Centrolenidae (Table 1). Eleven of these reproduce in temporary or permanent ponds near or distant from streams (Table 1). *Osteocephalus oophagus* occurred in all plots and was the most frequently encountered species, representing 74%

of all individuals. *Rhinella proboscidea*, *Leptodactylus knudseni* and *Osteocephalus taurinus* occurred in more than 50% of the plots (Table 1).

Eight species (*Allobates femoralis*, *Hypsiboas geographicus*, *H. lanciformis*, *Phyllomedusa bicolor*, *P. tarsius*, *P. tomopterna*, *Leptodactylus mystaceus* and *L. lineatus*) represented less than 2% of all individuals sampled (Table 1), and were excluded from analyses. *Rhinella marina*, a common species in open areas and found occasionally in the forested areas, was also excluded.

Effects of environmental variables on the number of species and on abundance

The number of species encountered per plot varied from one to nine (mean = 4.75; SD = 1.78). The model explained about 45% of the variance in the number of species (Nsp = 6.635–0.0260 Slope – 0.008 Distance of stream – 0.003 Number of trees + 0.468 Leaf litter volume; $R^2=0.420$; $F_{4,67}=12.127$; $P<0.01$). The number of species was negatively related to distance from stream ($t = -6.367$; $P<0.01$).

Table 2. Results derived from models of multiple regressions (abundance of species i = a + slope + distance of stream + number of trees + litter volume) and probabilities associated with effects of each variable on the abundance of anuran species at Reserva Florestal Adolpho Ducke, Manaus, Brazil. P = probabilities. Significant values are shown in italics.

Species	Constant	Slope	Distance from stream	Number of trees	Litter volume	R^2	F	P
Rhinella proboscidea	–0.393	0.007 P=0.459	0.0001 P=0.958	0.001 *P=0.045*	–0.007 P=0.959	0.081	$F_{4,66}$=1.448	0.228
Osteocephalus oophagus	2.278	–0.001 P=0.858	–0.00003 P=0.801	0.00001 P=0.969		0.0001	$F_{3,68}$=0.023	0.995
Osteocephalus taurinus	0.190	0.003 P=0.449	–0.001 *P=0.007*	0.00009 P=0.680		0.158	$F_{3,68}$=4.253	*0.008*
Leptodactylus knudseni	0.228	–0.002 P=0.497	0.0001 *P=0.028*	0.0001 P=0.497	0.011 P=0.822	0.125	$F_{4,67}$=2.385	0.060

The model did not explain the variation in the abundance of *R. proboscidea*, *L. knudseni* and *O. oophagus* (Table 2). For *R. proboscidea*, one plot was considered an outlier and was excluded. This plot has a high abundance of this species (16.8 individuals, mean by plot = 1.02; SD = 4.73), due to the high number of newly metamorphosed individuals found (see Menin et al., 2008 for details). However, there was a significant effect of number of trees (Table 2), which showed a positive relationship with the abundance of this species (Fig. 1A). For *L. knudseni* and *O. taurinus*, which reproduce in temporary ponds, a significant effect of distance from stream was detected (Table 2, Fig. 1B,C).

Effects of the environmental variables on species presence/absence

Distance from stream contributed negatively to species with reproduction in streams or temporary ponds at streams margins (*Allobates* sp., *D. minutus*, *H. cinerascens* and *L. rhodomystax*, Table 3). The number of trees

contributed negatively to the presence of *Allobates* sp. and positively to the presence of *A. spumarius* (Table 3). For *L. rhodomystax*, litter volume also contributed significantly to the model (Table 3). Although the model explained 61% of the variance for the presence of *V. oyampiensis*, no variable contributed significantly (Table 3). The model did not explain the distribution of *T. resinifictrix* (Table 3).

Effects of watersheds on the number and abundance of each species

There was no significant difference in the number of species per plot between watersheds (P=0.068). A total of 11 species were recorded in the western watershed, and ten in the eastern watershed. *Leptodactylus rhodomystax* and *Allobates* sp. occurred only in the western watershed, while *A. spumarius* occurred only in the eastern watershed (Table 1). There was no significant difference in abundance of the remaining species between watersheds (all P values >0.055).

Table 3. Results derived from models of logistic regressions (presence/absence = a + slope + distance of stream + number of trees + litter volume) and probabilities associated with effects of each variable on the presence/absence of anuran species at Reserva Florestal Adolpho Ducke, Manaus, Brazil.* = only trees with DBH >30 cm. P = probabilities. Significant values are shown in italics.

Species	Constant	Slope	Distance from stream	Number of trees	Litter volume	McFadden's Rho^2	χ^2	P
Allobates sp.	0.659	–0.118 P=0.051	–0.015 *P=0.002*	–0.007 *P=0.043*	1.619 P=0.089	0.340	25.019	*<0.001*
Atelopus spumarius	–10.192	–0.007 P=0.890	–0.005 P=0.182	0.010 *P=0.007*	0.459 P=0.586	0.223	13.721	*0.008*
Dendrophryniscus minutus	–0.737	–0.010 P=0.845	–0.020 *P<0.0001*	–0.003 P=0.253	1.306 P=0.096	0.423	38.745	*<0.0001*
Vitreorana oyampiensis	7.428	–0.064 P=0.360	–0.067 P=0.078	–0.008 P=0.083		0.615	41.824	*<0.001*
Hypsiboas cinerascens	3.477	0.043 P=0.607	–0.094 *P=0.045*	–0.002 P=0.675		0.724	62.914	*<0.0001*
Trachycephalus resinifictrix	0.295	–0.052 P=0.231	–0.003 P=0.249	0.004* P=0.840		0.026	2.239	0.524
Leptodactylus rhodomystax	–5.098	–0.113 P=0.075	–0.012 *P=0.013*	–0.003 P=0.418	2.150 *P=0.042*	0.225	13.048	*0.011*

Fig. 1. Regressions for statistically significant effects of predictor variables on log (density+1) for three species of aquatically-breeding frogs at Reserva Florestal Adolpho Ducke, Manaus, Brazil. The open circle is an outlier. A) *Rhinella proboscidea*, B) *Osteocephalus taurinus* and C) *Leptodactylus knudseni.*

DISCUSSION

Distance from stream was the variable that affected the richness and the distribution of the majority of anuran species. An increase in distance from stream resulted in a decrease in the number of species and individuals for *Allobates* sp., *D. minutus*, *H. cinerascens*, *O. taurinus* and *L. rhodomystax*, which reproduce in streams or temporary ponds (see also Menin et al., 2008); only the abundance of *L. knudseni* was positively influenced by distance from the stream. This indicates that species are found mainly near streams where reproductive sites are found. If rain volume is high, the streams overflow forming small ponds, used for reproduction. The abundance and presence of phytotelmata breeders (*O. oophagus* and *T. resinifictrix*) were not determined by any of the variables analysed. Rain can also create ponds isolated from streams in clay areas, where some species can reproduce (e.g. the Microhylidae *Chiasmocleis* spp. and *Ctenophryne geayi* and the hylid *Scinax* spp. are present in the RFAD but were not registered in this study; Zimmerman & Simberloff, 1996; Lima et al., 2006; Rodrigues et al., 2010). However, such water bodies are uncommon (Rodrigues et al., 2010), explaining the rarity of some species (e.g. *Phyllomedusa* spp.).

Small diurnal species (*A. spumarius*, *Allobates* sp. and *R. proboscidea*) were affected by tree density. A high number of trees represents a high abundance of trees with lower DBH (Castilho et al., 2006), which is common near water bodies. *Rhinella proboscidea* deposits its eggs in shallow ponds near small streams, headwaters of streams or ponds formed by rains (Menin et al., 2006); the majority of individuals found in the present study were juveniles and newly metamorphosed individuals.

As found for anurans with terrestrial reproduction (Menin et al., 2007), litter volume was not a good predictor of species abundance or occurrence except for *L. rhodomystax*. Litter layer depth has been studied for many herpetological communities in different regions. Some studies reported positive relationships between litter layer and species richness or abundance (Fauth et al., 1989; Giaretta et al., 1999; Vonesh, 2001), while other studies did not find any effect (Allmon, 1991; Menin et al., 2007). In studies conducted in central Amazonia, a higher production of litter was estimated in plane and clay areas (Luizão et al., 2004). The abundance and occurrence of many species in this study was influenced negatively by an increase in distance from stream and, consequently, by clay content.

The watersheds did not influence the abundance of the majority of species, but three species had differential distribution in the watersheds. *Atelopus spumarius* occurred only in the eastern watershed, while *L. rhodomystax* and *Allobates* sp. occurred only in the western watershed. In spite of the absence of adults of the latter two species, tadpoles of both species were found in the eastern watershed in aquatic habitats, but at very low densities (D. J. Rodrigues, pers. comm.). The absence or low density of these three species probably occurred due to tadpole predation (e.g. Hero et al., 1998) or water body permanence (e.g. Both et al., 2010). Fish are the main predators in aquatic
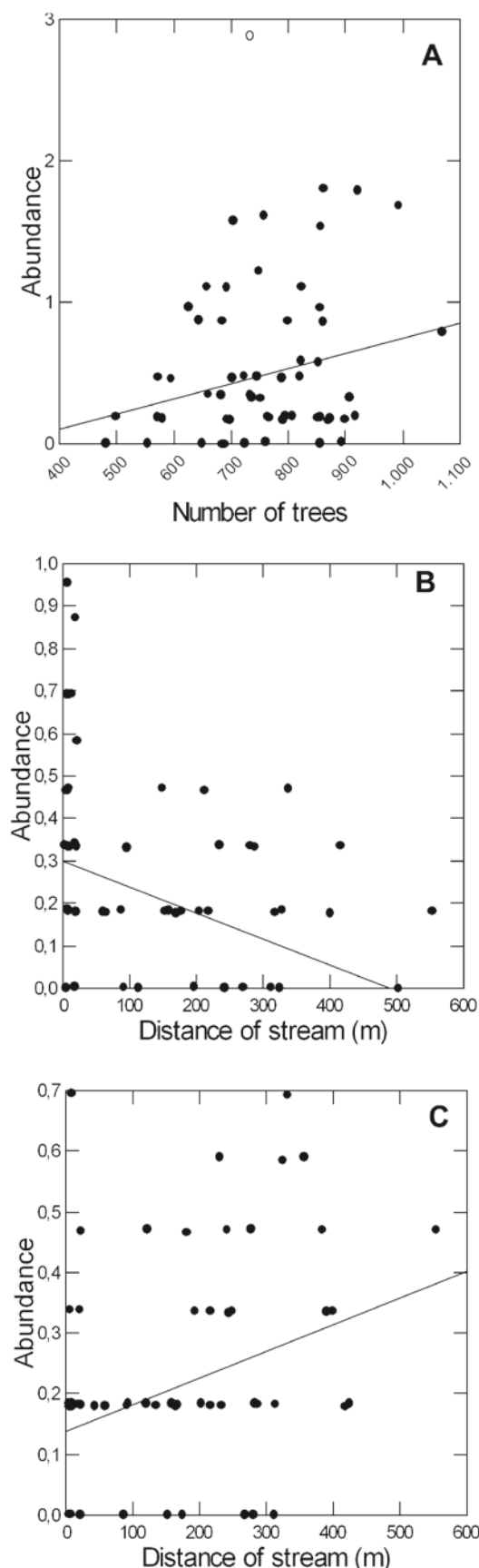
habitats, determining the composition of tadpole communities in central Amazonia (Hero et al., 1998). On the other hand, the streams of both watersheds in RFAD have different physical-chemical characteristics (Mendonça et al., 2005). In other studies in RFAD, a differential composition of fish (Mendonça et al., 2005), shrubs (Kinupp & Magnusson, 2005) and understory plants (Costa et al., 2005) was reported between the watersheds, although the fish assemblages in temporary ponds were similar (Pazin et al., 2006). This shows that apparently homogeneous areas can have abrupt discontinuities in species composition (Costa et al., 2005). Aquatic-reproducing frogs showed high beta diversity (Zimmerman & Bierregaard, 1986), in contrast to terrestrial-reproducing species which are distributed along all gradients and occurred in both watersheds (Menin et al., 2007).

Our results indicate that the majority of species studied occur along streams and can use the margins of streams as dispersal corridors, reducing the probability of finding these species far from streams. These results underline the importance of riparian zones for aquatic-breeding frogs (Parris & McCarthy, 1999; Eterovick & Barata, 2006; Keller et al., 2009) and other taxonomic groups (Drucker et al., 2008; Fraga et al., 2011), contrasting with results found for terrestrial-breeding anurans, which occupy the majority of habitats in RFAD (Menin et al., 2007). An understanding of the influence of environmental factors on the abundance and occurrence of species is necessary for effective conservation. When links between habitat structure and ecological requirements are identified, conservation strategies can be effectively elaborated and implemented. The forests along the margins of streams can be corridors for the dispersal of species that reproduce in this area, mainly because they maintain the microclimatic conditions required for survival (Stoddard & Hayes, 2005). These riparian areas support a characteristic species assemblage, showing a turnover in species pools between riparian and upland habitats (Sabo et al., 2005; Druker et al., 2008; Fraga et al., 2011). The removal of forests near streams (see Toledo et al., 2010 for discussion on a new Brazilian Forest Act proposal) could negatively affect amphibian populations, leading to local extinctions.

ACKNOWLEDGEMENTS

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