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Composition and ecology of a snake assemblage in an upland forest from Central Amazonia

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Abstract: Most species of Amazonian snakes have wide geographic distributions. However, local environmental factors influence the formation of assemblages in different localities. In this study, we investigated the composition of the assemblage and the effect of environmental variables on the distribution of the species inhabiting an upland forest in the Experimental Farm area of the Federal University of Amazonas in Manaus, Brazil. Data collection was carried out in 24 standardized plots. Each plot was sampled four times between July 2015 and April 2017 by active search method. We recorded 83 individuals from 29 species belonging to six families. The richness in the study area corresponded to 78% of the snake species and 100% of the families previously recorded for Manaus. As observed in other localities, the most abundant species was the Amazonian lancehead (*Bothrops atrox*). Multiple linear regression models did not detect any effect of environmental variables on species richness and abundance of individuals. However, quadratic polynomial regression models revealed that intermediate canopy opening percentages positively influence the richness and abundance of snakes. It is possible that the result is related to a tradeoff between the thermoregulation behavior of these animals and to their susceptibility to predation.

Key words: community ecology, Manaus, RAPELD, Serpentes, Squamata.

INTRODUCTION

Knowledge about assemblages of Amazonian snakes is usually limited to compiling species from faunistic inventories, often supplemented by natural history observations (e.g., Guyer and Donnelly 1990, Martins and Oliveira 1998, Bernarde et al. 2012, Fraga et al. 2013a, Prudente et al. 2018). From these studies has emerged the idea that the fauna of Amazonian snakes is distinct from the rest of the Neotropical region (Cavalheri et al. 2015) and that most Amazonian species have a wide geographic distribution, although the composition of the assemblages differs between localities throughout the biome (Bernarde et al. 2012). However, it has been pointed out that the density of snake sampling in the Amazon region is lower than the rest of the Neotropics (Guedes et al.

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2018), which may impair knowledge about which historical or environmental factors influence the composition of assemblages.

Much of what is known about environmental effects on the composition of Amazonian snake assemblages is due to the implementation of a modular and standardized system of samplings known as RAPELD (Magnusson et al. 2005, 2013). By means of an unprecedented sampling effort in the biome, it is known that assemblages are environmentally structured in relation to their distance from bodies of water (Fraga et al. 2011), a pattern which was also revealed by analyzing the abundance of individual species (Fraga et al. 2013b). Furthermore, it is known that environmental variables inhibit dispersion and consequently gene flow in different ways according to the characteristics of the species (Fraga et al. 2017). Understanding these environmental effects however, continues to be a challenge because of the difficulty in detecting these cryptic species in the midst of the dense forest (Fraga et al. 2014).

Although it has been home to many recent studies on snake assemblages, the Central Amazonia has only one area that can be considered sufficiently sampled: The Ducke Reserve, an area of mainland forest located in the municipality of Manaus (Fraga et al. 2013a). This scenario prevents extrapolations to predict the taxonomic composition of areas not yet sampled (Magnusson et al. 2013). Thus, the objective of the present study was to investigate the composition of the snake assemblage in a second location in Central Amazonia using the RAPELD sampling protocol, as well as to test the effect of potentially relevant environmental variables that were never previously investigated.

MATERIALS AND METHODS

STUDY AREA

The surveys were conducted in a forest belonging to the Experimental Farm area of the Federal University of Amazonas (FEX-UFAM), located at km 922 along the BR-174 highway near Manaus, Amazonas, Brazil (02º 37’ 17.1” and 02º 39’ 41.4” S, 60º 03’ 29.1” and 60º 07’ 57.5” W). FEX-UFAM occupies an area of 3000 hectares of upland tropical rainforest of primary closed canopy and understory with low luminosity. The average temperature ranges between 24.6ºC and 26.9ºC; the daily relative humidity varies between 75% (dry days) and 92% (rainy days) (Araújo et al. 2002), and the average annual rainfall is 2362 mm (Marques Filho et al. 1981). The rainy season usually begins in November and ends in May, with a drier period occurring from June to October (Marques Filho et al. 1981, Araújo et al. 2002, Bohlman et al. 2008). The area consists of a primary upland forest with a network of large streams that flood large areas along their banks when the larger rivers flood. There are also the headwaters of first and second order streams that flood small areas in response to local rains (Rojas-Ahumada et al. 2012).

DATA COLLECTION

The samples were conducted in 24 plots, 16 riparian (following the course of small streams) and 8 non-riparian plots (along the terrain contour). These grids were installed in 2007 by the Biodiversity Research Program (PPBio), according to the RAPELD biodiversity monitoring protocol devised by Magnusson et al. (2013). This system includes 59 km of trails divided between four trails of 8 km in the East-West direction, and nine of 3 km each in the north-south direction, totaling an area of 24 km^2. The grid consists of 41 sampling plots, 20 riparian and 21 non-riparian, each 250 m long and 10 m wide (Figure 1).

Data collection occurred between July 2015 and April 2017 with a total of 192 hours of standardized sampling effort distributed throughout the collection period. The method used was an active daytime search (Martins and Oliveira 1998)

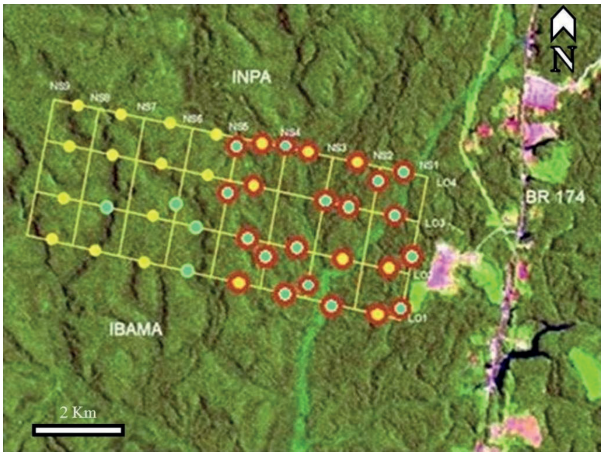

Figure 1 - RAPELD sampling grid located in the municipality of Manaus, Brazil. Green markers represent riparian plots and yellow plots represent non-riparian plots. Plots sampled in the present study are circled in red.

which consists of a visual search of up to five meters from the central line along each side of the plot. This method is based on locating animals in displacement or at rest by means of a detailed survey of all the micro-environments (adapted from Campbell and Christman 1982). Occasional records obtained by researchers or third parties in the area of FEX-UFAM were also used to determine the species assemblage. In addition, the records of the zoological collections of the Federal University of Amazonas and the National Institute of Amazonian Research were also consulted; both of which are located in Manaus, Amazonas. Species were identified at a specific level based on specialized references (Martins and Oliveira 1998, Fraga et al. 2013a, Uetz 2018). Only the records made in the sampling plots were considered in the ecological analyzes. The samplings were carried out under license number 7525-1 issued by the Biodiversity Information and Authorization System (SisBio / ICMBio).

ENVIRONMENTAL VARIABLES

The following environmental variables were evaluated: 1) Canopy Openness (%), measured with the aid of a forest densiometer, 2) Altitude (m), measured using a GPS device, 3) Distance of the plot from the nearest stream (m), measured with a tape-measure, 4) Depth of litter (mm), measured with a millimeter stick. The four variables were measured every 50 meters, totaling six points per plot. The value used in the analyzes was the arithmetic mean for each plot. Additional information on collection methods can be found on the PPBio web site at https://ppbio.inpa.gov.br/en/Data_Sampling (accessed in 2018).

DATA ANALYSIS

The first analysis used the Spearman test for a pairwise correlation between the predictor variables, aiming at the selection of a set of independent environmental variables. Later, we tested the normality of the data through the Shapiro-Wilk test and subsequently, simple linear regression analysis was performed for each of the four environmental variables (independent variables) in relation to abundance and snake richness per plot (dependent variables). These relationships were also tested using quadratic polynomial regression analysis.

RESULTS

We recorded a total of 83 individuals in 29 species distributed in 6 families: Aniliidae (n = 1), Boidae (n = 3), Colubridae (n = 21), Elapidae (n = 2), Leptotyphlopidae (n = 1) and Viperidae (n = 1). For the following analyzes and ecological parameters, only the records made in riparian and non-riparian plots were considered, which excludes the opportunistic sightings or other surveys. Within the plots therefore, 51 individuals belonging to 22 species were recorded (Table I). The most abundant species along the plots was *Bothrops atrox* (n = 14). The scientific collections in Manaus did not add more species to the study area.

Species richness in riparian plots (N = 16) ranged from 0 to 5, while richness in non-riparian plots (N = 8) ranged from 0 to 4. The abundance

TABLE I
Species recorded and their respective abundances in an area of upland forest in Central Amazonia between July 2015 and April 2017.

TAXON	Plot sightings		Occasional encounters	
	Riparian	Non riparian	Riparian	Non riparian
ANILIIDAE				
Anilius scytale (Linnaeus, 1758)	1			
BOIDAE				
Boa constrictor Linnaeus, 1758	2	1		1
Epicrates cenchria (Linnaeus, 1758)				1
Eunectes murinus (Linnaeus, 1758)			2	
COLUBRIDAE				
Atractus latifrons (Günther, 1868)	2			1
Atractus snethlageae Cunha & Nascimento, 1983				1
Atractus torquatus (Bibron & Duméril, 1854)	1			
Chironius multiventris Schmidt & Walker, 1943	3		2	
Dendrophidion dendrophis (Schlegel, 1837)	1		1	1
Drepanoides anomalus (Jan, 1863)		3		1
Drymoluber dichrous (Peters, 1863)		1		1
Erythrolamprus pygmaeus (Cope, 1868)	1			
Erythrolamprus reginae (Linnaeus, 1758)	1			2
Erythrolamprus typhlus (Linnaeus, 1758)	1			
Helicops angulatus (Günther, 1868)			1	
Imantodes cenchoa Linnaeus, 1758	4			1
Leptophis ahaetulla (Linnaeus, 1758)	2			2
Oxybelis fulgidus (Daudin, 1803)		2		2
Oxyrhopus vanidicus Lynch, 2009	3			2
Pseudoboa coronata Schneider, 1801	2			
Pseudoboa martinsi Zaher, Oliveira & Franco, 2008	1			
Siphlophis compressus (Daudin, 1803)		1		
Taeniophallus brevirostris (Peters, 1863)	1			
Taeniophallus nicagus (Cope, 1868)		2		
Xenodon rabdocephalus (Wied, 1824)			1	
ELAPIDAE				
Micrurus spixii Wagler, 1824				1
Micrurus hemprichii (Jan, 1858)		1		

TABLE I (continuation)

TAXON	Plot sightings		Occasional encounters	
	Riparian	**Non riparian**	**Riparian**	**Non riparian**
LEPTOTYPHLOPIDAE				
Epictia tenella Klauber, 1939				1
VIPERIDAE				
Bothrops atrox (Linnaeus, 1758)	11	3	1	6
Total abundance	37	14	8	24
Total species richness	16	8	6	15

of individuals in riparian plots (N = 16) varied between 0 and 6, while abundance in non-riparian plots (N = 8) varied between 0 and 4. According to simple linear regression models, none of the four environmental variables considered (canopy opening, altitude, distance from water and litter depth) were related to abundance and species richness per plot. According to quadratic polynomial regression models, the canopy openness percentage is related to the richness (Figure 2a) and abundance (Figure 2b) of snakes (Table II).

DISCUSSION

The assemblage studied represents a subset of the species observed over decades of sampling in both the Adolpho Ducke Forest Reserve (Fraga et al. 2013a) as well as within the metropolitan region of Manaus (Martins and Oliveira 1998, Fraga et al. 2014). The number of species observed in the FEX-UFAM forest corresponds to 78.37%, and the number of families corresponds to 100% of those recorded for Ducke Reserve, Manaus (Fraga et al. 2013a). This result indicates that the sampled forest, although not included in the national system of protected areas, represents an important biodiversity repository and that future samplings should add more species to the list presented here.

As for the studies that have been carried out in the Adolpho Ducke Forest Reserve (Fraga et al. 2013a), the most abundant snake species registered in FEX-UFAM was the Amazonian lancehead (*Bothrops atrox*) also known as *fer-de-lance* or *jararaca*. The species is a generalist in terms of diet and habitat and this may be one of the factors responsible for its high abundance (Martins et al. 2002, Bisneto and Kaefer 2019), as well as for its high rate of snakebites involving humans in the biome (Alcântara et al. 2018). Ecological studies at the meso and macroscale have indicated that this species is strongly associated with riparian environments (Turci et al. 2009, Fraga et al. 2013a, Alcântara et al. 2018) and most of the records of the species in the present study were made in this type of environment.

This study revealed a relationship between an assemblage of snakes and an environmental variable. This result was surprising since previous studies, even with a larger number of sampling units and effort, have revealed that snakes do not constitute a good taxonomic group for the detection of assemblage relationships with environmental variables, which is probably due to the difficulty in detecting individuals in forest environments (Fraga et al. 2011, 2014). Since canopy openness has never been evaluated as a predictor of the structure of a

TABLE II
Results of simple linear regression and quadratic polynomial regression analyses between environmental variables (independent variables) and richness and abundance of the snake assemblage (dependent variables). *Marginally significant results; **Significant results.

Environmental variables		Simple linear		Quadratic polinomial	
		Richness	Abundance	Richness	Abundance
Distance from stream	r^2	0.0070	0.0107	0.0664	0.0809
	P	0.6978	0.6299	0.3662	0.3351
Litter depth	r^2	0.0542	0.0834	0.0569	0.0904
	P	0.2737	0.1711	0.6714	0.8734
Elevation	r^2	0.0108	0.0171	0.1521	0.0898
	P	0.6287	0.5422	*0.0854	0.2357
Canopy openness	r^2	0.1275	0.1074	0.3897	0.4015
	P	*0.0867	0.1178	**0.0024	**0.0016

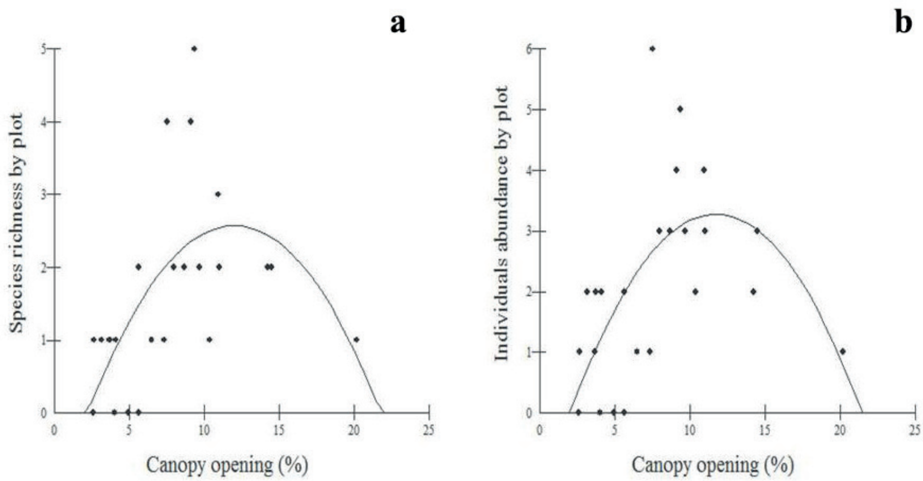

Figure 2 - Relationship between the percentage of canopy openness with (**a**) richness and (**b**) abundance of snakes in an upland forest in Central Amazonia.

community of Amazonian snakes, it is possible that the pattern detected in the present study, even with reduced sample effort, is due to the inclusion of this variable in the ecological models.

The intermediate canopy opening percentage (7-15%) had a positive influence on the richness and abundance of snakes and it is possible that this reflects a balance between the thermoregulatory behaviour of these ectotherms – where individuals would seek more open sites – and their susceptibility to attacks from visually oriented predators, a factor which would encourage individuals to search for more closed canopy sites. Thus, the search for intermediate sites along the canopy opening gradient would represent the final result of this trade off.

Snake thermoregulation occurs in several ways, such as respiratory mechanisms, water intake and transfer by conduction (Angilletta Jr. 2009). However, the direct absorption of heat via incident solar radiation on the body plays an important role in the optimization of morphophysiological functions and even on the survival of individuals (Angilletta Jr. 2009). Snakes are potential prey for a myriad of groups of visually oriented vertebrates, amongst which are birds (such as owls and eagles) and mammals such as felids, canids and the marsupial opossum, which is known to have immunity – Lethal Toxin Neutralizing Factor – against snake venom (Mushinski 1987, Domont et al. 1991, Motta-Junior et al. 2010). The risk of predation is mainly due to being in a state of vulnerability during displacement, foraging or thermoregulation (Fraga et al. 2013a). Thus, intermediate forest canopy openness values should represent more favorable conditions for the occurrence of snakes, representing the balance between solar radiation incidence (maximized in open environments) and protection against visually oriented predators (maximized under cover).

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AUTHOR CONTRIBUTIONS

GSM and ILK designed the study; GSM, ADB and JGS collected data; GSM and ILK analyzed data; GSM, TV and ILK wrote the paper with contributions of all authors.

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