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Fine-scale habitat heterogeneity explains the local distribution of two Amazonian frog species of concern for conservation

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ABSTRACT

To test the hypothesis that subtle differences in abiotic requirements can result in almost total spatial segregation, we sampled two species of diurnal frogs, *Atelopus spumarius* and *Allobates sumtuosus*, in a primary forest reserve in central Brazilian Amazonia. We conducted visual and acoustic surveys on three occasions over 2 months, in 40 streamside (riparian) plots distributed throughout the reserve's two major drainage basins, using a grid system that covers 64 km^2. On average, drainages differed in the pH of stream water and the number of connected and isolated streamside pools. Differences in abiotic characteristics of drainages were associated with the spatial distribution of frog species. The occurrence and density of *Allobates sumtuosus* was negatively related to stream pH and discharge and positively related to the number of isolated pools in plots. The occurrence and density of *Atelopus spumarius* was associated with streams with high discharge and pH near neutral. These results indicate that although very large reserves will probably contain sufficient landscape heterogeneity to accommodate different species of diurnal frogs, due to strongly patchy distributions, *in situ* studies using fine-scale species-distribution models will be necessary to assess the adequacy of small reserves in Amazonia that cover hundreds of square kilometers or less for the conservation of some anuran species.

Abstract in Portuguese is available with online material.

Key words: abiotic conditions; *Allobates sumtuosus*; Amazonia; amphibia; *Atelopus spumarius*; environmental drivers; RAPELD method; riparian zones.

In regions of high human population density, remnants of original habitat available for conservation are few, scattered, and small. Areas of native vegetation cover are often less than 100 km^2 and may be as small as a few square kilometers (Leroux *et al.* 2010). Management strategies concerned with delimitation or implementation of small conservation units must consider environmental variation at the scale of the remnant, and how this variation influences the occurrence and local densities of the species that the reserves are intended to conserve (Groves *et al.* 2002).

Some species have discontinuous distributions in response to fine-grained variations in environmental characteristics, such as physicochemical characteristics of water bodies or soil and the structure of forest understory (Vormisto *et al.* 2000, Browne *et al.* 2009). Changes in these variables can occur among spatially proximate points and within narrow ranges of thresholds (Wiens 1989, 2000), often resulting in discontinuous distributions of the species under study. To predict the occurrence of such taxa, it is necessary to model species distributions at a finer resolution than one square kilometer.

Recent studies have attempted to evaluate the geographic distribution of species and to identify priority areas for conservation over large areas, commonly using variables that represent environmental characteristics at coarse scales (*e.g.,* Bernardo-Silva *et al.* 2012, Serra *et al.* 2012). However, conservation of species with patchy distributions requires evaluation at a finer scale due to subtle variations in key environmental features and the fact that the target species may be confined within small natural remnants (*e.g.,* Sharma *et al.* 2014).

Species distributions of anuran, fish, bird and plant assemblages in central Amazonian *terra firme* forests frequently reveal discontinuities in response to micro-topographic gradients (Costa *et al.* 2005, 2008, Menin *et al.* 2011, Bueno *et al.* 2012, Ribeiro *et al.* 2012, Rojas-Ahumada *et al.* 2012) or between streamside areas more or less influenced by sporadic flooding (Drucker *et al.* 2008, Espírito-Santo *et al.* 2013). To date, most studies on vertebrate species distributions in these forests have primarily investigated how environmental gradients relate to observed differences between species assemblages occurring in streamside versus upland areas Fraga *et al.* 2011, Menin *et al.* 2011, Bueno *et al.* 2012, Ribeiro *et al.* 2012, Rojas-Ahumada *et al.* 2012). However, how environmental gradients within streamside (*i.e.,* riparian) zones affect species spatial distributions and densities remains poorly understood.

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Due to their biphasic life cycle, many amphibians have complex ecological requirements and often need specific breeding sites for reproduction. For this reason, amphibians are good models for studies investigating variations in occurrence and local density of individuals and their relationships with environmental variables, such as physicochemical differences among water bodies and their adjacent marginal areas (*e.g.,* Keller *et al.* 2009, von May *et al.* 2010). In this study, we sampled two species of mainly terrestrial diurnal frogs, *Atelopus spumarius* and *Allobates sumtuosus*, in Reserva Ducke (RFAD), a 64 km^2 area of *terra firme* forest in central Brazilian Amazonia; we then used these species as models to test the hypothesis that fine-grained differences in abiotic conditions associated with specific reproductive requirements can result in almost complete spatial segregation of the two species. The distribution of these two species across RFAD is poorly known, but the few records available suggest that they occur in opposite sectors of the reserve (Menin *et al.* 2011). As both species inhabit similar habitats in streamside areas, they represent a useful study system to test for the existence of fine-scale habitat segregation.

METHODS

STUDY SPECIES.—The terrestrial diurnal frog *Allobates sumtuosus* (Morales 2002) (family Dendrobatidae) lays its eggs in gelatinous nests on dead leaves on the forest floor, usually between January and April. After the tadpoles hatch, males transport them from nests to small isolated rainwater pools (Lima *et al.* 2006). *Allobates sumtuosus* occurs mainly alongside streams, but some individuals occur near isolated pools far from streams (Lima *et al.* 2006). All species of *Allobates* studied so far are territorial and adults defend small areas where they mate and lay eggs during the reproductive season (Kaefer *et al.* 2012). The identity and distribution of this species remained obscure for more than a decade following its description, and information on ecological factors associated with its occurrence and local abundance remains limited (Simões *et al.* 2013). The IUCN Red List cites *Allobates sumtuosus* as 'data deficient' with unknown population trends (Salas 2004).

The terrestrial diurnal frog *Atelopus spumarius* (Cope 1871) (family Bufonidae) occurs mainly along the margins of forest streams, where males call intensely between December and April (Lima *et al.* 2006). The frogs deposit their eggs in small ponds connected to streams, and larval development occurs on the streambed (Gascon 1989, Hödl 1990, Lima *et al.* 2006). Most studied species of *Atelopus* are territorial and remain within a small area for the whole reproductive season (Crump 1986, Lötters 1996). Many species of *Atelopus* are vulnerable to the removal of native vegetation and to infection by the chytrid fungus *Batrachochytrium dendrobatidis*, which has already resulted in many clades becoming extinct or suffering extreme population declines (La Marca *et al.* 2005, Lips *et al.* 2008). The IUCN Red List cites *Atelopus spumarius* as 'Vulnerable' with decreasing population trend (Azevedo-Ramos *et al.* 2010). Further information about the morphology, behavior, and natural history of *A. sumtuosus* and *A. spumarius* can be found in the Guide to the Frogs of Reserva Ducke (http://ppbio.inpa.gov.br/guias).

STUDY AREA.—We conducted the study over a 64-km^2 trail system within RFAD (59°55′ W, 2°57′ S), a 100 km^2 forest remnant situated north of Manaus, Amazonas State, Brazil (Fig. S1). The reserve has a humid tropical climate and with predominantly dense evergreen *terra firme* forest vegetation (IBGE 1992). Canopy height in riparian areas varies between 25 and 30 m and has a dense understory of stemless palms, shrubs, and herbaceous vegetation (Ribeiro *et al.* 1999). The reserve covers two major drainage basins, separated by a central plateau oriented N–S (Fig. S1). Both drainages contain first-, second-, and third-order streams, the margins of which have narrow alluvial terraces that vary between 18 and 78 m in width (Rodrigues 2006). After strong rains, overflow from the streams inundates the streamside terraces, but water levels drop within a few hours after rain stops. Pools occur along the alluvial terraces, and these may endure for few days to 12 months. The pools and streams generally have saturated levels of dissolved oxygen (Pazin *et al.* 2006).

SPATIAL DESIGN.—We used 40 linear sampling plots established in streamside areas, with 20 plots distributed in each of the reserve's main drainage basins (eastern and western), over the 64-km^2 trail system that covers most of the reserve, excluding only a 1-km buffer zone along the reserve edge (Fig. S1). We distributed the plots to systematically cover the two drainages where streams crossed the trail system and placed them at least 1 km apart (Fig. S1). We established most plots (N = 29) alongside narrow first- and second-order streams, but we placed eleven plots beside third-order streams (with water discharge >0.1 m^3/s).

Plot characteristics followed the RAPELD system, a spatially standardized sampling method for use in long-term ecological research. This method allows comparisons among sampling sites as well as understanding ecological process within the sites (Magnusson *et al.* 2013). RAPELD modules use uniformly distributed trails and plots in which environmental variables are measured using the same protocols. The RAPELD system has been used for a variety of taxa in sites throughout the world (Magnusson *et al.* 2013). Guidelines for RAPELD sampling units along riparian zones area are available on http://ppbio.inpa.gov.br/instalacao/riparias. Riparian RAPELD plots have a 250-m-long central line that follows the stream bank in 10-m linear segments and a minimum distance between the stream margin and the nearest point on the center line of 1.5 m. Organisms can be counted along plots in strips that begin at the stream margin and varied in width depending on the species' biology. At RFAD, *Atelopus spumarius* occurs primarily within the first 3 m of stream margins. Therefore, we sampled the species within 4-m-wide strips (totaling 1000-m^2 sampling area per plot) (Fig. S2). *Allobates sumtuosus* occurs at greater distances from streams, so we sampled it within 10-m-wide strips (totaling 2500-m^2 sampling area per plot).

DATA COLLECTION.—We collected data on density of the two species in all plots on three occasions: 10–25 January, 6–21 February, and 25 February to 10 March 2013. These months encompass the peak reproductive season of both species, when vocal activity facilitates their detection. Neither species is known to be migratory, and individuals can be found throughout the year, though they are harder to detect when not calling. Therefore, we believe that the data on densities reflect the distribution of these species throughout the year. We carried out counts between 0600 and 0900 h and between 1620 and 1730 h, the hours of peak activity of the two species (Lima *et al.* 2006). Also, we alternated morning and afternoon surveys between plots in sequential sampling occasions. During each sampling event, one person conducted visual and auditory searches; this person walked along the sampling plot steadily at about 250 m/h. As the number of calling individuals varies with weather conditions, we used the largest number of individuals recorded per plot during any of the three sampling occasions as the index of relative density of the species in the analyses described below.

In each plot, we measured environmental variables describing the riparian zone and the adjacent stream. We counted the number of isolated pools within 10 m of the stream and the number of pools connected to the stream channel. We measured understory cover along a line running parallel to and 50 cm distant from the plot center line using an aluminum rod 1.5 cm in diameter and 150 cm in length, which we positioned vertically and moved along the line. At each 2 m, we recorded whether any part of the rod touched the vegetation, giving a maximum of 125 records per plot (adapted from Bullock 1996). We used the number of rod touches in each plot to represent the understory-vegetation cover in each plot. We did not measure canopy openness because it does not vary significantly between RFAD drainage basins (Rodrigues 2006).

We collected soil samples to a depth of 10 cm at six points along the plot (50 m between samples) and estimated the physical structure of the soil using the percentage of clay in a pooled 5-g sample derived from the six subsamples. Technicians at the Laboratório Temático de Solos e Plantas (LTSP) of Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus conducted the physical analyses following standard methods (Embrapa 2009). We used percentage clay content in the soil in the analyses because it strongly associates with species composition and distribution of ground-dwelling arthropods that commonly serve as food for the litter frogs in this region (Franklin *et al.* 2005, Aguiar *et al.* 2006).

The width, depth, flow velocity, and discharge of streams in RFAD do not vary significantly between seasons, except during spates of strong rainfall (Espírito-Santo *et al.* 2008). In this study, we measured the characteristics of streams in the middle of the dry season (1–30 September 2012). We measured the width of the stream adjacent to each sampling unit every 50 m at six points distributed along the stream using a tape measure stretched from one bank to the other, perpendicular to the stream course. At the same points, we estimated water velocity (in m/sec) by launching a 1-cm diameter silicon ball in the current at the middle of the stream and recording the time elapsed until it moved a distance of 1 m. We measured stream depth at the same points as stream width and water velocity; at each point, we made nine measurements of depth at regular intervals across the stream along a transect perpendicular to the stream bank. To estimate stream size, we used average width, depth, and velocity of the six sampling points, multiplying the average cross-sectional area by the average depth of the stream, and discharge (in m^3/sec), by multiplying the average cross-sectional area by average water velocity (Mendonça *et al.* 2005). We took all measurements on rainless days.

We measured the pH of streams and pools with a digital potentiometer (Aqua-Check^{TM} Water Analyzer, Analytical HI). We sampled these characteristics at the end of the rainy season, when the larvae of the two focal species were already present in pools (*Allobates sumtuosus*) and streams (*Atelopus spumarius*). According to Gascon (1989) and Lima *et al.* (2006), the larvae of these species occur in streams or pools between January and May, but the tadpoles are more abundant in March, when we measured the chemical properties of the streams.

The reader can access details of the methods used to obtain the environmental variables in the field and the raw data in the Public Data Repository of the Program for Research on Biodiversity (Repositório Público de dados do Programa de Pesquisas da Biodiversidade) through links provided in Appendix S1.

STATISTICAL ANALYSES.—To test for the existence of environmental differences between the main drainages, we conducted analyses of variance (ANOVA) with one factor (drainage) and two levels (eastern or western drainage). Table 1 lists the environmental variables used in ANOVA tests. We conducted Shapiro–Wilk tests of residuals to verify the assumption of normality. The pH in streams was correlated with the average pH of pools connected to streams ($r = 0.68$) and isolated pools ($r = 0.55$). Since frequent flooding from streams influences pool pH, stream pH (pH) was used as a proxy for pool pH. The remaining environmental variables, number of connected pools (NCP), number of isolated pools (NIP), understory-vegetation cover (UVC), soil clay content (SCC), and stream discharge (SD) showed only weak correlations (Table S1), and these predictor variables showed little multicollinearity (tolerance >0.6, in all cases).

TABLE 1. *Standard deviation (SD) and arithmetic mean (AM) of the environmental variables obtained in 20 riparian sampling sites located in each drainage basin. The two last columns are ANOVA test results for differences in environmental characteristics between basins.*

	Western drainage		Eastern drainage		ANOVA test	
Environmental variables	SD	AM	SD	AM	$F_{1,38}$	P
Number of connected pools	1.89	4.90	1.51	6.25	6.20	0.017
Number of isolated pools	1.80	6.90	2.41	5.15	6.75	0.013
Connected pools pH	0.95	3.83	2.20	5.41	8.68	0.05
Isolated pools pH	0.87	3.58	2.31	4.90	5.62	0.023
Stream pH	1.39	4.02	1.05	7.60	83.55	0.001
Stream discharge (m^3/sec)	0.10	0.09	0.11	0.09	0.002	0.96
Vegetation cover in understory	10.5	74.4	8.91	73.6	0.059	0.80
Clay content (%)	5.48	8.18	5.27	9.76	0.86	0.35

We used a correlogram based on Moran's I to identify and quantify possible spatial autocorrelation in the predictor and response variables because the presence of autocorrelation in both the predictor and response variable can induce type I errors in statistical tests (Legendre 1993). As we found no significant autocorrelation in either the response or predictor variables at any distance class ($P > 0.05$ in all cases, Moran's Statistics: $-0.3 > 0 < 0.3$), the statistical tests did not require an adjustment for autocorrelation.

The factors that determine where a species occurs can differ from the factors that determine its density in the sites where it occurs, so we also tested a zero-inflated Poisson regression (Zuur *et al.* 2009). Nevertheless, this returned results similar to multiple regression with Gaussian error structure and we used the latter, as the partial plots are more easily interpreted. In RFAD, *Allobates sumtuosus* occurred in both main drainages and we used a logistic regression model to evaluate the possible relationship between the variation in five environmental variables (NIP, UVC, SCP, pH, and SD) in 40 plots and *A. sumtuosus* occurrence (presence/absence). We selected these variables based on their presumed importance to *A. sumtuosus* natural history traits and because they had weak collinearity. As the density of *A. sumtuosus* varied in the plots in which it occurred, we evaluated the same predictor variables using a multiple linear regression model to investigate possible relationships between them and the density of *A. sumtuosus* in the 26 plots in which we recorded the species.

We recorded *Atelopus spumarius* in only ten plots, distributed exclusively in the eastern drainage. Therefore, we tested fewer predictor variables (NCP, pH, and SD) using a logistic regression model to evaluate possible relationships between their variation in 40 plots and *A. spumarius* occurrence (presence/absence) across both drainages. Predictor variables all relate to stream characteristics because *A. spumarius* tadpoles develop in streams. The density of *A. spumarius* varied within the eastern drainage, and we used a multiple linear regression model to evaluate the relationship among the same three predictor variables and local density of *A. spumarius* in the 20 plots located in the eastern drainage.

RESULTS

Environmental differences between drainage basins.—Isolated pools (breeding sites for *A. sumtuosus*) were more frequent in the western drainage ($N = 40$, $F_{1,38} = 6.75$, $P = 0.013$), whereas pools connected to streams (breeding sites for *A. spumarius*) were more frequent in the eastern drainage ($N = 40$, $F_{1,38} = 6.20$, $P = 0.017$; Fig. S3). Stream pH was significantly more acidic in the western than in the eastern drainage ($N = 40$, $F_{1,38} = 83.55$, $P < 0.0001$; Fig. S3). Understory-vegetation cover, soil clay content, and stream discharge did not differ significantly between drainages (Table 1).

Distribution and local densities of *Allobates sumtuosus* and *Atelopus spumarius*.—We detected *Allobates sumtuosus* in 26 of 40 plots (Fig. S4). The maximum number of individuals in any of the three sampling occasions in the western basin varied from 1 to 19 individuals per plot. The sum of the maximum number of individuals recorded per plot in the three sampling occasions in the western drainage was 136, and the species was encountered in all plots in that basin. In contrast, the maximum number of individuals in three sampling occasions in the eastern drainage was four individuals per plot, and we recorded *Allobates sumtuosus* in only six plots in that basin. The sum of maximum numbers of individuals recorded per plot during the three sampling occasions in that basin was 13 individuals. *Atelopus spumarius* was recorded in ten plots, all located in the eastern drainage (Fig. S4). The maximum local density ranged from one to nine individuals per occupied plot. The raw counts of individuals of both species in each of the three sample occasions are provided on Table S2. There was no record of either species in eight plots, all located in the eastern drainage. The two species co-occurred in only four plots, which were insufficient to undertake analyses of potential interactions.

Relationships between environmental factors and density and distribution of *Allobates sumtuosus*.—The variation in presence/absence of *Allobates sumtuosus* in 40 plots could be substantially explained (McFadden's $\rho^2 = 0.59$) by a model composed of number of isolated pools (NIP), stream discharge (SD), stream pH (pH), understory-vegetation cover (UVC), and soil clay content (SCC) ($PA = 19.63 + 0.19\ NIP + 3.23\ SD - 1.6\ pH - 0.1\ UVC - SCC$; $\chi^2 = 25.9$, $P = 0.001$, Null-model deviance = 30.6). Stream pH ($Z = 2.07$, $P = 0.04$) was the predictor variable that best explained the occurrence of the species in the logistic model (Table S3).

The multiple linear regression model explained 60% of the variation in *A. sumtuosus* density (ALSD) in a model that included the predictor variables listed above ($ALSD = 2.63 + 0.94\ NIP - 27.83\ SD - 0.94\ pH + 0.07\ UVC + 0.25\ SCC$; $R^2 = 0.60$, $F_{5,20} = 5.92$, $P = 0.002$). The local density of *A. sumtuosus* was positively related to the number of isolated pools within sampling plots (Fig. 1A) and negatively related to discharge and pH of streams adjacent to plots (Fig. 1B and C, respectively). *Allobates sumtuosus* is distributed widely in riparian areas in RFAD and occurred in plots located alongside streams with pH varying from 2.02 to 8.21 and discharge between 0.003 and 0.430 m^3/sec. However, the species occurred at very low densities (<2 individuals encountered per plot) in ponds with pH < 3. The number of isolated pools in plots where *A. sumtuosus* occurred ranged from 1 to 11. The lowest densities of *A. sumtuosus* (1–4 individuals/2500 m^2) were recorded in plots with fewer isolated pools (1–3), adjacent to streams that were less acidic (pH 5.00–8.21) and with high stream discharge (0.10–0.43 m^3/sec).

Relationships between environmental factors and presence/absence of *Atelopus spumarius*.—The logistic regression model indicated that much of the variation (McFadden's $\rho^2 = 0.25$) in the presence or absence of *A. spumarius* (PA) in Reserva Ducke

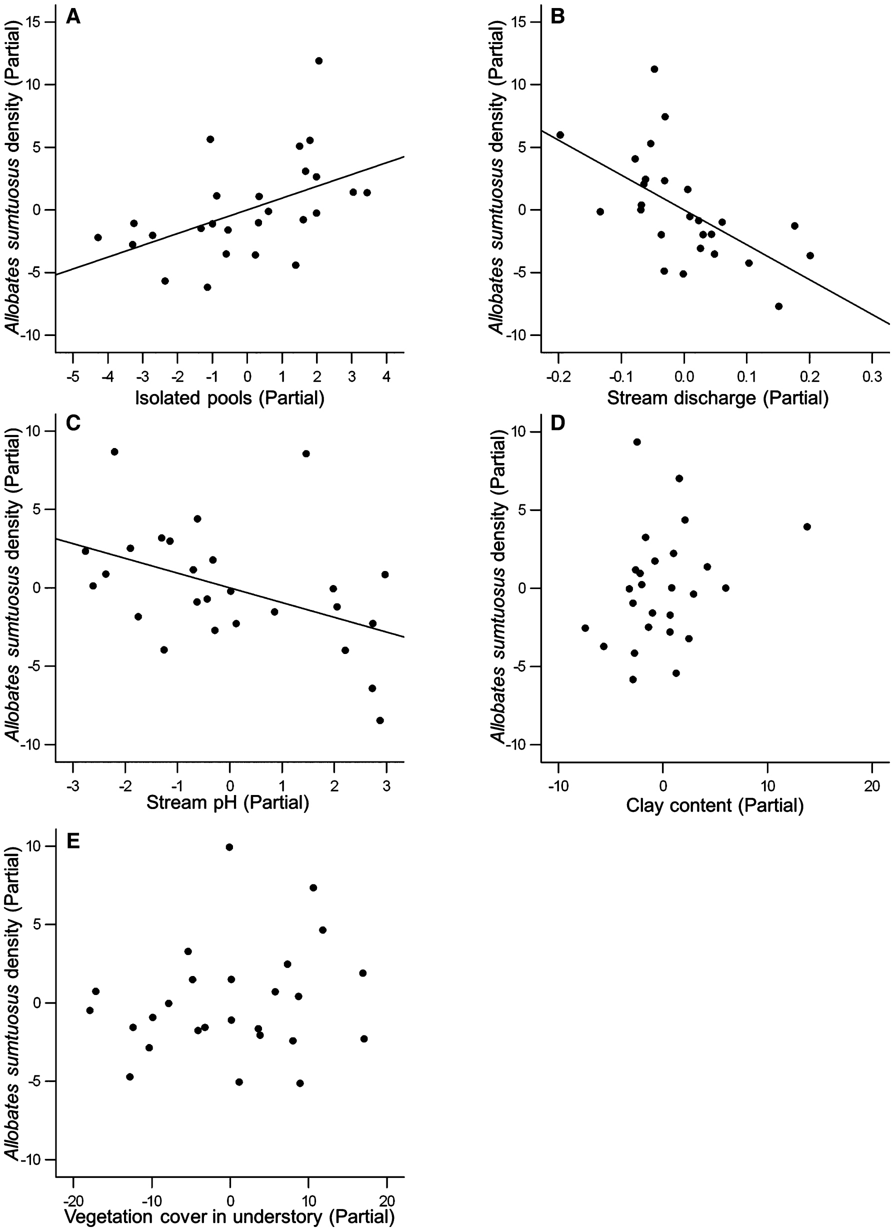

FIGURE 1. Partial regressions derived from multiple linear regression analyses showing the relationship between *Allobates sumtuosus* densities and (A) isolated pools, (B) stream discharge (m^3/sec), (C) stream pH, (D) clay content, and (E) vegetation cover in the understory in 26 riparian study plots in Reserva Ducke, Manaus, Amazonas, Brazil. Regression lines are only shown for statistically significant relationships.

could be explained by a model that included pH, stream discharge (SD), and number of connected pools (NCP) (PA = − 10.2 z+ 0.65 pH + 10.6 SD − 0.02 NCP; $\chi^2 = 22.5$, $P = 0.001$, null-model deviance = 16.7). Stream discharge ($Z = 2.1$, $P = 0.03$), pH ($Z = 2.02$, $P = 0.04$), and number of connected pools ($Z = 2.01$, $P = 0.04$) contributed significantly to the model (a classification of the logistic regression models is given in Table S4).

The density of *A. spumarius* was strongly associated with riparian areas adjacent to streams with less acidic water (Fig. 2). The species was found in plots with 4–10 connected pools, located along streams with pH of 5.0–8.21 and discharge from 0.01 to 0.43 m^3/sec. The multiple linear regression explained 37% of the variation in *A. spumarius* density (ATSD) (ATSD = 10.421 − 0.9 PH + 14.69 SD − 0.63 NCP, $R^2 = 0.37$, $F_{3,16} = 3.18$, $P = 0.05$). The density of *A. spumarius* was positively associated with riparian areas adjacent to streams with higher discharge (Fig. 2). Within the eastern drainage, the densities of *A. spumarius* were higher in plots with intermediate numbers of connected pools adjacent to streams (7), with pH near neutral (6.38–8.15) and intermediate discharge (0.108–0.165 m^3/sec) (Fig. 3).

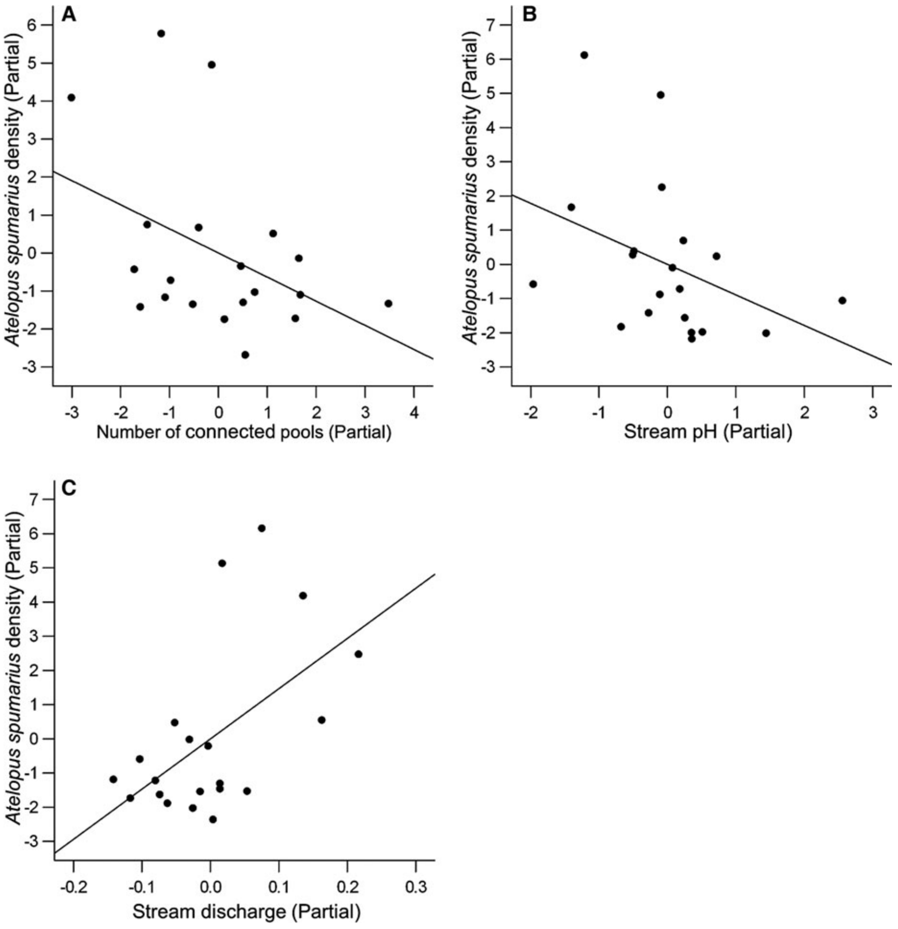

FIGURE 2. Partial regressions derived from multiple linear regression analyses showing the relationship between *A. spumarius* densities and (A) connected pools, (B) stream pH, and (C) stream discharge in 20 riparian plots in the eastern drainage in Reserva Ducke, Manaus, Amazonas, Brazil.

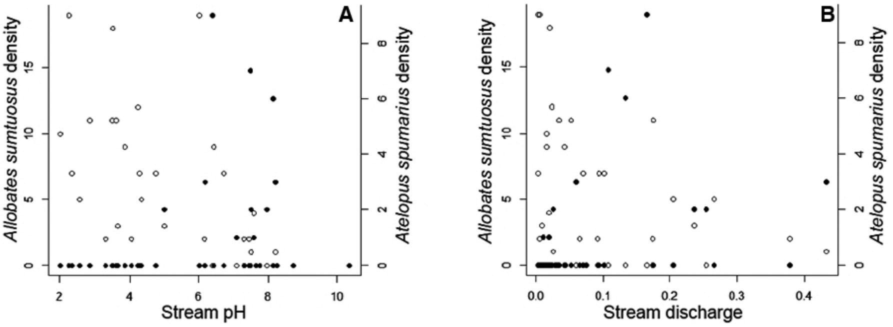

FIGURE 3. Variation in local density of *Allobates sumtuosus* (open circles, left vertical axis) and *Atelopus spumarius* (closed circles, right vertical axis) in relation to (A) stream pH and (B) stream discharge (m³/sec) variation in 40 plots distributed in Reserva Ducke, Manaus, Amazonas, Brazil.

DISCUSSION

The spatial distributions of *Allobates sumtuosus* and *Atelopus spumarius* were not random across riparian environments within the same landscape. Subtle variations in environmental characteristics of riparian zones and adjacent streams appear to act as ecological filters, influencing the occurrence and density of the two frog species. Variation in physicochemical characteristics of water bodies inhabited by larvae appears to be more important for both the establishment of adult individuals of these species and the determination of their local densities, than characteristics of the streamside areas they inhabit. These findings suggest that species surveys conducted at small spatial scales, which evaluate associations between species and environmental variables measured *in situ,* can greatly benefit the planning of conservation strategies for tropical frogs and other riparian organisms.

To guide actions for conservation of endangered frog species, several recent studies have used techniques of species-distribution modeling (SDM) in which key variables obtained by remote methods were used to locate areas that potentially contained suitable habitat and reproductive resources (*e.g.,* Giovanelli *et al.* 2008, Gómez-Rodríguez *et al.* 2008, Bernardo-Silva *et al.* 2012). However, the environmental variables used in those studies were derived from data collected and interpolated at relatively coarse scales. Moreover, the effectiveness of demarking new nature reserves based on the resulting distribution models strongly depends on large areas being available for conservation. Application of the results of these models for establishment of protected areas could result in the inclusion of extensive areas of unsuitable habitat and may or may not include areas with the ecological requirements necessary for persistence of the species. Thus, information generated by large-scale SDM should be used with caution when delimiting small reserves for vulnerable species (Loiselle *et al.* 2003). Environmental variables measured in the field, as well as data based on the relative abundance or density of target species, are needed to predict their local distribution and to foster appropriate local-scale management decisions by ensuring the establishment of protected areas of sufficient size and habitat complexity (Gómez-Rodríguez *et al.* 2008, Costa *et al.* 2010).

For the reasons given above, use of SDM to define reserves for endangered species should generally be a two-stage process. Coarse-scale information can be used to locate potential reserves. Subsequently, surveys should be undertaken to verify that the species does occur in the selected locality. If the reserve is so small that it might not contain all of the environmental variation expected for the region, further SDM based on locally measured variables, such as described in this study, should be undertaken.

The two species of diurnal frogs investigated in this study were encountered in riparian zones containing either a large number of isolated pools (*Allobates sumtuosus*) or pools connected to streams (*Atelopus spumarius*), reflecting the conditions for larval development required by each species. Environmental characteristics associated with water bodies and their riparian zones differ between the two drainages within the reserve, and these differences potentially limit the occupancy of *A. sumtuosus* and *A. spumarius* to RFAD's western and eastern drainages, respectively. Additionally, within the area in which each species occurs, their local density varies mainly in relation to physical and chemical properties of the adjacent streams. Consequently, whereas all areas of continuous streamside *terra firme* may typically be regarded as comprising almost identical habitat (*e.g.,* riparian zones *sensu* Pinheiro 2007), they encompass environmental mosaics that may act as ecological filters for some species.

Local distributions and abundances of frogs in assemblages associated with riparian areas are usually considered to be influenced by local soil characteristics, stream width, or vegetation structure (Parris & McCarthy 1999, Afonso & Eterovick 2007, Keller *et al.* 2009, Menin *et al.* 2011, Ribeiro *et al.* 2012, Rojas-Ahumada *et al.* 2012). Our results indicate that factors not previously considered in previous studies, such as pH, need to be investigated to understand distributions of adults of some Amazonian frog species. These effects may relate to particular stages in the life history. Species with life histories similar to that of *A. sumtuosus* (which spawns on leaf litter and transports larvae to isolated pools) may have reduced success in areas experiencing sporadic flooding from larger streams. Such floods inundate much of the alluvial terraces, potentially washing eggs and larvae into the stream, where they would be subject to predation by fish (Gascon 1992, Hero *et al.* 1998, Parris & McCarthy 1999, Rodrigues 2006). For species with long larval stages in perennial streams and larger water bodies, such as *Atelopus spumarius* (Zimmerman & Simberloff 1996, Gawor *et al.* 2012), greater light incidence and discharge should result in greater production of algae and associated invertebrates, both of which are eaten by tadpoles (Gawor *et al.* 2012).

Some of the pH values we measured were less than 2.9, which are very low values for streams in undisturbed landscapes. As the distribution of both species, and especially that of *Atelopus spumarius*, is apparently restricted by low pH, further studies of the factors affecting pH variation in these forest streams should be undertaken to determine whether the low values represent natural spatial variation or a long-term trend.

Allobates sumtuosus occurred alongside streams with a wide pH range (2.02–8.21). However, tadpoles of *Allobates sumtuosus* may be less tolerant to alkaline than to acidic pools and also to extremely acidic pools, as the species occurs at very low densities on the banks of streams with pH above 5 and below 3. In contrast, adults of *Atelopus spumarius* were restricted to banks of streams with a limited pH range. This is not likely to be associated with the ecology of adult individuals, which have a terrestrial lifestyle, but it possibly relates to a restricted physiological tolerance of larvae to a range of pH values that are close to neutral (6.15–8.21). Field and laboratory studies have demonstrated that amphibian larval tolerance to water pH varies both inter- and intraspecifically (Pierce 1985). Suboptimal water pH can also result in development of abnormalities and reduced growth rate (Pierce 1985), and it has been suggested to influence the occurrence and abundance of amphibians in temperate regions. For example, *Rana arvalis* spawns more frequently in more acidic waters (Leuven *et al.* 1986), and the Pennsylvanian salamander (*Ambystoma jeffersonianum*) avoids breeding in alkaline ponds (Horne & Dunson 1994).

Besides the physical variables we analyzed, biotic factors may influence the spatial distribution of *Allobates sumtuosus* and *Atelopus spumarius* in RFAD. The species co-occurred in four plots, where their relative densities were negatively correlated. This could suggest that biotic interactions, rather than environmental filtering, regulate the species' density and occurrence (Kraft *et al.* 2015), because asymmetrical competition has been documented among other diurnal frogs (Lehtinen 2005, Twomey *et al.* 2008). However, the natural histories of *Allobates sumtuosus* and *Atelopus spumarius* are very distinct (Lima *et al.* 2006), which makes it difficult to pinpoint any ecological factor likely to trigger competitive interactions between them. Given the strength of the relationships observed between environmental variables and the distributions of the two species, we believe that gradual changes in streamside characteristics favor each species differently, allowing their relative densities to peak in nonoverlapping regions of the environmental clines across the reserve. Dissimilarity in species–habitat relationships has been proposed as a mechanism regulating the spatial distributions of European salamanders (*Salamandra salamandra* and *S. atra*) in mountainous terrains, with species co-occurring only in a narrow contact zone, with no evidence of competitive interaction (Werner *et al.* 2014).

We demonstrated that, even within a relatively small area (64 km^2) of the same forest vegetation type, floodplains bordering small streams contain sufficient environmental variation to limit the occurrence of frog species. Small environmental variations that are difficult to perceive, such as incremental differences in discharge rate and pH of streams, seem to be more effective environmental filters to the distribution of these species than factors associated with the terrestrial habitat of adult frogs. Thus, occurrence mapping of species based solely on traits of the terrestrial environment may not be sufficient to develop distribution models that are effective for species management. For example, despite occurring in both of the major catchments of RFAD, *Allobates sumtuosus* occurred only in low densities in the eastern drainage. Density data reveal that those areas are probably suboptimal for the species and may not be adequate for it to maintain demographic processes. At the local scale, where mass effects may result in dispersing individuals occupying suboptimal conditions, modeling algorithms based on species relative densities will probably be more useful for conservation planning than models based on presence–absence data. Field studies are more demanding and sometimes more costly than studies based only on remote-sensing and museum records. However, they seem to be an essential complement to the use of remote-sensing surrogates when defining the location of small reserves in Amazonia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Links to directly access to the data and metadata collected at Reserva Ducke and used to do the analyses presented in the present study.

FIGURE S1. Location of the study area in Reserva Ducke, in Manaus, Amazonas State, Brazil.

FIGURE S2. Schematic representation of sampling plots for riparian environments installed in Reserva Ducke, Manaus, Amazonas, Brazil.

FIGURE S3. Local-scale variation of the main environmental predictors of *Allobates sumtuosus* and *Atelopus spumarius* occurrences and densities in 40 riparian plots in Reserva Ducke, Manaus, Amazonas, Brazil.

FIGURE S4. Distribution of *Allobates sumtuosus* and *Atelopus spumarius* and localities where neither species was recorded in riparian study plots in the Reserva Ducke, Manaus, Amazonas, Brazil.

TABLE S1. *Results of Pearson's multiple linear correlation analyses among eight selected environmental variables in 40 plots distributed along the Reserva Ducke.*

TABLE S2. *The raw number of individuals of* Allobates sumtuosus *and* Atelopus spumarius *recorded in each sampling occasion in the western and eastern plots located in the Reserva Ducke, Manaus, Amazonas.*

TABLE S3. *Classification table of the logistic regression model used to investigate the relationship among three environmental variables on presence/absence of* Allobates sumtuosus *in 40 plots located at Reserva Ducke, Manaus, Amazonas, Brazil.*

TABLE S4. *Classification table of the logistic regression model used to investigate the relationship among three environmental variables on presence/absence of* Atelopus spumarius *in 40 plots located at Reserva Ducke, Manaus, Amazonas, Brazil.*

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