

Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in Central Amazonia: mesoscale spatial patterns

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Abstract: Many studies suggest that edaphic variables are major determinants of frog distributions. However, leaf-litter depth and soil characteristics are influenced by distance from streams, so the apparent relationship between edaphic characteristics and species distributions could be an artefact of the dependence of species on free water for reproduction. Therefore, we investigated the effect of edaphic variables on the mesoscale distribution of frog species not dependent on free water for reproduction. We evaluated the effects of soil texture, pH, slope, number of trees and leaf-litter volume on the distribution of nine terrestrially reproducing anuran species in the Reserva Ducke, a 100-km² terra firme forest preserve in central Amazonia. Diurnal and nocturnal assemblages of anuran species were sampled in 72 plots systematically distributed across the reserve. We sampled the diurnal anuran assemblage by visual encounter in 250 × 1-m plots and the nocturnal assemblage in 250 × 20-m plots using both auditory and visual surveys. The majority of terrestrially breeding anuran species were influenced by topographic and/or edaphic variables, such as slope, soil clay content and pH. However, responses to environmental predictors differed among species. Most species occurred throughout all environmental gradients and relationships with soil characteristics were subtle, indicating that these species occur in the majority of habitats in Reserva Ducke. The results of this study indicate that terrestrially breeding frogs are habitat generalists that show little mesoscale beta diversity associated with habitat variation.

Key Words: abundance, beta diversity, Brazil, clay, community structure, distribution patterns, frogs, soil, slope

INTRODUCTION

Most studies on habitat use by vertebrates in tropical forests have been based on differences in distributions of individuals among types of habitats (Duellman 1999, Emmons 1984, Rosenberg 1990) or along large altitudinal gradients (Fauth *et al.* 1989, Giaretta *et al.* 1999). However, the use of coarse differences or habitat type assumes that microhabitats are relatively homogeneous and discrete (Watling 2005). In contrast, many studies have shown distributions of understory plants and trees to be related to soil and topographic features (Clark *et al.* 1999, Kahn & Castro 1985, Kinupp & Magnusson 2005, Lescure & Boulet 1985). Such studies with animals are rare, but Vasconcelos *et al.* (2003) found that ant assemblages are sensitive to local variation in vegetation and soil.

Topographic factors influence soil characteristics (Chauvel *et al.* 1987), and, consequently, forest structure and dynamics (Bellingham & Tanner 2000, Castilho *et al.* 2006, Webb *et al.* 1999). These variations in forest structure and composition across topographic gradients generate microhabitat variability, which may affect demographic patterns in animal assemblages (Catling & Burt 1995, Vasconcelos *et al.* 2003).

Topography, climate and vegetation type are generally considered the most important factors determining distribution of anuran species on a macroscale (Duellman 1999). Vegetation structure, litter cover and soil influence the distribution of some anuran species (Fauth *et al.* 1989, Hadden & Westbrooke 1996, Pearman 1997). Structurally simple habitats may contain fewer species, so that local species richness is also associated with structural diversity of the habitat (Ernst & Rödel 2005, Ernst *et al.* 2006, Heinen 1992).

Most studies have examined local-scale tropical anuran diversity in leaf-litter frog assemblages (Allmon 1991, Fauth *et al.* 1989, Inger & Colwell 1977, Lieberman 1986, Scott 1982). In these studies, species richness

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increased with litter depth and humidity (Fauth *et al.* 1989), or abundance of litter arthropods (Lieberman 1986). Edaphic factors, such as soil humidity (Vonesh 2001) and pH (Wyman 1988), may affect the occurrence of some species.

Many proposed relationships with soil and leaf-litter characteristics may be artifacts of other processes. Many species of frog require free water for reproduction (Haddad & Prado 2005), and are thus restricted to areas, such as bottomlands around streams, which by their nature have a limited range of soil and leaf-litter characteristics (Luizão *et al.* 2004). Zimmerman & Bierregaard (1986) suggested, considering all species in the community, that frogs are not a useful group for the study of forest fragmentation because their distributions depend more on presence of aquatic breeding sites than on area and other characteristics of forest fragments. This results in high beta diversity and, hence, natural variance in occurrences. However, many neotropical frog species are not dependent on free water for reproduction (Haddad & Prado 2005). These species deposit their eggs in soil or leaf-litter and potentially could occur in any part of the forest. Detection of beta diversity is related to the scale and location of the study. High beta diversity for plants at both local and landscape scales (Jones *et al.* 2006, Poulsen *et al.* 2006, Tuomisto *et al.* 2003) has been observed in western Amazonian, while other studies have found that plants often show little beta diversity (Costa *et al.* 2005, Kinupp & Magnusson 2005), except at large-enough scales (> 10 km) for differences in species occurrences to be explained by dispersal limitation (Hubbell 2001). Distributions of understory plants (on spatial scales of 1–10 km) are also often associated with soil and leaf-litter characteristics, but show little mesoscale (< 10 km) beta diversity; most species occur across the majority of ecological gradients present in Central Amazonian forests (Costa *et al.* 2005, Kinupp & Magnusson 2005).

Nine species of anuran with tadpoles that develop completely in terrestrial habitats occur in non-inundated (terra firme) forest in the region of Manaus, Amazonas, Brazil (Zimmerman & Simberloff 1996). As these species lack aquatic larvae, they may show habitat relationships that differ from aquatic-breeding species. These species are ideal organisms to test whether edaphic or topographic factors affect distributions at a local scale, independent of the presence of free water. Three of the nine species are small (snout-vent length < 20 mm), four species are intermediate in size (25–40 mm) and two species are large (> 90 mm).

In order to determine levels of mesoscale beta diversity in central Amazonian anurans, we studied the effects of soil and topography on the distributions of nine terrestrially reproducing species in 64 km² of terra firme forest near Manaus. In this study, we show that terrestrially breeding frogs in central Amazonia show little mesoscale

beta diversity, and that their responses to edaphic and topographic gradients are more similar to those of understory plants than to aquatic-breeding frogs.

METHODS

Study area

Our study took place at Reserva Florestal Adolpho Ducke (RFAD, 02°55′–03°01′S, 59°53′–59°59′W), adjacent to the city of Manaus, Amazonas state, Brazil. The reserve covers 10 000 ha of terra firme (non-flooded) rain forest, a well-drained forest not subject to seasonal inundation. The forest is characterized by a 30–37-m-tall closed canopy, with emergents growing to 40–45 m (Ribeiro *et al.* 1999). The understory contains abundant sessile palms (*Astrocaryum* spp. and *Attalea* spp.; Ribeiro *et al.* 1999). The climate is characterized by a rainy season from November to May and a dry season during the rest of the year (Marques Filho *et al.* 1981). Mean annual temperature is approximately 26 °C (Marques Filho *et al.* 1981) and mean annual rainfall was 2489 mm between 1985 and 2004.

Data collection

We sampled the anuran assemblage during three diurnal samples (November–December 2002, February–April 2003 and January–February 2004) and five nocturnal samples (November–December 2002, March–May 2003, November–December 2003, January–March 2004 and April–May 2004). Data were collected in 72 plots systematically distributed over a 64-km² grid formed by 8-km long trails (see Figure 1 in Costa *et al.* 2005). Each plot was at least 1 km distant from any other. Plots were 250 m long and positioned to follow altitudinal contour lines, and thus minimize altitudinal and soil variation within each plot (Magnusson *et al.* 2005). All plots were at least 1 km from the edge of the reserve. Diurnal surveys required a mean of 46 d to cover all plots within the reserve, and nocturnal surveys required a mean of 49 d to survey all 72 plots.

Diurnal surveys lasted about 2 h per plot and were conducted between 08h00 and 16h00 by two people walking along a 250 × 1-m (0.025 ha) plot. Observers visually scanned and carefully turned over the leaf-litter, detecting individuals by visual encounter.

We sampled the nocturnal anuran assemblage by simultaneous visual encounter surveys and auditory sampling (Crump & Scott 1994, Zimmerman 1994). These methods are complementary and adequate to survey distribution and abundance of anurans in long- and short-term studies (Doan 2003). We sampled each plot for about 1 h between 18h30 and 22h00. Every 5 m,

the two observers stopped and recorded the number of vocalizing individuals of each species and searched the litter and vegetation for anurans. All individuals located visually or by their call within 20 m of the centre line of the plot were recorded, so that approximately 1 ha was searched per plot. We pooled the number of individuals recorded by the two methods in analyses.

Voucher specimens were deposited in the Amphibians and Reptiles Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA-H) in Manaus, Amazonas, Brazil. The nomenclature in this study is in accordance with Amphibian Species of the World (<http://research.amnh.org/herpetology/amphibia/index.php>).

Environmental parameters

The topographic parameters used were altitude and slope of each study plot. The altitude of each plot was obtained from direct field measurements by a professional surveyor. Slope measurements were taken with a clinometer every 50 m, perpendicular to the main axis of the plot, totalling five measurements per plot. We used the mean of the five measurements to represent the slope of the plot (range = 0.67°–27.8°).

Previous studies measured soil characteristics (clay content and pH) at the same points as slope, by collecting six samples to a depth of 5 cm. Samples were combined for each plot and analysed at the Soil Laboratory of the Agronomy Department at INPA. Clay content methodology is described in Embrapa (1997) and pH methodology in Embrapa Solos (1999). Soil clay content varied from 1.6% near streams to 87.7% on ridges. Values for pH varied from 3.4–4.9.

A previous study determined the number of trees per plot for three different diameter at breast height (dbh) classes. Individuals with 1 cm ≤ dbh < 10 cm were counted in 250 × 4-m plots; individuals with 10 cm ≤ dbh < 30 cm were counted in 250 × 20-m plots and individuals with dbh ≥ 30 cm were counted in 250 × 40-m plots (Castilho *et al.* 2006).

We measured litter volume twice during the study, at five points, spaced every 50 m along each plot trail. At each point, the litter in a 60 × 60-cm area was collected and compressed in a bucket (24 cm high by 24 cm diameter), graduated in litres. We used a circular board the same diameter as the bucket to compress the litter three times, as much as possible. We then removed the board and measured the volume. We use mean litter volume for each plot in analyses.

Data analysis

Leptodactylus (Lithodytes) aff. andreae and *Anomaloglossus stepheni* were recorded in both diurnal and

nocturnal samples, but much higher abundances of both species were recorded during diurnal samples. We use only diurnal abundance data in analyses of these species.

We tested for spatial auto-correlation of independent variables with Mantel tests, using the RT software package (RT – a Program for Randomization Testing, Version 2.1. Centre for Applications of Statistics and Mathematics, University of Otago, Otago). We calculated association matrices of independent variables as the difference in the value of the variable between plots. We used the Euclidean Distance coefficient to calculate the geographic distance matrix.

We used multiple regressions to investigate the effects of independent variables (slope, clay content, number of trees, volume of litter and pH) on the abundance of each species and on the number of species per plot. The mean abundance of each species per plot, based on the five nocturnal samples or on the three diurnal samples, was used in analyses (data on abundance of each species is available from <http://ppbio.inpa.gov.br/Eng/inventarios/ducke/anuros>). Abundance data were transformed ($\log(x+1)$) before analyses to reduce the effect of extreme values. We did not include altitude in regression models because it was correlated with clay content (Pearson correlation $r = 0.94$).

For species found in < 50 plots, we analysed presence/absence data using logistic regression (Model: presence/absence = a + slope + clay content + number of trees + litter volume + pH). We used SYSTAT 8.0 (SYSTAT: The System for Statistics, Evanston, Illinois, USA) for all regression analyses.

Species sizes used in analyses come from Lima *et al.* (2006) and were transformed (1/maximum length of male). Independent variables in regressions models are abbreviated as follows: clay (clay content), trees (number of trees) and litter (volume of litter).

RESULTS

We detected three species of Leptodactylidae, three Brachycephalidae, two Microhylidae and one species of Aromobatidae during our sampling (Table 1). *Leptodactylus (Lithodytes) aff. andreae*, *Anomaloglossus stepheni*, *Eleutherodactylus fenestratus* and *Eleutherodactylus zimmermanae* occurred in all plots. *Eleutherodactylus fenestratus* was the most frequently encountered species, representing 41% of all individuals. The number of plots where each species was recorded was significantly (number of plots = 20.9 + 875 × (1/maximum length of male); $R^2 = 0.581$; $F_{1,7} = 9.73$; $P = 0.017$) and negatively associated with species size, with smaller species occurring in more plots (Figure 1).

Table 1. Number of plots where each species was recorded at Reserva Florestal Adolpho Ducke, Manaus, Brazil. Diurnal species (*Anomaloglossus stepheni* and *Leptodactylus (Lithodytes) aff. andreae*) were sampled only by visual sampling. The Microhylidae, which are subterranean, were sampled only by auditory sampling.

| Species | Number of plots | Visual sampling | Auditory sampling | Total of individuals |
|--|-----------------|-----------------|-------------------|----------------------|
| Aromobatidae | | | | |
| <i>Anomaloglossus stepheni</i> | 72 | 1352 | – | 1352 |
| Brachycephalidae | | | | |
| <i>Eleutherodactylus fenestratus</i> | 72 | 334 | 6368 | 6702 |
| <i>Eleutherodactylus ockendeni</i> | 41 | 6 | 105 | 111 |
| <i>Eleutherodactylus zimmermanae</i> | 72 | 5 | 1689 | 1694 |
| Leptodactylidae | | | | |
| <i>Leptodactylus (Lithodytes) aff. andreae</i> | 72 | 3957 | – | 3957 |
| <i>Leptodactylus pentadactylus</i> | 28 | 50 | 12 | 62 |
| <i>Leptodactylus stenodema</i> | 21 | 11 | 23 | 34 |
| Microhylidae | | | | |
| <i>Synapturanus mirandaribeiroi</i> | 45 | – | 1459 | 1459 |
| <i>Synapturanus cf. salseri</i> | 48 | – | 996 | 996 |

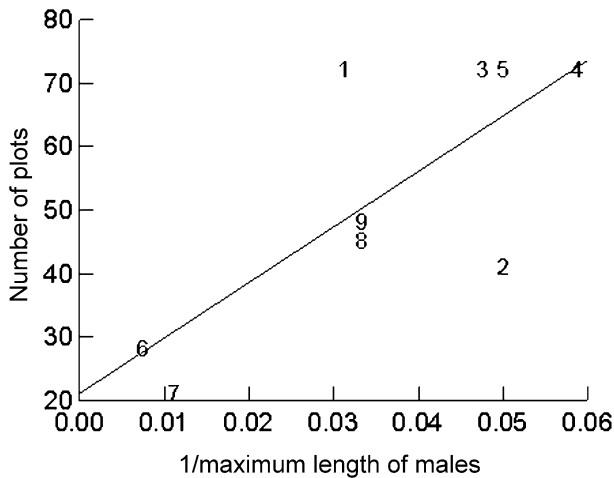


Figure 1. Maximum snout-vent length of males per species and number of plots in which each species was recorded at Reserva Florestal Adolpho Ducke, Manaus, Brazil. 1 = *Eleutherodactylus fenestratus*, 2 = *Eleutherodactylus ockendeni*, 3 = *Eleutherodactylus zimmermanae*, 4 = *Anomaloglossus stepheni*, 5 = *Leptodactylus (Lithodytes) aff. andreae*, 6 = *Leptodactylus pentadactylus*, 7 = *Leptodactylus stenodema*, 8 = *Synapturanus mirandaribeiroi*, 9 = *Synapturanus cf. salseri*.

Spatial auto-correlation

There was no correlation between the geographical distances among plots and the variables slope, clay content or number of trees (Mantel tests: $P=0.41$, $P=0.18$ and $P=0.94$, respectively). There was a significant correlation between the geographical distances between plots and pH and litter volume ($P < 0.0001$ in both cases). However, the variance explained by geographical distance was small for pH ($r^2 = 0.08$) and litter volume ($r^2 = 0.10$).

Effects of environmental variables on abundance

We used models containing only the significant variables ($P < 0.05$) to construct graphs illustrating the effects of these variables. The number of species encountered per plot varied from four to eight (mean = 6.54; SD = 0.99; $N = 72$). The model explained about 15% of the variance in the number of species (number of species = $2.24 + 0.020\text{Slope} - 0.003\text{Clay} + 0.002\text{Trees} - 0.010\text{Litter} + 0.597\text{pH}$; $R^2 = 0.147$; $F_{5,66} = 2.27$; $P = 0.058$). The number of species was significantly ($t = 2.34$; $P = 0.022$) and positively related to the number of trees. The other variables did not contribute significantly to the model ($P > 0.22$ in all cases).

The model explained about 53% of the variance in the abundance of *Anomaloglossus stepheni* (abundance of *A. stepheni* = $0.64 - 0.047\text{Slope} - 0.009\text{Clay} + 0.001\text{Trees} + 0.058\text{Litter} + 0.302\text{pH}$; $R^2 = 0.526$; $F_{5,66} = 14.6$; $P < 0.001$). There were significant (Table 2) and negative relationships with slope and clay content (Figure 2).

The model explained about 37% of the variance in the abundance of *Eleutherodactylus fenestratus* (abundance of *E. fenestratus* = $2.86 + 0.020\text{Slope} + 0.006\text{Clay} - 0.00004\text{Trees} - 0.031\text{Litter} - 0.075\text{pH}$; $R^2 = 0.374$; $F_{5,66} = 7.88$; $P < 0.001$). Slope and clay content (Figure 2) showed significant (Table 2) positive effects on the abundance of this species.

The model explained about 16% of the variance in the abundance of *Eleutherodactylus zimmermanae* (abundance of *E. zimmermanae* = $3.39 + 0.005\text{Slope} - 0.008\text{Clay} + 0.001\text{Trees} - 0.203\text{Litter} - 0.344\text{pH}$; $R^2 = 0.165$; $F_{5,66} = 2.60$; $P = 0.033$). There was a significant (Table 2) and negative effect of clay content on the abundance of this species (Figure 2).

The model explained about 13% of the variance in the abundance of *Leptodactylus (Lithodytes) aff. andreae*

Table 2. Probabilities associated with effects of variables on the abundance of four species of anuran at Reserva Florestal Adolpho Ducke, Manaus, Brazil, derived from models of multiple regressions (Abundance of species $i = a + \text{Slope} + \text{Clay content} + \text{Number of trees} + \text{Litter volume} + \text{pH}$). b = standardized regression coefficient; P = probabilities. Significant values are shown in bold.

| Species | | Slope | Clay content | Number of trees | Litter volume | pH |
|--|-----|----------------|----------------|-----------------|---------------|--------|
| <i>Anomaloglossus stepheni</i> | b | -0.601 | -0.518 | 0.179 | 0.045 | 0.141 |
| | P | < 0.001 | < 0.001 | 0.060 | 0.602 | 0.192 |
| <i>Eleutherodactylus fenestratus</i> | b | 0.398 | 0.552 | -0.013 | -0.038 | -0.054 |
| | P | < 0.001 | < 0.001 | 0.904 | 0.705 | 0.663 |
| <i>Eleutherodactylus zimmermanae</i> | b | 0.047 | -0.384 | 0.130 | -0.126 | -0.128 |
| | P | 0.698 | 0.007 | 0.299 | 0.272 | 0.369 |
| <i>Leptodactylus (Lithodytes) aff. andreae</i> | b | -0.341 | -0.199 | -0.114 | 0.061 | -0.176 |
| | P | 0.007 | 0.163 | 0.371 | 0.602 | 0.228 |

(abundance of *L. (L.) andreae* = $4.49 - 0.020\text{Slope} - 0.003\text{Clay} - 0.0004\text{Trees} + 0.060\text{Litter} - 0.292\text{pH}$; $R^2 = 0.131$; $F_{5,66} = 1.98$; $P = 0.092$). There was a

significant effect of slope (Table 2), which showed a negative relationship with the abundance of this species (Figure 2).

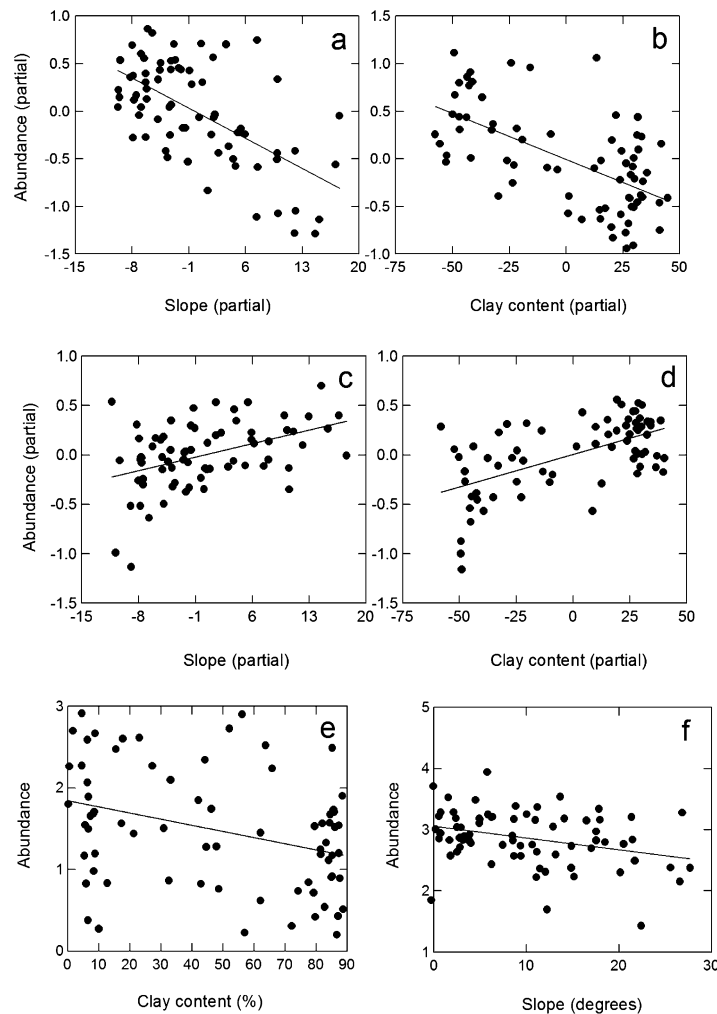


Figure 2. Regressions or partial regressions for statistically significant effects of predictor variables on log(density + 1) for four species of terrestrially breeding frog at Reserva Florestal Adolpho Ducke, Manaus, Brazil. *Anomaloglossus stepheni* (a, b) ($r^2 = 0.383$, $P < 0.001$; $r^2 = 0.379$, $P < 0.001$); *Eleutherodactylus fenestratus* (c, d) ($r^2 = 0.192$, $P < 0.001$; $r^2 = 0.330$, $P < 0.001$); *Eleutherodactylus zimmermanae* (e) ($r^2 = 0.110$, $P = 0.004$); *Leptodactylus (Lithodytes) aff. andreae* (f) ($r^2 = 0.093$, $P = 0.009$).

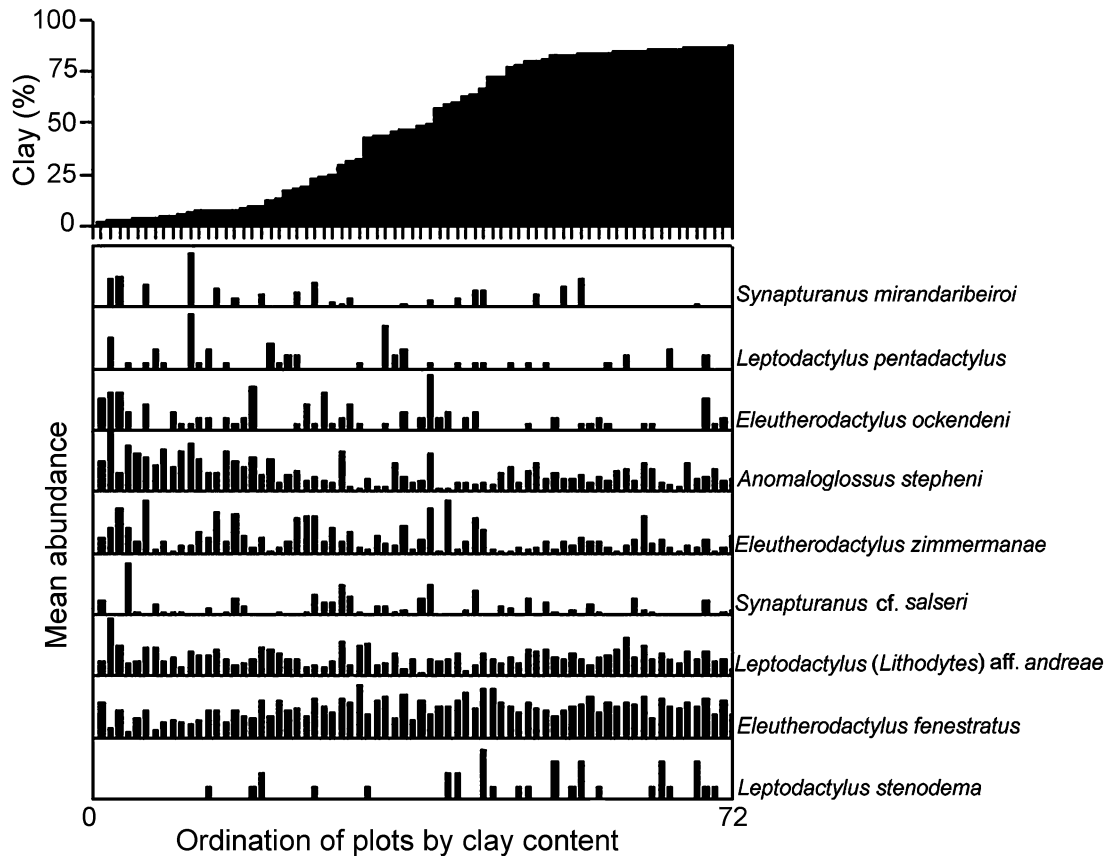


Figure 3. Distribution of anuran species with terrestrial reproduction along clay content gradient in study plots at Reserva Florestal Adolpho Ducke, Manaus, Brazil.

In spite of some species exhibiting relationships with clay content, most species occurred across the whole gradient (Figure 3).

Effect of environmental variables on presence/absence

For *Eleutherodactylus ockendeni*, only the number of trees contributed significantly (Table 3) and negatively to the presence of this species among plots (presence/absence of *E. ockendeni* = $-9.31 + 0.005\text{Slope} - 0.017\text{Clay} + 0.009\text{Trees} + 0.080\text{Litter} + 0.889\text{pH}$; MacFadden’s $\text{Rho}^2 = 0.169$; $\chi^2 = 16.6$; $P = 0.005$).

Only pH contributed significantly (Table 3) and negatively to the *Leptodactylus stenodema* model (presence/absence of *L. stenodema* = $19.1 - 0.063\text{Slope} + 0.006\text{Clay} - 0.002\text{Trees} - 0.189\text{Litter} - 4.252\text{pH}$; MacFadden’s $\text{Rho}^2 = 0.194$; $\chi^2 = 16.9$; $P = 0.004$).

Only pH contributed significantly (Table 3) and positively to the model of *Synapturanus cf. salseri* (Presence/absence of *S. cf. salseri* = $-16.8 + 0.063\text{Slope} -$

Table 3. Probabilities associated with effects of variables on the presence/absence of five anuran species at Reserva Florestal Adolpho Ducke, Manaus, Brazil, derived from models of logistic regressions (Presence/Absence = $a + \text{Slope} + \text{Clay content} + \text{Number of trees} + \text{Litter volume} + \text{pH}$). Significant values are shown in bold.

| Species | Slope | Clay content | Number of trees | Litter volume | pH |
|-------------------------------------|-------|--------------|-----------------|---------------|--------------|
| <i>Eleutherodactylus ockendeni</i> | 0.903 | 0.115 | 0.003 | 0.895 | 0.479 |
| <i>Leptodactylus pentadactylus</i> | 0.287 | 0.383 | 0.586 | 0.177 | 0.549 |
| <i>Leptodactylus stenodema</i> | 0.192 | 0.578 | 0.332 | 0.785 | 0.016 |
| <i>Synapturanus mirandaribeiroi</i> | 0.127 | 0.514 | 0.076 | 0.837 | 0.254 |
| <i>Synapturanus cf. salseri</i> | 0.155 | 0.847 | 0.878 | 0.077 | 0.034 |

$0.002\text{Clay} - 0.0004\text{Trees} + 1.17\text{Litter} + 3.16\text{pH}$; MacFadden’s $\text{Rho}^2 = 0.152$; $\chi^2 = 13.9$; $P = 0.016$).

For *Leptodactylus pentadactylus* (MacFadden’s $\text{Rho}^2 = 0.066$; $\chi^2 = 6.4$; $P = 0.272$) and *Synapturanus mirandaribeiroi* (MacFadden’s $\text{Rho}^2 = 0.056$; $\chi^2 = 5.3$; $P = 0.379$) none of the variables contributed significantly to the model (Table 3).

DISCUSSION

The distributions of most of the widely distributed species in the reserve (present in > 50 of 72 plots) were significantly associated with slope or clay content. In contrast, these variables were not related to the distributions of any of the less amply distributed species. The distributions of the less amply distributed species were more likely to be influenced by soil pH or tree density. Despite the significant effects of the predictor variables, the models explained little of the variance in species density or occurrence, and most species occurred throughout the majority of the environmental gradients. The number of occupied plots was negatively associated with species size, with larger species occurring at lower average densities, but this may be a sampling effect.

Another study conducted in central Amazonia found no differences in total number of anuran individuals in plots differing in soil and/or slope (Allmon 1991). However, soil type was analysed using gross categories. In a study conducted in Costa Rica, the pattern of distribution of terrestrially breeding frogs was edaphically biased, showing relationships among the abundance of species with soil drainage (Watling 2005). A study conducted in Australia found higher species richness and abundance of anurans in sites with clay soil, presumably because these had greatest water availability (Woinarski *et al.* 1999) and were closer to reproduction sites.

The presence of *L. Stenodema* and *S. cf. salseri* were influenced by soil pH. However, *L. stenodema* occurred in more acid soils, while *S. cf. salseri* occurred in soils with higher pH. Wyman (1988) and Wyman & Hawksley-Lescault (1987) reported that amphibian species were encountered in soils with higher pH, suggesting a possible habitat selection related to oviposition sites. According to Pierce (1985), the early developmental stages of amphibians can be severely affected by low pH because it affects ionic regulation. However, Vonesh (2001) did not detect effects of soil pH on the distribution of anurans in Africa. Therefore, although some species may be affected by soil pH, it appears that the distributions of most anurans are independent of natural variation in soil pH.

Only the occurrence of *E. ockendeni* was influenced by tree density. Overall species richness in plots was also positively related to the number of trees. Tree density generally has little effect on litter anurans in primary tropical forests (Allmon 1991, Giaretta *et al.* 1999, Vonesh 2001). On the other hand, in other tropical amphibian communities, the vegetation structure influenced the richness and composition of terrestrial and arboreal anuran species (Ernst & Rödel 2005, Ernst *et al.* 2006, Pearman 1997). In these studies (Ernst & Rödel 2005, Ernst *et al.* 2006, Pearman 1997), the densities of some species decreased, indicating sensitivity of this species to habitat degradation. Tree

density had a negative effect on the abundance of ant species in the central Amazon (Vasconcelos *et al.* 2003).

Litter-layer depth is often measured in studies of herpetological communities. Some studies have shown positive relationships between litter depth and anuran abundance or species richness (Fauth *et al.* 1989, Giaretta *et al.* 1999, Heinen 1992, Lieberman 1986, Vonesh 2001). These relationships can be related to a greater number of microhabitats (Fauth *et al.* 1989) or refuges (Lieberman 1986). However, other studies report litter depth having no significant influence on the anuran community (Allmon 1991, Scott 1976, this study). Study plot size may influence potential mean depth effects and averaging may mask effects seen in small-scale studies (C.F.D.Rocha, personal communication). Differences among studies may be related to different methods quantifying litter characteristics (volume, depth, or dry mass) or to unmeasured difference in litter quality, which may vary with topography and/or seasonally. Litter decomposes faster in the rainy season, often resulting in a shallower litter layer (Luizão & Schubart 1986).

As a group, frogs show high beta diversity largely due to variation in the availability of aquatic breeding sites (Ernst & Rödel 2006, Zimmerman & Bierregaard 1986). However, most plant studies have measured species distributions at this scale using systematically or randomly placed plots. Some groups of plants, such as some palms (C. Castilho, pers. comm.) and ferns (Costa *et al.* 2005), have species that are closely associated with watercourses, and these would probably show beta diversity patterns more similar to aquatic-reproducing frogs, if these plants were included in surveys.

Systematically distributed plots, such as those used in this study, mostly reveal terrestrially breeding frogs. The species of frog studied vary in size and foraging height, but they showed little mesoscale (1–10 km) beta diversity. Some species tended to be more common in some soil and topographic conditions, but all occurred across most of the edaphic gradients present in Reserva Ducke, which are typical of much of central Amazonia. In our models, edaphic and topographical variables explained 6–20% of the variance in abundance (or presence/absence) of the seven anuran species, a rate similar to that for understorey plants (Costa *et al.* 2005, Kinupp & Magnusson 2005).

Our data indicate that terrestrially breeding frog species should not be lumped with species of aquatic-breeding frog for analyses of habitat relationships, because the presence of reproduction sites are important for the latter group (Ernst & Rödel 2005, 2006). Zimmerman & Bierregaard (1986) suggested that frogs are not good indicator species for fragmentation studies because their distributions are largely determined by the presence of water bodies suitable for reproduction. We disagree with that generalization.

Habitat variation among our study sites was subtle, indicating that it is probably insufficient to exclude most of the species from any locality within the reserve. Reserva Ducke is large and includes most of the habitats found in terra firme forest in central Amazonia (Ribeiro *et al.* 1999), so our results are likely to apply to most areas with relatively intact forest. However, all of the terrestrially breeding species we studied are forest specialists, and our surveys during the past 25 y indicate that they are rare or absent from regrowth forest and small forest fragments in the Manaus area. Species such as these, which occur in most situations in intact forest, but which are sensitive to human disturbances, are ideal candidates for studies of forest fragmentation.

At the scale of our study, terrestrially breeding frogs show little mesoscale beta diversity associated with habitat variation, suggesting that models based on dispersal limitation being developed for plants (Hubbell 2001) may apply to some animal groups.

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