

The Effect of Riparian Zones on Species Diversity of Frogs in Amazonian Forests

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We investigated the effects of riparian zones, and associated environmental variables, on the composition and number of species of frogs per sample unit in an Amazonian forest. Sample plots in riparian (up to 10 m from water bodies) and non-riparian areas were distributed over a 25 km² sampling grid to obtain a representative sample of habitats in each category. Each plot was sampled three times, over two rainy seasons. The riparian plots harbored more and different species than the non-riparian plots. In riparian areas near streams, the species composition changed along the gradient associated with stream width. The higher number of individuals and species in riparian plots highlights the importance of water courses and associated riparian areas for the conservation of anuran diversity in Amazon rainforests.

Nós investigamos os efeitos das zonas ripárias e variáveis ambientais associadas ao número e composição de espécies de anuros em uma floresta amazônica. Parcelas ripárias (até 10 m dos corpos d'água) e não ripárias foram distribuídas sobre uma grade de 25km² para obter uma amostra representativa dos habitats em cada categoria. Cada parcela foi amostrada três vezes, durante duas temporadas de chuva. As parcelas ripárias abrigaram mais espécies e possuíram uma composição de anuros diferente das parcelas não ripárias. Em áreas ripárias, à beira de riachos, a composição de espécies mudou ao longo do gradiente associado com a largura dos riachos. Os maiores números de indivíduos e de espécies em parcelas ripárias destacam a importância dos cursos de água e respectivas áreas ciliares para a conservação da diversidade de anuros na floresta amazônica.

SABO et al. (2005) examined global patterns of species richness between riparian and non-riparian areas in seven continents, with a range of taxa from desert soil fungi to tropical-forest primates, and concluded that riparian areas do not have higher species richness than non-riparian areas. However, they found that species composition differs between the two areas, and concluded that although riparian areas do not have higher alpha diversity, they increase regional species diversity by increasing beta diversity. The review by Sabo et al. (2005) included only four studies of anurans, a group that might be expected to show strong differences in species richness between riparian and non-riparian areas, and those studies only recorded two to 11 species of frogs. Because of the temperate North American bias, most of the species of amphibians included in the review by Sabo et al. (2005) were salamanders.

Plant and animal species do not homogeneously occupy riparian areas, and stream characteristics, such as size, flow rate, and surrounding vegetation influence the structure of animal (Parris and McCarthy, 1999; Keller et al., 2009) and plant (Drucker et al., 2008) communities. Recent studies that investigated the influence of environmental gradients on adult anuran assemblages in the Amazon concluded that the assemblages respond mainly to distance from streams and factors associated with stream characteristics (Condrati, 2009; Rojas-Ahumada et al., 2012). In contrast to the results of Sabo et al. (2005), those authors concluded that Amazonian riparian zones hold more species of frogs per sampling unit than non-riparian areas.

Previous studies in the Amazon, although concordant, were conducted in humid forest near the center of the Amazon forest using almost identical species assemblages

with similar evolutionary histories. Northern and southern Amazonia have distinct anuran assemblages, possibly because rainfall seasonality is reversed between the north and south, and this allows for a test of whether the pattern of higher species density in riparian areas found in previous studies holds for a largely independently derived Amazonian anuran fauna in drier peripheral Amazon rainforests of the northern hemisphere.

Sabo et al. (2005) noted that few studies had sufficient replication to assess beta diversity within riparian and non-riparian areas. Alpha diversity (number of species collected per sampling unit) is a characteristic of the experimental design as well as the biotic community. Zones with high alpha diversity, but low beta diversity, may harbor less species overall than zones with low alpha diversity, but high beta diversity.

Riparian areas are severely impacted by human activities (Bren, 1993), and many researchers have stressed the importance of water bodies and riparian areas for the conservation of animal species. To evaluate the contribution of riparian areas to overall species richness, it is necessary to have representative samples of riparian and non-riparian areas, and evaluate the contribution of different zones with species-accumulation curves. In this study, we used a RAPELD sampling grid (Magnusson et al., 2005) to obtain samples of the overall anuran community in proportion to their occurrence in the landscape in both riparian and non-riparian zones, and this allowed evaluation of differences in overall species richness, as well as differences in alpha diversity.

MATERIALS AND METHODS

Study area.—This study was conducted in the Estação Ecológica de Maracá (ESEC Maracá), a river island formed

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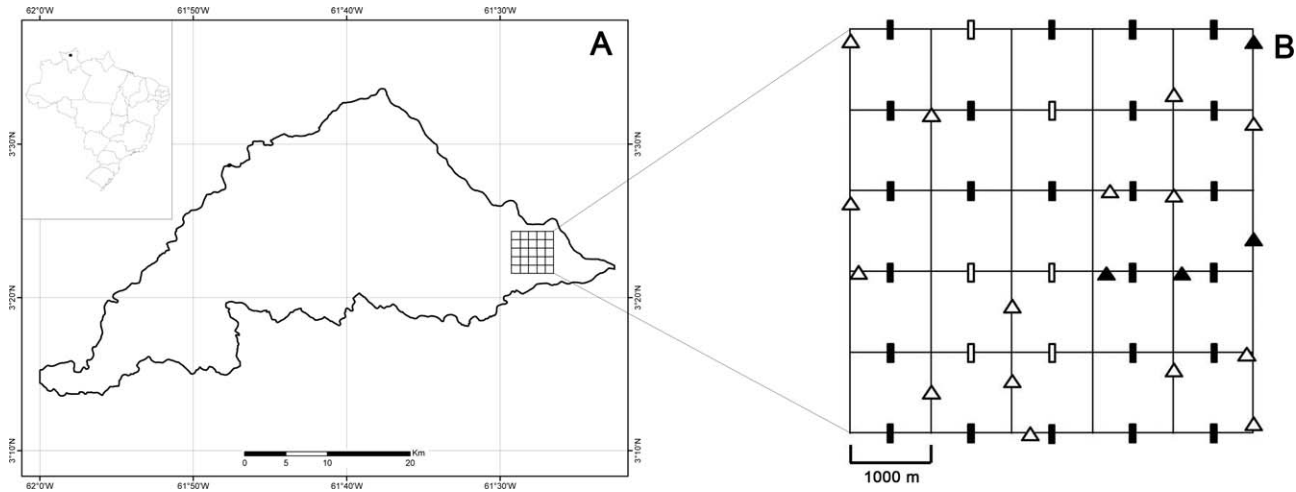


Fig. 1. (A) Map of Brazil showing the location of Maracá Island (black square) and location of the 25 km² RAPELD grid indicated by the 5 km long access tracks on eastern end of Maraca island; (B) Distribution of plots in the sample site. Lines represent the trails; rectangles represent the 30 evenly distributed plots: black rectangles are plots in non-riparian areas and white rectangles are uniformly distributed plots in the riparian zone. The white triangles are shoreline plots near streams and black triangles are shoreline plots near lakes.

by the Uraricoera river in the northern region of the state of Roraima, Brazil (between 3°15' and 3°35'N, 61°22' and 61°54'W), located at the junction of the Roraima-Rupununi savanna with the Amazon Rainforest (Fig. 1). The island covers an area of approximately 103,796 ha, with predominance of semi-deciduous rain forest that is not subject to long-term seasonal flooding (Milliken and Ratter, 1998). Mean annual temperature is approximately 26°C (range in daily maxima 21–46°C). Annual rainfall ranges from 1750–2250 mm, with a pronounced dry season between October and March and a rainy season between April and September.

Sampling design.—The eastern end of ESEC Maracá has a research site of the Program for Research in Biodiversity (PPBio) of the Brazilian Ministry of Science and Technology that follows the RAPELD spatial model (for more details see http://ppbio.inpa.gov.br/Port/instalacao/instalacaogrades/document_view; Magnusson et al., 2005). The sampling site is composed of a 5 × 5 km grid (25 km²) formed by six trails running from east to west and another six running from north to south equidistant by 1 km. The PPBio installed thirty 250 m long plots at 1 km intervals along the east–west trails, giving uniform coverage of the 25 km² grid (Fig. 1). The center lines of the plots follow altitudinal contour lines to minimize variation in altitude, soil conditions, and water-table depth within each plot. These 30 plots were considered the uniformly distributed plots.

Six (20%) of the evenly distributed plots were less than 10 m from streams and were considered riparian plots (Fig. 1). We used a broad definition of riparian areas as those that are transitional between terrestrial and aquatic ecosystems (e.g. streams, rivers, lakes, and dams). Such broad definitions are used in laws relating to riparian areas, such as the Brazilian Forest Code (Law 4771/65). To obtain more samples of different types of riparian zones, we installed 19 additional 250 m long plots along the margins of water bodies; 15 on the margins of terra-firme streams and four on the margins of lakes (Fig. 1). The center lines of these 19 shoreline plots followed the margins of streams or lakes and were about 2 m from the edge of the water. Unlike the uniformly distributed plots, the center lines of these plots

did not follow altitudinal contours, but were slightly inclined due to the gradual fall in altitude along the streams.

Sampling of anuran assemblages.—Each of the 49 plots was visited three times, over two rainy seasons (August 2008, May and June 2009). Two complementary methods, visual and auditory, were used simultaneously for sampling frogs (Rödel and Ernst, 2004; Menin et al., 2007). The surveys were always conducted by the same two observers, who recorded all frogs vocalizing up to 10 m from the center line of each plot and any that were seen up to 15 m from the line. In each of the surveys, the species assemblage was sampled during late afternoon between 1700–1900 h, and at night between 1900–2300 h. We maintained spatial rather than temporal standardization, and spent about 85 min in active search in each plot per survey. However, the total time spent in each plot per survey varied between 15–20 min during the day and 60–95 min at night due to time spent capturing and measuring individuals.

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

Environmental variables.—For each of the uniformly distributed plots, the following environmental variables were available: proportion of canopy opening, slope, altitude, proportion of clay in the soil, and tree density. The researchers responsible for the collection of the environmental variables in the evenly distributed plots and the values of all environmental variables can be found online in the PPBio website (<http://ppbio.inpa.gov.br>). Methods of collection are given in the site and summarized below.

Canopy openness was estimated by R. Braga-Neto and G. Zuquim using hemispherical photographs taken at six equidistant points, 50 m apart. A Nikon Coolpix 4500 camera was used with a hemispherical lens converter, supported on a tripod 1 m above the ground. The photographs were taken in the early morning (from 0530–0830 h) and late afternoon (from 1600–1800 h) to avoid

direct incidence of sunlight on the lens. The images were analyzed in the GLA (Gap Light Analyzer) program (www.ecostudies.org/gla). For analyses, an average of the six points per plot was used. The mean amplitude of canopy openness per plot was 2.93–5.88%.

Altitude was measured by a professional topographer at the beginning of each plot and, as the uniformly distributed plots followed the altitudinal contour lines, the value is constant along the center line of the plot. Altitude varied from 54.9–82.5 m. Slope measurements were made with the aid of a clinometer at six equidistant points, 50 m apart, along the center line of the plot by F. B. Baccaro and R. N. O. de Araújo, and we used the mean of the measurements to represent the slope of each plot, which varied from 1.3–16.3°. Analyses of soil characteristics for each plot undertaken by T. P. Pimentel were based on a composite of six samples per plot taken at six equidistant points, 50 m apart by F. B. Baccaro. Proportion of clay in the soil (soil particle size <0.002 mm) ranged from 1.5–13.5% in the sampled plots.

Castilho et al. (2006) established a hierarchical design to sample trees by diameter class at breast height (dbh): trees with dbh \geq 30 cm were sampled in about 1 ha (40 m strip along the plot); sub-samples of about 0.5 ha (20 m strip) and about 0.1 ha (4 m strip) were used to sample trees with 10 cm \leq dbh < 30 cm and 1 cm \leq dbh < 10 cm, respectively. The data for sub-samples were extrapolated to 1 ha, and we used the tree density per hectare, which ranged from 1952–9152, in analyses.

In 15 of the shoreline plots that were along streams, we measured width and maximum depth of the stream, water velocity, and herbaceous and shrub cover. Depth and width were measured at six equidistant points, 50 m apart. For both width and the depth, we used the mean of the six measurements for the analysis. Both measurements were taken only once during the study between 2 and 23 June 2009, a time of year when the streams in the study area showed little variation in size. The mean depth of the streams ranged from 2.1–19.3 cm and mean width from 21.8–231 cm.

Water velocity was estimated as the time a plastic rectangle (5 cm \times 3 cm) released in the center of the stream took to travel one meter on the water surface, determined at six equidistant points, 50 m apart (Dias et al., 2009). We used the average of six points for the analysis, which ranged from 0–0.282 m/s. Water velocity measurements were taken at the same times as with the width and depth measurements.

Cover of herbaceous and shrub vegetation was estimated from point quadrates. A 2 m high wooden rod with a diameter of about 2 cm was placed vertically at 2 m intervals along the center line of the plot and a record was made each time it made contact with a plant (adapted from Magnusson et al., 2008). Relative cover of herbs and shrubs in plots ranged from 49.6–81.6%.

The small number (four) of shoreline plots near lakes did not justify analyses of habitat variables. To compare riparian areas with more upland areas, we include all shoreline plots, whether near lakes or rivers, and six of the evenly distributed plots that were within 10 m of streams, as riparian plots, giving 25 riparian plots and 24 upland plots.

Data analysis.—We used t-tests to compare riparian and non-riparian plots for differences in the number of species and

the number of individuals. As data for number of individuals were not normally distributed, we used log transformations to satisfy the assumptions of the t-test (Sokal and Rohlf, 1995). Since, the number of species between riparian and non-riparian areas could simply be an artifact of the difference in the number of individuals collected in each of those areas (Gotelli and Graves, 1996). Thus, rarefaction curves were constructed by 1,000 randomizations based on the number of individuals in order to analyze whether differences in richness exist between riparian and non-riparian plots independent of differences in frog abundance between the areas.

In community ecology studies, each species potentially represents a dimension, and it is difficult to interpret more than three dimensions (Legendre and Legendre, 1998). Ordination techniques reduce the dimensionality of data, summarizing a data set with many variables into a small number of synthetic variables that allows description of the dominant trends in species composition (McCune and Grace, 2002). Nonmetric Multidimensional Scaling (NMDS) was used as an ordination technique to reduce the dimensionality of the data by ordering the plots in relation to species composition. Separate analyses were undertaken for the 30 evenly distributed plots, all 49 plots, and the 15 shoreline plots near streams. We used the ordination with 30 evenly distributed plots to evaluate the influence of environmental variables on species composition, all 49 plots to assess differences in species composition between riparian (25 plots) and non-riparian plots (24 plots), and the 15 shoreline plots near streams to evaluate the influence of stream characteristics on species composition.

Two sets of ordination were carried out for each group of plots, one based on the presence and absence of species, and the other using the species-abundance data. At the scale of this study, ordinations with presence-absence data generally show patterns based on the less common species, since the most common species tend to occur in the majority of the plots and contribute little to qualitative differences. At the scale of this study, abundance data generally reveal patterns for the most common species which show large differences in abundance between plots. To avoid temporal differences due to the season of sampling, analyses were based on abundance matrices that used the maximum abundance of each species recorded in any of the three sampling campaigns conducted in each plot. *Leptodactylus fuscus* and *Rhinella cf. merianae* were not included in the NMDS, as they occurred mainly in open areas.

The scores of a one-dimensional NMDS, which represents the strongest pattern for the community composition, were used as the dependent variable in multiple regression analyses to investigate the effects of environmental variables for uniformly distributed plots and shoreline plots near streams. Twenty-nine plots were used in the regression model for evenly distributed plots, since canopy-openness data were not available for one of the plots. Data on current velocity and stream depth were not included in the multiple regression model because they were positively correlated with the width of the stream (Pearson correlation $r = 0.77$ and $r = 0.86$, respectively).

Statistical tests are compromised by spatial autocorrelation only when both the predictor and response variables are autocorrelated (Legendre et al., 2002). To test for spatial autocorrelation in the dependent and predictor variables, we generated correlograms using Moran's I, which detect

Table 1. Number and Percentage (in Brackets) of Plots Where Each Frog Species Was Recorded During the Study in the ESEC Maracá (Roraima, Brazil) in August 2008, and May and July 2009.

| | Riparian areas (n = 25) | Non-riparian areas (n = 24) |
|---|----------------------------|--------------------------------|
| Allophrynidae | | |
| <i>Allophryne ruthveni</i> | 2 (8) | 0 (0) |
| Bufoidea | | |
| <i>Rhaebo guttatus</i> | 5 (20) | 1 (4.2) |
| <i>Rhinella marina</i> | 6 (24) | 7 (29.2) |
| <i>Rhinella</i> cf. <i>merianae</i> | 3 (12) | 1 (4.2) |
| Hylidae | | |
| <i>Dendropsophus</i> cf. <i>microcephalus</i> | 2 (8) | 0 (0) |
| <i>Hypsiboas crepitans</i> | 16 (64) | 10 (41.7) |
| <i>Hypsiboas geographicus</i> | 2 (8) | 0 (0) |
| <i>Hypsiboas multifasciatus</i> | 20 (80) | 5 (20.8) |
| <i>Phyllomedusa</i> <i>hypochondrialis</i> | 1 (4) | 0 (0) |
| <i>Scinax ruber</i> | 1 (4) | 2 (8.3) |
| <i>Trachycephalus typhonius</i> | 1 (4) | 1 (4.2) |
| Leiuperidae | | |
| <i>Physalaemus ephippifer</i> | 18 (72) | 4 (16.7) |
| Leptodactylidae | | |
| <i>Leptodactylus</i> aff. <i>andreae</i> | 22 (88) | 22 (91.7) |
| <i>Leptodactylus bolivianus</i> | 21 (84) | 21 (87.5) |
| <i>Leptodactylus fuscus</i> | 1 (4) | 1 (4.2) |
| <i>Leptodactylus knudseni</i> | 12 (48) | 18 (75) |
| <i>Leptodactylus lineatus</i> | 4 (16) | 4 (16.7) |
| <i>Leptodactylus mystaceus</i> | 10 (40) | 11 (45.8) |
| <i>Leptodactylus</i> gr. <i>podicipinus-wagneri</i> | 20 (80) | 0 (0) |
| Microhylidae | | |
| <i>Elachistocleis surumu</i> | 5 (20) | 0 (0) |

spatial autocorrelation in different distance classes (Legendre and Legendre, 1998).

All statistical tests were conducted with the statistical software R version 2.12.1 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria; <http://www.R-project.org>), using the vegan package to prepare the NMDS and rarefaction curves (Oksanen et al., 2008), and the pgrmss package to construct correlograms (Giraudeau, 2011).

RESULTS

We encountered 1,076 individuals belonging to 20 anuran species from six families (Table 1). The two families with the highest number of recorded species were Leptodactylidae and Hylidae (seven species each), followed by Bufoidea (three), Allophrynidae (one), Leiuperidae (one), and Microhylidae (one). The number of species recorded per plot in the 49 plots ranged from one to 11 (mean = 5.71, SD = 2). *Allophryne ruthveni*, *Dendropsophus* cf. *microcephalus*, *Phyllomedusa hypochondrialis*, *Hypsiboas geographicus*, *Leptodactylus* gr. *podicipinus-wagneri*, and *Elachistocleis surumu* were found only in riparian plots.

The two most widely distributed species, *Leptodactylus* aff. *andreae* and *Leptodactylus bolivianus*, were recorded in more than 85% of the plots. Eleven species had restricted

distributions and were recorded in less than 20% of the plots, while seven species had intermediate occurrences, and were recorded in 25–62% of plots (Table 1). Similar patterns were found for non-riparian plots, and few differences were found between the results for all plots combined and results for non-riparian plots (Table 1). However, in the riparian plots *Hypsiboas multifasciatus*, *L. aff. andreae*, *L. bolivianus*, *L. gr. podicipinus-wagneri*, and *Physalaemus ephippifer* had wide distributions, occurring in more than 70% of the plots, nine species showed restricted distributions and were recorded in less than 20% of the plots, while six species had intermediate distributions, and were recorded in 25–64% of the riparian plots (Table 1).

Uniformly distributed plots.—The ordination of plots in species space, represented by a single NMDS axis, captured 60% of the variance in the association matrix using binary data and 70.5% of the variance using species-abundance data. Thus, we used the NMDS in one dimension as a dependent variable in the multiple regression analyses for qualitative and quantitative data. The dependent variables did not show significant spatial autocorrelation at any distance class ($P > 0.11$ in all cases).

The species composition based on presence–absence data (Fig. 2) was significantly influenced by the altitudinal gradient ($R^2 = 0.281$, $P = 0.034$, $n = 29$). However, this association was weak, explaining only about 28% of the variance in the dependent variable. Species composition based on presence–absence data was not influenced by canopy openness, slope, amount of clay in the soil, or number of trees ($P > 0.17$ in all cases). *Hypsiboas geographicus*, *Leptodactylus* gr. *podicipinus-wagneri*, and *Physalaemus ephippifer* occurred mainly in the lower extreme of the altitude gradient, while the other species occurred throughout the gradient. None of the environmental variables influenced the species composition derived from species-abundance data ($P > 0.15$ in all cases).

Differences between riparian and non-riparian areas.—The number of species recorded in riparian plots ranged from four to 11 (mean = 6.88, SD = 1.69), and one to eight in non-riparian plots (mean = 4.5, SD = 1.53). The number of individuals recorded ranged from 10 to 93 in riparian plots (mean = 30.8, SD = 18.6), and 4 to 22 in non-riparian plots (mean = 12.8, SD = 5.1). The riparian plots harbored a significantly higher number of species ($t = 5.16$, $df = 47$, $P < 0.0001$) and individuals ($t = 5.58$, $df = 47$, $P < 0.0001$) per plot than non-riparian plots.

Since the number of individuals differed between riparian and non-riparian plots, differences in number of species could simply be an artifact of the difference in the number of individuals. Therefore, we used rarefaction curves based on the number of individuals to evaluate differences between the areas in number of species independent of differences in number of individuals. Even when we standardized the abundance of species in the riparian plots to that of the total number of individuals recorded in the non-riparian plots (307 individuals) using the rarefaction curve based on number of individuals (Fig. 3), the species richness of riparian plots (mean of 18 species, with 95% CI of 15–20) was substantially greater than that of non-riparian plots (14 species). This suggests that the difference in the number of species found in the riparian and non-riparian plots was not due only to differences in the number of individuals recorded.

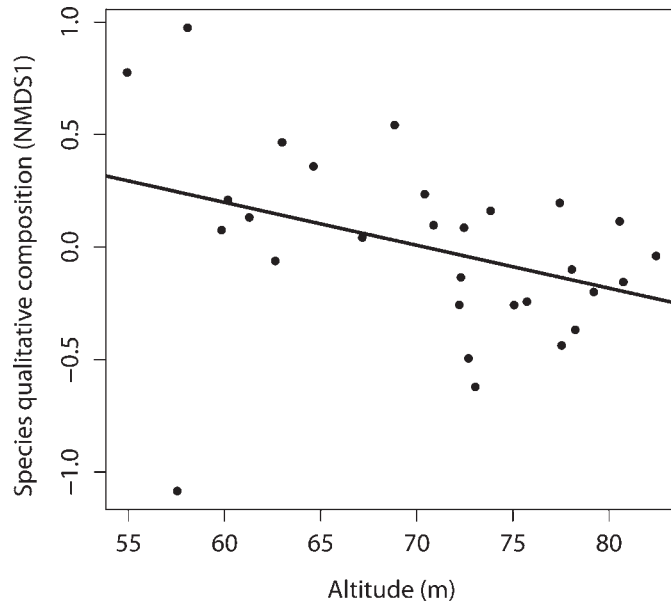


Fig. 2. Relationship between altitude of the plots and anuran species composition represented by one-dimensional Nonmetric Multidimensional Scaling (NMDS), based on the species presence–absence matrix from 29 plots evenly distributed over 25 km².

Since a single NMDS axis explained 54% of the variation in the association matrix based on binary data and 60% of the abundance data, these were used to represent the ordination of plots in species space. The composition of frog species represented by the NMDS axis differed between riparian and non-riparian plots for both presence–absence ($t = 5.62$, $df = 47$, $P < 0.0001$) and species-abundance ($t = 6.47$, $df = 47$, $P < 0.0001$) data, indicating distinct assemblages in the two habitats.

Influence of environmental variables on assemblages along streams.—To test for association with stream characteristics, we carried out an ordination of the 15 shoreline plots that were along streams. The first dimension of the NMDS captured 58% of the variance in differences among plots for presence–absence data and 77% for abundance data.

Multiple regression ($R^2 = 0.326$, $n = 15$) indicated that species composition, based on presence–absence data was influenced ($P = 0.03$) by the stream width (Fig. 4), but not by vegetation cover ($P = 0.95$). For abundance data, neither stream width ($P = 0.26$) nor percentage vegetation cover ($P = 0.31$) influenced species composition.

DISCUSSION

The composition of anuran species in northern Amazonia changed along the altitudinal gradient. Altitude does not directly influence anurans, but represents other variables that act as environmental filters, such as soil characteristics, vegetation, and distance from water bodies. On Maracá Island, altitude is not as strongly associated with soil structure and vegetation (this study) as it is in Central Amazonia (Chauvel et al., 1987; Condrati, 2009). Composition was not related to soil or vegetation variables in this study, so distance from water bodies or soil humidity is likely to be the principal variable affecting anurans associated with the altitude gradient on Maracá Island.

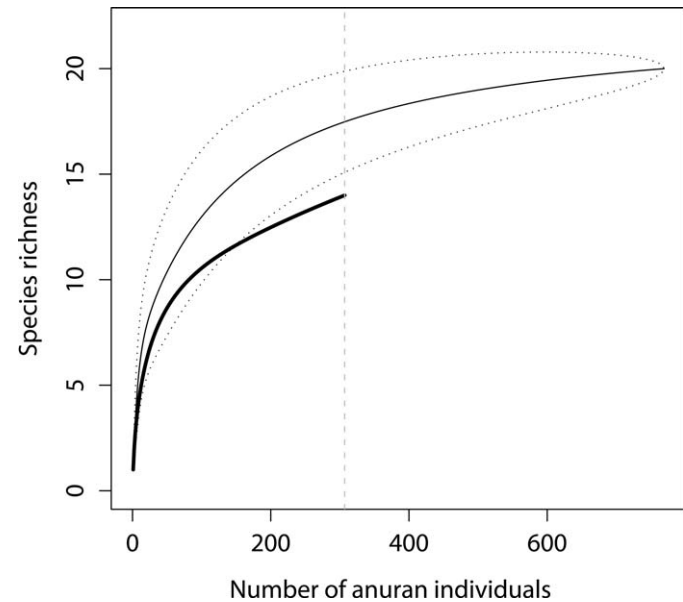


Fig. 3. Rarefaction curve based on the number of anuran individuals recorded in non-riparian (thick solid line) and riparian (thin solid line) plots with upper and lower 95% CI (dotted lines). The vertical dashed line represents the total number of individuals (307) found in non-riparian plots.

The influence of distance from water bodies has been reported in Central Amazonia for understory plants (Drucker et al., 2008), understory birds (Bueno et al., 2012), and amphibians (Rojas-Ahumada et al., 2012). Although altitude does not directly affect the biota, it is useful as a surrogate because it is easily obtained from topographic maps, and it may be an important tool for management and conservation plans. The amphibian assemblages from pristine forests in the Republic of Cameroon responded simultaneously to the altitudinal gradient and the ecotone caused by the presence of forest streams (Hofer et al., 2000).

In this study, and studies in central Amazonia (Condrati, 2009; Rojas-Ahumada et al., 2012), riparian areas had higher numbers of anuran species than non-riparian areas; a pattern that differs from the general pattern suggested by Sabo et al. (2005). The presence of breeding habitats is a critical factor that influences the distribution of anuran species, since larvae of many species depend on water for development (Zimmerman and Bierregaard, 1986), and water bodies influence anuran assemblages in tropical forests in Ivory Coast (Ernst and Rödel, 2006) and Singapore (Bickford et al., 2010). With the exception of *Leptodactylus* aff. *andreae*, all species we sampled depend on water for reproduction, which probably explains the strong influence of water bodies per se on the composition of frog species on Maracá Island.

Streams do not increase beta diversity only by creating differences between riparian and non-riparian areas. The anuran assemblages change along the stream-size gradient. A similar pattern was found by Condrati (2009) in central Amazonia. Besides the presence of water bodies, structural variables (e.g. width, depth, and water velocity) influence the richness, abundance, and species composition of animals that are totally dependent on water, such as fish (Mendonça et al., 2005), or partially dependent, such as anurans (Parris and McCarthy, 1999; Eterovick and Barata, 2006; Afonso and Eterovick, 2007).

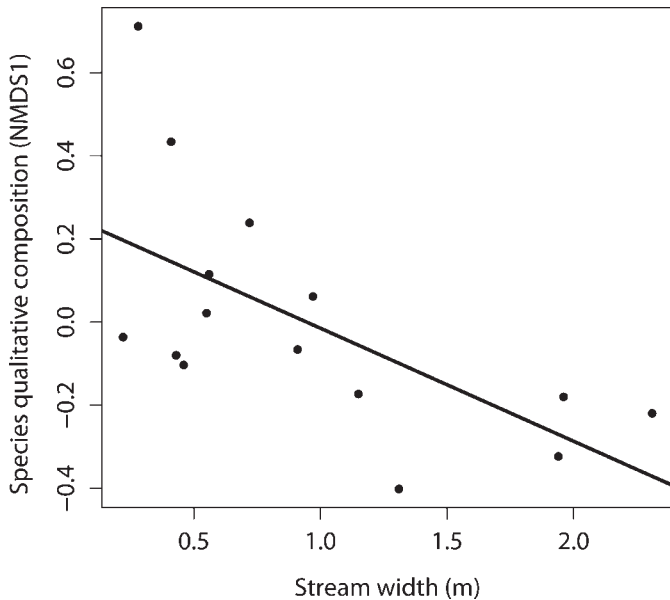


Fig. 4. Relationship between stream width and the composition of anuran species represented by a one-dimensional Nonmetric Multidimensional Scaling (NMDS) analysis, applied to a presence–absence data for 15 shoreline plots near streams.

Keller et al. (2009) attributed the effect of stream size on an anuran assemblage in a forest in Southeast Asia to the increase in sunlight reaching ground level and, consequently, to an increase in productivity in larger streams. However, in southeastern Brazil, in a contact zone between Cerrado and Atlantic Forest, the number of species of anurans recorded in plots was negatively related to the size of the stream (Afonso and Eterovick, 2007). Therefore, increased light penetration and productivity are not the only factors influencing the change in composition of anuran species, especially when differences in stream size are not large, as in our study (maximum stream width = 2.1 m).

Heterogeneity of the breeding sites could influence the change in species composition of adult anurans in lotic habitats (Afonso and Eterovick, 2007; Keller et al., 2009). The structural components of the riparian microhabitat (e.g., rapids, pools, substrate, etc.) seem to be the main influences on habitat use by species of frogs that breed in forest streams in Indonesia (Gillespie et al., 2004). Thus, the change in the composition of frog species along the stream-width gradient on Maracá Island may reflect the presence of habitats that are favorable for the development of tadpoles, such as stagnant water and pools in streams.

The hydroperiod of temporary ponds influences the spatial distribution of species of adult frogs (Santos et al., 2007; Silva et al., 2011) and tadpoles (Eterovick, 2003). All streams that we investigated on Maracá Island are temporary, and the hydrological dynamics should be similar to that of temporary ponds, where size may reflect hydroperiod, as demonstrated by Santos et al. (2007) in southeastern Brazil. Thus, hydroperiod should also influence the spatial distribution of adult frogs along streams on Maracá Island.

We recorded different anuran species compositions in riparian and non-riparian areas, as well as a greater number of individuals and species in plots in the riparian zone, similar to the results found of Condrati (2009) and Rojas-Ahumada et al. (2012) in central Amazonia. Riparian areas are severely impacted by human activities (Bren, 1993), and

many researchers have stressed the importance of water bodies and riparian areas for the conservation of animal species. Moreover, revisions of the Brazilian Forest Code (4771/65) may result in reduction of both forest and riparian areas protected by law, and this may endanger the fauna of these areas, especially amphibians, through habitat fragmentation and habitat split (Becker et al., 2007). Riparian forest buffers, up to 200 m wide, in a temperate region were not enough to maintain amphibian abundances in riparian areas, because many species depend on both riparian and non-riparian areas to complete their life cycle (Marczak et al., 2010). Because frogs are the prey of many other species (Duellman and Trueb, 1994), the influence of riparian areas is likely to extend along the food chain. Riparian zones in Amazonian rainforest support higher species densities of understory plants (Drucker et al., 2008), understory birds (Bueno et al., 2012), and frogs (Rojas-Ahumada et al., 2012; this study) than surrounding areas, highlighting their importance for biodiversity conservation in Amazonian rainforests.

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