PRIMARY RESEARCH PAPER

Tadpole richness in riparian areas is determined by niche-based and neutral processes

Alexandre Pinheiro de Almeida ·
Domingos de Jesus Rodrigues ·
Michel Varajão Garey · Marcelo Menin

Abstract In this study, we evaluate the effects of spatial and environmental factors on the structure of tadpole assemblages in Central Amazonia testing the following hypotheses: (1) environmental factors are more important than spatial ones in tadpole richness distribution and (2) habitat structure variables are more important than biotic variables in tadpole richness distribution. Tadpoles were sampled at 20 riparian plots between February and June 2010. Spatial and environmental components explained the major part of the variation in observed and estimated tadpole richness, respectively. Among all fitted models, the best model that explains species richness distribution is the one that contains only the number of ponds. Our results showed that tadpole richness in streamside ponds is influenced by niche-based processes and can be explained by local factors related to habitat structure. Predator density was not an important biotic factor in our study, contradicting the results found by other studies conducted in tropical areas. However, neutral processes are also important because spatial variation can explain the spatial distribution of species richness, probably as a result of dispersal limitation. Therefore, our results contribute to understanding of the local and landscape features which influence the amphibian species diversity in a tropical forest.

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A. P. de Almeida · M. Menin
Programa de Pós-Graduação em Diversidade Biológica, Instituto de Ciências Biológicas, Universidade Federal do Amazonas, Manaus, AM, Brazil

D. de Jesus Rodrigues
Instituto de Ciências Naturais, Humanas e Sociais, Universidade Federal de Mato Grosso, Sinop, MT, Brazil

D. de Jesus Rodrigues · M. Menin
Instituto Nacional de Ciência e Tecnologia de Estudos Integrados da Biodiversidade Amazônica, Ministério da Ciência, Tecnologia e Inovação, Conselho Nacional de Desenvolvimento Científico e Tecnológico – INCT-CENBAM/MCTI/CNPq, Manaus, Brazil

M. V. Garey
Instituto Latino-Americano de Ciências da Vida e da Natureza, Universidade Federal da Integração Latino-Americana, Foz do Iguaçu, PR, Brazil

M. Menin (✉)
Departamento de Biologia, Instituto de Ciências Biológicas, Universidade Federal do Amazonas, Av. General Rodrigo O. Jordão Ramos, 3000, Manaus, AM 69077-000, Brazil
e-mail: menin@ufam.edu.br

Introduction

Species richness on a local scale can be affected by environmental filtering, species interactions, as well as historical and stochastic processes (Morin, 1999; Ricklefs & Lovette, 1999; Hubbell, 2001). Studies developed on a spatial mesoscale in tropical areas, such as rainforests of Central Amazonia, have shown the strong effects of certain factors, such as topography, edaphic gradients, number of ponds, and size of riparian zones, on the assemblage structure of different taxonomic groups (Costa et al., 2005; Pazin et al., 2006; Drucker et al., 2008), including amphibians (Menin et al., 2007, 2011; Rojas-Ahumada et al., 2012).

Amphibians are considered sensitive to variation in habitat quality due to a life cycle generally involving both aquatic and terrestrial phases (Duellman & Trueb, 1994). Moreover, they are considered poor dispersers, with high site fidelity being a consequence of their physiology and behavior (Duellman & Trueb, 1994; see a review in Smith & Green, 2005). Streams and ponds are important habitats for anuran reproduction in tropical zones (Zimmerman & Bierregaard, 1986; Eterovick & Barata, 2006; Rodrigues et al., 2010), with species having reproductive modes associated with lentic or lotic water being dependent on the presence of these water bodies in riparian areas (Menin et al., 2011; Rojas-Ahumada et al., 2012). Considering that the majority of the Central Amazonian anuran species is aquatic breeders (Lima et al., 2012), the habitat choice for oviposition by adults (e.g. Evans et al., 1996) will influence the distribution of tadpoles in the habitats. Besides, the permanence and survival of tadpoles in the environments chosen by the adults could also be influenced by inter and intraspecific interactions (e.g. predation and competition; Hero et al., 1998, 2001; Azevedo-Ramos & Magnusson, 1999; Barnett & Richardson, 2002), as well as the quality and structure of the water bodies (e.g. favorable conditions for tadpole development; Evans et al., 1996; Alford, 1999; Klaver et al., 2013). However, analysis of the prevalence of these factors—predators and habitat structure—and their effect on the pattern of species richness in tropical aquatic communities remains scarce.

Tadpoles are preyed upon by a variety of vertebrate and invertebrate species, representing an important source of food (e.g., Azevedo-Ramos et al., 1992), including coupled cycles of predator-tadpole abundance (Bertoluci et al., 2013). Predators can influence tadpole community structure in two different ways. First, the predation may reduce competition among tadpoles (Heyer, 1976), positively influencing the species richness (Both et al., 2009, 2011) and determining the species composition (Hero et al., 1998). Secondly, predators can decrease amphibian richness, although not all species are equally affected by predators (Hecnar & M'Closkey, 1997). Moreover, larger ponds near streams have greater density of fishes (Pazin et al., 2006), and small ponds distant from streams have greater density of aquatic invertebrates (Hecnar & M'Closkey, 1997), causing alterations in the composition (Gascon, 1992; Azevedo-Ramos et al., 1999; Hero et al., 2001) and species richness of tadpoles. Thus, the influence of predators on species richness remains unclear in tropical environments: its effects on the tadpole assemblages and its interactions with other environmental variables are probably different from that found in temperate areas.

A recurrent pattern in studies of community ecology is the positive relationship between species diversity and environmental heterogeneity; this relationship has been observed for different taxa, including amphibians (see Tews et al., 2004). Due to the difficulty in characterizing habitat heterogeneity, many studies used different habitat structure variables as a proxy of environmental heterogeneity (e.g., Both et al., 2011). In the same way, structural characteristics of aquatic environments, such as water chemistry (Rome et al., 1992), hydroperiod, depth, and size of the water bodies (Rossa-Feres & Jim, 1996; Eterovick & Fernandes, 2002; Peltzer & Lajmanovich, 2004; Strauß et al., 2010; Both et al., 2011), canopy openness (Halverson et al., 2003), and availability of temporary ponds (Rodrigues et al., 2010) were also determinants of tadpole assemblage structure. Water quality appears to be a limiting factor for aquatic organisms because extreme physical and chemical characteristics of the water, such as low or high pH, prevent the survival of organisms (Rome et al., 1992; Moore & Townsend, 1998). The dissolved oxygen in the water can also

have a strong influence on the behavior of tadpoles, making them more susceptible to predation under conditions of low dissolved oxygen (Moore & Towsend, 1998). The pond area (Azevedo-Ramos et al., 1999; Peltzer & Lajmanovich, 2004; Urban, 2004) and the hydroperiod (Azevedo-Ramos et al., 1999; Both et al., 2011) exert an influence on the species richness and composition of species. Larger ponds support a greater number of species (Rodrigues, unpublished data) and can store water for longer periods, so the highest number of species could be related to a species-area effect (Pazin et al., 2006). Ponds with greater depth tend to have greater hydroperiods, permitting the complete development of the tadpoles (Peltzer & Lajmanovich, 2004; Both et al., 2011). In contrast, shallower ponds are ephemeral, but are occupied by an exclusive set of species with shorter larval periods (Peltzer & Lajmanovich, 2004; Both et al., 2009, 2011).

Many of the studies cited were conducted on a small spatial scale, using a small number of water bodies. Studies using a greater spatial scale (e.g., Rodrigues et al., 2010) are more recent and have permitted the determination of environmental gradients influencing the pattern of species distribution. The choice of areas for biodiversity conservation is based on medium to large scale studies and on richness and endemism patterns (Kerr, 1997), but it does not consider the effects of environmental gradients. The knowledge of the factors and their effects on a larger spatial scale can be used to develop conservation strategies for anuran species in Amazonia. In this study, we addressed two questions to evaluate the effects of spatial and environmental factors on the structure of tadpole assemblages in a spatial mesoscale in a *terra firme* forest in Central Amazonia: (1) Are environmental factors (biotic and abiotic variables) more important than spatial ones in tadpole richness distribution? We predict that environmental factors will have a greater influence on species richness than spatial variables, due to the spatial scale studied. In smaller spatial scales, dispersion tends to not limit species distribution (e.g., Smith & Green, 2005), favoring habitat selection by the species. (2) Are habitat structure variables more important than biotic variables in tadpole richness distribution? According to previous results for tropical tadpole assemblages (e.g., Hero et al., 2001; Both et al., 2011), we predict

that predator abundance has greater influence on the richness pattern than habitat structure.

Materials and methods

Study area

The study was conducted at the Fazenda Experimental of the Universidade Federal do Amazonas—UFAM (FE-UFAM: 02°37′17.1″ and 02°39′41.4″ S, 60°03′29.1″ and 60°07′57.5″ W; Fig. 1). The FE-UFAM is located at km 38 of the BR-174 highway. The FE-UFAM covers an area of 3,000 ha and has not yet been characterized in terms of flora, topography and climate, but the Fazenda UFAM's vegetation is located in extensive forest area. The forest of the region is classified as *terra firme* rain forest, with fairly dense canopy and an understory with low light, characterized by the abundance of palm trees such as *Astrocaryum* spp. and *Attalea* spp. (Guillaumet & Kahn, 1982). Tree height is between 35 and 40 m, with emergent trees reaching 50 m (Ribeiro et al., 1999). The area of the FE-UFAM also includes construction and farming areas, a green primary forest of *terra firme* featuring large streams that flood wide areas, in response to the flooding of major rivers, as well as headwaters and first and second order streams flooding small areas in response to daily rainfall. The relief is fairly rugged (altitude range 42–130 m a.s.l), including areas of slopes with steep inclinations (variation range 0.6°–26.1°). Temporary ponds form along flat areas along the margins of streams and may retain water from a few days to more than six months (Pazin et al., 2006), sometimes being subjected to irregular inundation by the streams during heavy rains (Rodrigues et al., 2010).

The climate is Am according to the Köppen-Geiger system (tropical monsoon, without a dry season) and the precipitation of the driest month is greater than 100 mm (Peel et al., 2007). Variation in the air temperature is very low between months, with an average between 24.6 and 26.9°C (Araújo et al., 2002). Average annual rainfall is 2,362 mm (Marques Filho et al., 1981). The rainy season usually occurs from November to May, with March, April, and May usually having greater rainfall (Marques Filho et al., 1981; Araújo et al., 2002).
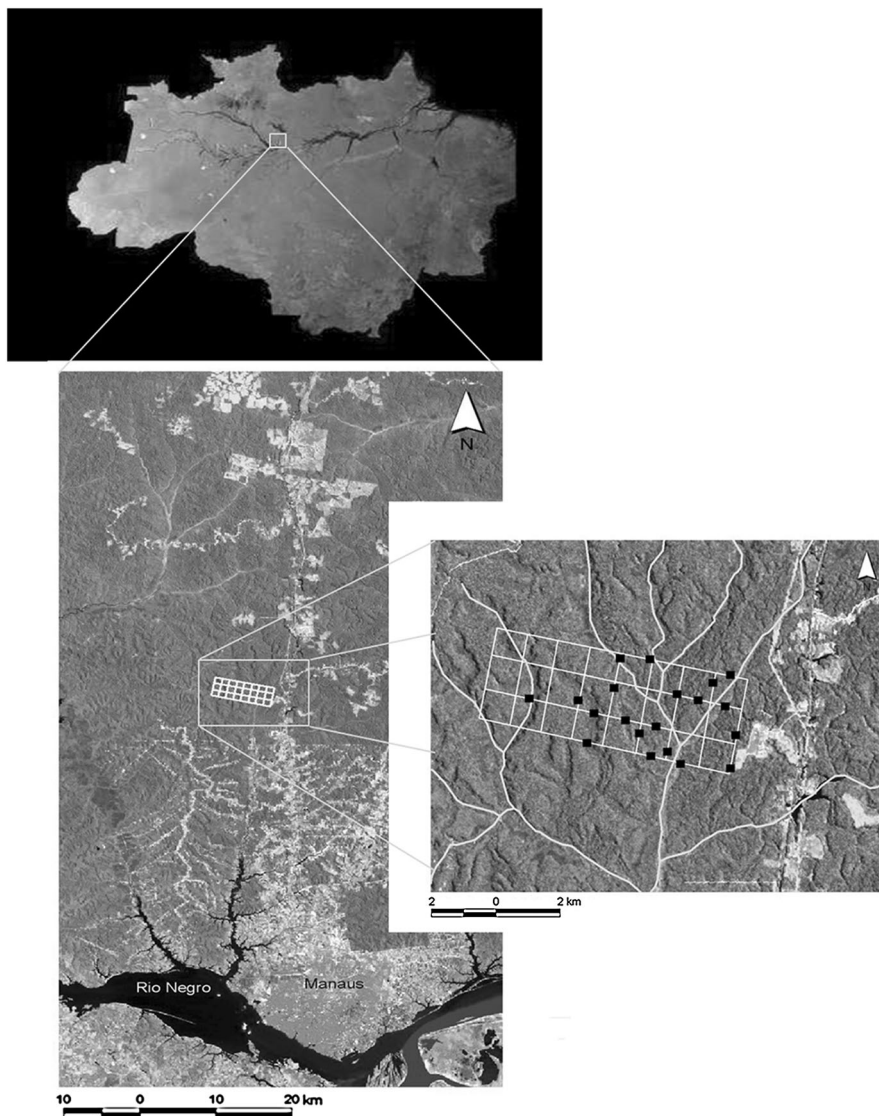
Data collection

Two diurnal sampling events were carried out during the rainy season (February–March 2010, April–May 2010) and one at the end of the rainy season/beginning of the dry season (June 2010; period in which there are persistent ponds along the stream margins due to great availability of water in the soil). Data were collected in 20 permanent riparian plots (Fig. 1), which corresponded to 50 m stretches along the margins of first and second order streams. The width of each plot varied according to the width of the valley (see "Results" section) that corresponded to the width of

the floodplain (the lowland areas around streams subject to flooding, measured until the beginning of slope). The plots were at least 500 m from one another.

The tadpoles and predators (aquatic frogs, turtles, fishes and aquatic insects of the orders Heteroptera, Coleoptera and Odonata) were collected in ponds found in each plot by sweeping a dip-net through the whole pond area (Gascon, 1991; Shaffer et al., 1994), including the leaf litter and the bottom substratum, until no more specimens were found in a 15 min interval (Rodrigues et al., 2010). The leaf litter was removed and inspected for tadpoles. We collected,

identified, and returned the tadpoles and predators to the pond. Those unable to be identified in the field were taken to the laboratory for further inspection. The tadpoles were identified following Hero (1990). Fishes were identified by a specialist (Jansen Zuanon—National Institute for Amazonian Research). Aquatic insects were identified following the identification keys of Triplehorn & Johnson (2011). Voucher specimens of those unable to be identified in the field were fixed and identified in the laboratory. All material was deposited in the Paulo Bührnheim Zoological Collection at the Universidade Federal do Amazonas, Manaus, Brazil (CZPB-UFAM 84–110).

Environmental parameters

We measured the following parameters at each plot: the width of the stream, the width of the valley, the canopy openness, the number of ponds, the distance from each pond to the stream, the area and depth of each pond, and the depth of the leaf litter layer at the bottom of each pond (recorded for each sampling period). Measurements followed those established by Mendonça et al. (2005) and Pazin et al. (2006). The stream width was measured at four equidistant points along the stream channel. For valley width, we considered the lowland areas around streams subject to flooding, which were measured at four equidistant points perpendicular to the stream channel. The number of ponds was determined by counting the water bodies within each plot. Ponds connected to one another during the rainy season were considered as a single water body. Pond area was measured by counting squares of a nylon grid (10 cm mesh) extended over the pond. Water depth and leaf litter layer were measured in the center of the pond in small ponds and at four equally spaced points in ponds larger than 1 m^2. Canopy openness was estimated with a spherical densiometer (Robert & Lemmom Forest Densiometer, model C) at four points located in each quarter of the plot. We calculated the volume of each pond applying the formula: volume = surface area × average depth (Masser & Jensen, 1991) to calculate predator density. For each plot, we used the average of pond volume across the three sampling events in our analysis.

The variables pond area and depth, leaf litter depth, and canopy openness were measured for each sampling event. We used the average across the three sampling events for all environmental variables in the analysis.

Data analysis

The spatial structure of tadpole assemblages was modeled using Principal Components of Neighbor Matrices analysis (PCNM, Borcard & Legendre, 2002; Dray et al., 2006), using SAM 4.0 software (Rangel et al., 2010). We applied the PCNM using the minimizing residual short-distance spatial autocorrelation, to create the spatial variables. For this, we used the geographical coordinates of the central point of each plot to calculate Euclidian distances between plots. To calculate the PCNM eigenvectors, we used a truncation maximum distance that connects all sampling units, under minimum spanning tree criterion (Rangel et al., 2006). The procedure recovered two PCNM axes (cumulated $R^2_{adj} = 0.40$; $P = 0.013$) that were used as spatial variables.

For statistical procedures, we used the total species richness per plot and the estimated richness. We employed the Jackknife 2, a non-parametric richness estimator index used to estimate the expected species richness per plot. The independent variables measured were transformed by Z-score, so that each variable had an average equal to zero and a standard deviation equal to one. To verify the presence of multicollinearity among independent variables, we used two methods in conjunction, following Zuur et al. (2010). We calculated the Variance Inflation Factors (VIF) using the *car* packages (Fox & Weisberg, 2011) in the statistical software R (R Core Team, 2012) in which values VIF > 3 indicate the presence of multicollinearity. We also graphically analyzed the distribution of all variables, through an inspection of graphical results of the Principal Component Analysis (PCA) using the statistical software SAM (Rangel et al., 2010). First, we excluded from subsequent analyses the collinear variables based on higher values of VIFs and, thereafter, we used the graph of PCA to eliminate variables that showed collinearity between covariates according to the eigenvectors of the covariance matrix. Thus, the first variable to be removed from the analysis was the water depth, after which we executed the analyses again, and also excluded the variable pond area. These variables were excluded from all subsequent analyses.

To assess the influence of environmental and spatial variables on species richness of tadpoles in plots, we implemented a partial regression analysis (Legendre & Legendre, 1998). The partial regression analysis allows the dependent variable variation to be separated into: pure environmental, pure spatial, spatially structured environmental variation, and unexplained (Borcard et al., 1992; Legendre & Legendre, 1998). With this analysis, we seek to understand the contribution of space and environment in the pattern of species richness distribution. This analysis was carried out using SAM software (Rangel et al., 2010).

To evaluate the influence of the independent variables on the pattern of tadpole species richness or estimated species richness (dependent variables) in the plots, we fitted generalized linear models (GLM) using the package *nlme* (Pinheiro et al., 2012). We applied the GLM function with a Poisson distribution to determine the optimal model. We generated a global model containing all the independent variables (width of the stream, width of the valley, canopy openness, number of ponds, distance from each pond to the stream, and predator density). For each response variable (observed and estimated richness), we generated a priori eighteen models, including a global model, models with only a single variable that were present in global model, and complex models including two or three variables, and including the interaction between two variables. The number of explanatory variables in models does not exceed six, applied the rule of thumb $n/3$ (n = number of plots) (Crawley, 2007). Applying the information-theoretical approach, we seek to understand what or which independents variables (biotic and abiotic) better predicts the distribution of species richness.

We used Akaike's Information Criteria to rank models (ΔAICc), and Akaike weights calculated to evaluate the relative support of each model (Burnham & Anderson, 2002; Burnham et al., 2011). For model selection, we applied criteria based on the likelihood-based inference (Lucaks et al., 2007; Burnham et al., 2011), using the evidence ratios, that is the relative likelihood of model I versus model j (Burnham & Anderson, 2002). The Akaike weights were used to evaluate model selection uncertainty, which quantify the probability that the model is a best of those considered, given a data (Burnham & Anderson, 2002; Lucaks et al., 2007; Richards et al., 2011). We calculated for each model the percentage of deviance explained as a measure of model goodness-of-fit (Zuur et al., 2009). Within each analysis, models were considered for interpretation of their parameters if they: (1) had ΔAICc of less than 4.0, (2) were included in the set of best supported models with combined Akaike weights of 0.70 (70% confidence set), (3) had an evidence ratio relative to the best supported model lower than 3 (Burnham & Anderson, 2002; Burnham et al., 2011). This approach has the advantage that the cutoff remains unaltered by sample size and, consequently, by the addition or deletion of a model (Burnham & Anderson, 2002).

Results

Environmental characteristics of plots

The number of ponds per plot varied from zero to 13 (mean 3.7 $\pm$ 1.9). Ponds were relatively small (mean 1.7 $\pm$ 0.59 m², range 0.17–10.84 m²), shallow (mean 6.76 $\pm$ 5.16 cm, range 1.35–30.5 cm), with a 4.77 $\pm$ 2.22 cm (range 0.2–12.75 cm) leaf litter layer, and a variable distance from stream margins (mean 14.78 $\pm$ 20.78 m, range 0.5–125 m). Stream width varied from 1.62 to 5.5 m (mean 2.93 $\pm$ 0.95 m), valley width varied from 26 to 259 m (mean 82.66 $\pm$ 74.2 m), and canopy openness varied from 11 to 14% (mean 12.44 $\pm$ 0.95%).

Assemblage composition of tadpole and predator species

A total of 2,092 individual tadpoles of nine species belonging to six families were recorded in the three sampling events (Table 1). *Allobates sumtuosus* (Aromobatidae) was the most abundant species, representing 75.8% of the individuals collected and detected in 19 of the 20 plots. Another eight species were found in one to seven plots (Table 1). We found three species in the first sampling period, six species in the second sampling period and eight species in the third sampling period. Plot richness ranged from zero to five species (mean = 1.28 $\pm$ 1.13).

Predator species found in the plots were adults of anurans (*Pipa arrabali* and *Pipa pipa*), small turtles (*Platemys platycephala*), fishes (Characidae, Cichlidae, Erythrynidae, Gymnotidae, Lebiasinidae,

Table 1 Number of plots where each species was recorded and number of individuals detected in three samplings at the Fazenda Experimental of the Universidade Federal do Amazonas, Manaus, Brazil

Family/Species	Number of plots	Number of individuals			
		February–March 2010	April–May 2010	June 2010	Total
Aromobatidae					
Allobates sumtuosus	19	20	837	728	1,585
Bufonidae					
Amazophrynella manaos	7	0	12	69	81
Centrolenidae					
Vitreorana oyampiensis	2	0	1	1	2
Hylidae					
Dendropsophus cf. *brevifrons*	1	0	0	3	3
Hypsiboas cinerascens	3	0	0	32	32
Osteocephalus taurinus	8	51	96	120	267
Leptodactylidae					
Leptodactylus riveroi	1	0	0	51	51
Leptodactylus rhodomystax	6	7	63	4	74
Microhylidae					
Chiasmocleis hudsoni	2	0	7	0	7
Number of species	–	3	6	8	9
Number of individuals	–	78	1,006	1,007	2,092

and Rivulidae), larvae of Odonata, and adults of Coleoptera (Dytiscidae, Gyrinidae) and Heteroptera (Belostomatidae).

Partitioning variation in species richness between spatial and environmental variables

Spatial and environmental components jointly explained 60.4% of the variation in tadpole richness in plots ($R^2_{adj} = 0.604$, $P = 0.002$). The pure environmental component accounts for the greatest fraction of variation in species richness (37%). The pure spatial component explained about 26.5% of the variation in species richness, while the spatially structured environmental component (i.e. variance shared between environmental and spatial variables) explained 13.4% of variation in species richness. The remaining 23.1% was related to unexplained variation. Regarding estimated species richness (estimated richness was 11 species), the environmental and spatial variables explained 54.6% of variation in the species richness ($R^2_{adj} = 0.546$, $P = 0.045$). However, the spatial component explained the greatest fraction of the variation (37.9%). The pure environmental component explains 34.2% of variation in species richness. The spatially structured environmental component

explained 1.6% of variation in estimated species richness, while the remaining 26.3% was related to unexplained variation.

Effects of environmental variables on species richness

Among all fitted models with independent variables, the best model that explains species richness distribution is the one that contains only the number of ponds per plot (Table 2, Supplementary material S1 and S2). This model explains 21% of the variation in observed and estimated species richness between sites (Table 2). Plots with more ponds contained more tadpole species observed and estimated (Fig. 2A, B). However, evaluating the observed and estimated species richness, four models were equally parsimonious, with three models in common for both richness parameters: (1) with only number of ponds, (2) with number of ponds and valley width, and (3) with only valley width (Table 2). We found higher estimated species richness in the plots with smaller valley width (Fig. 2C, D). The random model to observed species richness and the model with number of ponds and canopy cover for estimated richness were equally important.

Table 2 The six most parcimonius a priori models used to examine the relationship between observed and estimated tadpole species richness and abiotic and biotic variables in 20 riparian plots at a *terra firme* forest in Central Amazonia, Brazil

Models	k	ΔAICc	wAICc	Deviance	%DE
Observed richness					
Number of ponds	2	0.0	0.21	7.83	32.79
Valley width	2	0.7	0.15	8.57	26.47
Number of ponds + valley width	3	1.0	0.13	6.03	48.23
Random model	1	1.3	0.11	11.66	0
Number of ponds + canopy cover	3	2.5	0.06	7.51	35.56
Number of ponds + predators density	3	2.6	0.06	7.62	34.66
Estimated richness					
Number of ponds	2	0	0.21	19.11	21.56
Number of ponds + valley width	3	0.2	0.19	19.84	32.61
Valley width	2	0.7	0.15	16.42	18.58
Number of ponds + canopy cover	3	1.9	0.08	18.17	25.39
Number of ponds + predators density	3	2.4	0.06	18.71	23.23
Number of ponds + valley width + number of ponds × valley width	4	2.7	0.54	15.70	35.57

k = number of parameters; ΔAICc = difference in corrected Akaike's Information Criteira; wAICc = weights of corrected Akaike's Information Criteria; %DE = percent deviance explained in the response variable by the model under consideration

Discussion

Our results showed that both environmental and spatial variables influence the patterns of tadpole species richness in areas of *terra firme* in the Central Amazonia Forest. We found that a large portion of the variation of observed tadpoles species richness in Central Amazon Forest is determined by environmental variables (number of ponds and valley width), while the variation of estimated species richness was greatly influenced by spatial factors. The spatial distribution of tadpoles may be determined by reproduction site chosen by adults, mainly because of the isolated effects of environmental and spatial factors. This result highlights the importance of both niche and neutral process in spatial distribution of tadpoles. Spatial effects and landscape influences are interpretable entirely in terms of adult habitat use (Van Buskirk, 2005). Our study area contained large streams that flood large areas, as well as headwaters and first and second order streams that flood small areas in response to daily rainfall, and a fairly rugged relief, including areas of slopes with steep inclinations (Rojas-Ahumada & Menin, 2010). These factors may affect the spatial distribution of tadpoles, where species are widespread (e.g., *Allobates sumtuosus* and *Osteocephalus taurinus*) and show high abundance in the plots, while other species are rarer (*Vitreorana oyampiensis* and *Dendropsophus* cf. *brevifrons*), and only found in restrict areas of Central Amazonia forests (Menin et al., 2009; Lima et al., 2012). Although dispersal limitation tended to be a limiting factor at different spatial scales (Cottenie, 2005; Smith and Green, 2005; but see Girdler & Barrie, 2008), possibly including adult anurans in *terra firme* forests of Central Amazonia, there is little evidence of dispersal limitation for adults of anurans that live in riparian zones in the same study area (Rojas-Ahumada et al., 2012). On the other hand, spatial effects on ecological communities can be an artifact caused by the close interrelation of space and environment (Bjorholm et al., 2008). Although dispersal may not be limiting to adults the environmental effects of abiotic variables may play a major role in preventing them colonize distant ponds because the pure environmental effects that were the most important to explain a larger variation of observed species richness. Therefore, the attribution of observed spatial patterns to dispersal processes must be performed cautiously (Diniz-Filho et al., 2003; Landeiro et al., 2011). According to some studies (e.g. Diniz-Filho et al., 2003; Landeiro et al., 2011; Rojas-Ahumada et al., 2012), much of the variation attributed to spatial variables may be due to the effects of unmeasured environmental variables, such as the
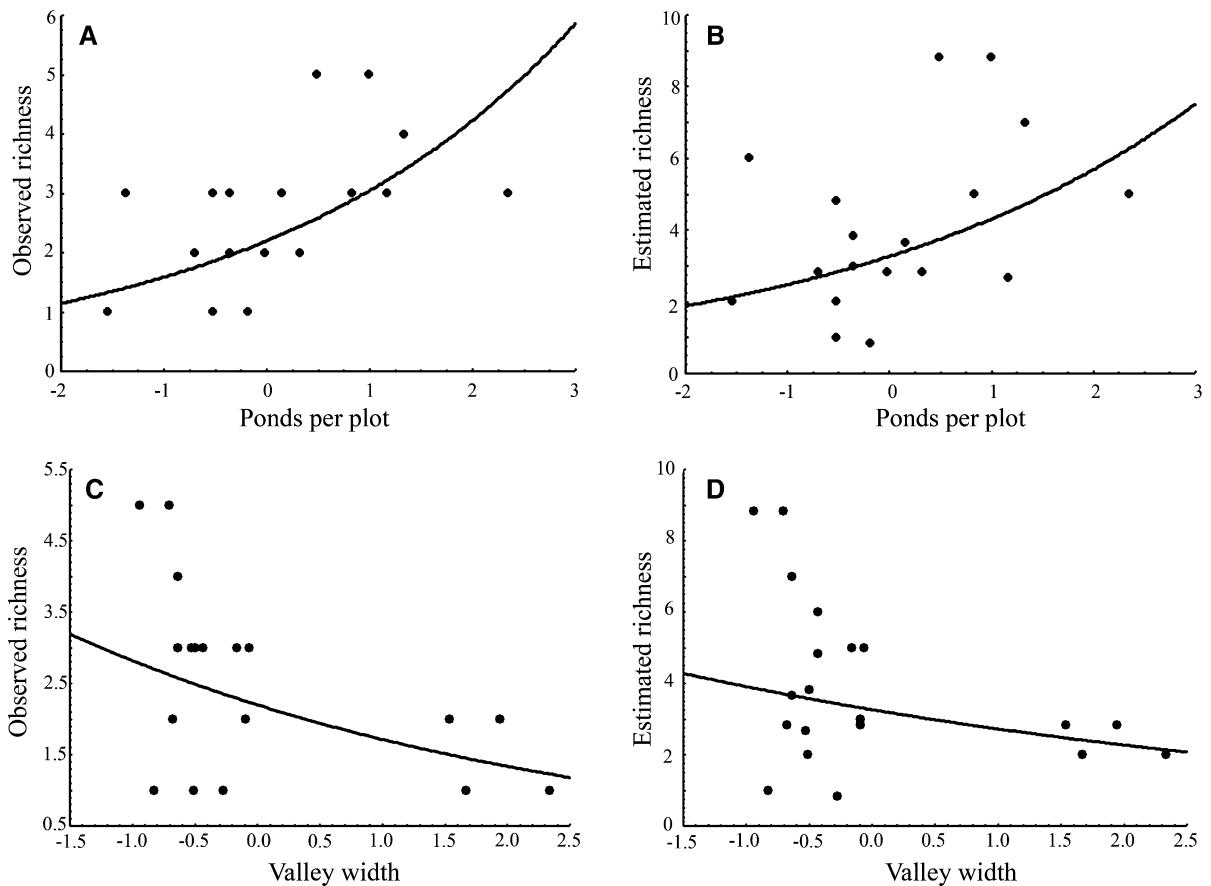
Fig. 2 Relationship between observed (**A** and **C**) and estimated (**B** and **D**) tadpole richness per plot and the number of ponds and valley width in the Fazenda Experimental of the Universidade Federal do Amazonas, Manaus, Brazil

physical and chemical characteristics of the water (Hecnar & M'Closkey, 1996).

According to Akaike weights value (Lucaks et al., 2007; Richards et al., 2011), the best model to explain the variation in estimated and observed richness is the pond availability. The greater number of ponds allows for wider habitat diversity available to adults for reproduction. The landscape structure directly affects the distribution of adults (Lomolino & Smith, 2003) because they may select specific sites for reproduction, thus influencing the distribution of tadpoles among habitats and reducing contact with predators (Evans et al., 1996; Alford, 1999; Eterovick & Barros, 2003). The availability of reproductive habitats is another critical factor limiting the distribution of most species of frogs in Central Amazonia (Zimmerman & Bierregaard, 1986), as observed in this study, where the number

of ponds within the plots was related to species richness. In addition, the number of ponds in a plot can lead to the stability of the tadpole assemblage, because when a pond dries out, the ponds nearby can harbor the individuals and contribute toward the maintenance of local species richness. Another important factor in the ecology of tropical temporary ponds near streams (Pazin et al., 2006) is the effects of lateral inundation of streams, which may either make possible the transfer of individuals between ponds, enabling their escape from predators, or add predators from the stream.

The canopy openness over the ponds was identified as an important factor determining the assemblage distribution of fishes (Pazin et al., 2006) and anuran larvae (Schiesari, 2006). Open-canopy ponds receive higher incidence of solar radiation, and have higher temperature and dissolved oxygen levels (Halverson

et al., 2003; Schiesari, 2006). These factors can influence the hydroperiod and, consequently, affect the distribution of anuran larvae and aquatic invertebrates (Werner & Glennemeier, 1999; Halverson et al., 2003). However, species open-canopy specialist can be more affected by closed-canopy condition than canopy cover generalist (Skelly et al., 2002). This environmental gradient can act as a selective sieve for the distribution of anuran larvae.

The valley width (or the floodplain width) represents a potential area for the formation of temporary ponds and a direct relationship is expected between the valley width and the number of ponds. According to Hodnett et al. (1997), valleys in the *terra firme* forest in Amazonia are frequently flooded in response to daily rainfall, with this variation being more pronounced in small streams (Zweimüller, 1995). However, a negative relationship was found between tadpole species richness and valley width, contradicting the initial prediction. This discordance can be related to negative or weak correlation between the valley width and the number of ponds found in our study area. Unfortunately, the effect of the floodplain size on tadpole assemblages is poorly known. The only study which analyzed this variable does not found influence on the structure of tadpole assemblage in another area in Central Amazonia (Rodrigues, unpl. data).

Predator density was not an important biotic factor in our study, contradicting the results found by many studies conducted in tropical areas (e.g., Gascon, 1992; Hero et al., 1998, 2001; Azevedo-Ramos et al., 1999). However, these studies were developed on a smaller spatial scale and the predator–prey interactions can be more important in local ponds than in a spatial mesoscale. Moreover, invertebrate predators can be influenced by the same environmental variables as tadpoles (Both et al., 2009) and their effects can be diluted at this spatial scale.

In spite of the density of predators being considered an important biotic variable influencing the structure of tadpole assemblages in tropical environments (e.g., Hero et al., 2001), our data suggest that environmental features (number of ponds and valley width) are the major proximal factors in streamside ponds in *terra firme* forests of Central Amazonia. Moreover, the influence of niche-based processes forming tadpole assemblages may be more relevant than that of neutral processes (Hubbell, 2001), as found in stream tadpole assemblages in Madagascar (Strauß et al., 2013).

Therefore, the contribution of local and landscape features has important implications for anuran conservation projects that use ponds within tropical forests.

In conclusion, environmental and spatial variables explain the spatial variation of tadpole species richness occurring on a spatial mesoscale in a forest in Central Amazonia, contradicting the data obtained by other studies in smaller spatial scales in tropical areas in which predation is the proximal factor influencing the assemblage structure. From the perspective of our study developed over a short period of time (one rainy season), the tadpole species richness in streamside ponds is influenced by niche-based processes and neutral processes. Our results showed that tadpole species richness in streamside ponds in *terra firme* forests of Central Amazonia is influenced by niche-based processes and can be explained by local factors related to habitat structure in the plots. However, neutral processes are important because spatial variation can explain the spatial distribution of species richness, probably as a result of dispersal limitation that reflects the biology and dispersal abilities of the species.

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