

Diversity of reptiles in flooded and unflooded forests of the Amanã Sustainable Development Reserve, central Amazonia

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Abstract. Brazilian Amazonia harbours approximately 46% of all squamate reptiles distributed in Brazil. However, this species richness is considered to be underestimated due to the lack of sampling in many areas of the region. We determined the species composition of squamate reptiles of the Amanã Sustainable Development Reserve in two main habitats found in Amazonia: flooded and unflooded forests. Sampling was made from October 2013 to February 2014 in 40 plots within the reserve. Specimens records were obtained from pitfall traps with drift fences, time constrained visual searches and occasional encounters. We detected a total of 512 individuals (30 lizard species, 25 snake species and one amphisbaenian species). The number of species of both lizards and snakes were not significantly different in flooded versus unflooded forests. Sampling-based rarefaction curves for lizard species in both forests showed a tendency toward stabilization whereas stabilization of rarefaction curves for snake species was not observed. Species composition varied between both forests indicating that the local pool of species is determined by the complementarity of the species between the two types of forests. Differences in the species composition could be explained by ecological and historical factors, indicating that the maintenance of both habitats is needed in order to protect the biodiversity of this region.

Keywords. Diversity, flooding pulse, lizards, snakes

Introduction

Brazil houses the third largest diversity of reptilians in the world with 753 species of squamate reptiles (Costa and Bérnils, 2018). Currently, 189 species of snakes, 140 lizards, and 18 amphisbaenians are found in the Brazilian Amazonia (Prudente and da Silva, 2017; Avila-Pires and Ramalho, 2019), representing approximately 46% of the squamate species reported in Brazil. However, this species richness is considered to be underestimated due to the presence of many cryptic species (Funk et al., 2012) and to constant description of new species (e.g., Colli et al., 2015; Passos et al., 2016; Bernarde et al., 2018; Melo-Sampaio et al., 2019).

At the local scale, studies on lizards and snakes in Brazilian Amazonia were performed mainly in unflooded (*terra-firme*) forests (e.g., Martins and Oliveira, 1998; Bernarde and Abe, 2006; Vitt et al., 2008; Fraga et al., 2013), limiting the understanding of species distribution and development of conservation strategies in different habitats such as flooded (*várzeas and igapós*) forests, which were sampled only in a few studies (e.g., Waldez et al., 2013). Sampling of squamate reptiles in flooded and unflooded forests, aiming at evaluating the complementary species diversity in these different forest types, remains scarce (e.g., Neckel-Oliveira and

Gordo, 2004; Pantoja and Fraga, 2012; Waldez et al., 2013). In studies carried out in the Brazilian Amazonia, the forest mosaic was a determining factor for the regional diversity of the area (Pantoja and Fraga, 2012; Waldez et al., 2013).

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In central Amazonia, rainforests are composed of a mosaic of seasonally flooded and unflooded forests (Hess *et al.*, 2003). Flooded forests represent about 20% of the Amazon basin area and due to the hydrological pulse, this habitat is defined by seasons of flood and drought (Junk *et al.*, 1989) also playing a key role in the regional biodiversity (Ramalho *et al.*, 2018). These two types of forests differ in some aspects: soils of flooded forests (*várzeas*) have high concentrations of nutrients while unflooded forests are more floristically diverse (Haugaasen and Peres, 2006). On the other hand, the mean number of trees, basal area and aboveground dry biomass are similar between the two types of forests (Haugaasen and Peres, 2006).

In the flooded forests the seasonal flooding has a great influence over different biological species groups such as plants (Collevatti *et al.*, 2009), non-flying mammals (e.g., Haugaasen and Peres, 2005), amphibians and reptiles (e.g., Waldez *et al.*, 2013; Ramalho *et al.*, 2016), birds (e.g., Beja *et al.*, 2010), and bats (Pereira *et al.*, 2009) causing great mortality during dryer periods (Junk, 1997). Genetic and phenotypical variations in species occurring in these two forests can also be detected, showing different ecological adaptations in response to variations in the structure of the forest (Rocha *et al.*, 2014; Gibbs *et al.*, 2018). Moreover, historical factors such as climatic changes along the time could affect the diversification of closely related species in these two habitats (e.g., Collevatti *et al.*, 2009).

In the present study we investigate the species richness and composition of squamate reptiles in flooded and unflooded forests of the Amanã Sustainable Development Reserve, a protected reserve at the lower Solimões River located in the Jaú area of endemism (Borges and Silva, 2012), a poorly known area in the Brazilian Amazonia. According to a small set of previous available studies (e.g., Neckel-Oliveira and Gordo, 2004; Waldez *et al.*, 2013), and the differences between flooded and unflooded forests regarding to soil and floristic structure (e.g., Haugaasen and Peres, 2006), we predicted that i) the unflooded forest was richer in squamate reptile species due to their particular habitat characteristics such as the lower degree of disturbances and the higher floristic diversity when compared to flooded forests, which is subjected to higher frequency of floods, and ii) the regional pool of species is composed of local assemblage complementarities (high beta-diversity) between the two types of forests. We also compared the data obtained from different sampling methods to access species richness and composition in these two types of forests.

Material and Methods

Study area.—We conducted this study in the Amanã Sustainable Development Reserve (hereafter referred as RDS Amanã; Fig. 1), which covers areas distributed in the municipalities of Maraã, Codajás, Coari and Barcelos, in state of Amazonas, Brazil. RDS Amanã comprises approximately 2,350,000 hectares (Ayres *et al.*, 2005) and is located in the interfluvial region between Negro and Solimões rivers and connected to the Jaú National Park, an area of great importance to the conservation of squamate reptiles in Brazilian Amazonia (Neckel-Oliveira and Gordo, 2004). RDS Amanã contains a mosaic of seasonally flooded (*várzea* and *igapó*) and unflooded (*terra-firme*) forests (Pereira *et al.*, 2009). At the western area of the reserve, the Amanã Lake is formed by the black water draining from the unflooded forests surrounding it. The south region of the reserve is composed mostly by flooded forests which are part of the flooding basin of the Japurá River (Pereira *et al.*, 2009). The reserve also has areas with silt soils dominated by savanna and *campinaranas* environments (Valsecchi and do Amaral, 2009).

According to the Köppen-Geiger system, the climate in the region is Af (tropical rainforest without a dry season) and the precipitation in the driest month is greater than 60 mm (Peel *et al.*, 2007). This region is characterized by a rainy season from December to June and a dry season from July to November, with a mean annual rainfall of 2,200 mm (Ayres, 1995). During the flood season, the water level can increase by up to 10.6 m on the middle Solimões River (Ramalho *et al.*, 2009). The vegetation is composed mainly by trees of the Sapotaceae, Lecythidaceae, Euphorbiaceae, Myristicaceae, Leguminosae, Mimosidae, Caesalpinioideae and Faboideae families (Ayres, 1995; Pereira *et al.*, 2009).

Data collection.—Sampling was conducting in two events, (1) from October to December 2013 and (2) from January to February 2014 in the areas named Amanã Lake and Paranã do Amanã (unflooded forest), São José and near Tambaqui River (south of the RDS Amanã, flooded forest) (Fig. 1). The geographical coordinates of each sampling area can be found in Table 1. To minimize the effects of flooding pulse on the samplings and to allow the use of pitfall traps, we conducted our study during the presence of terrestrial habitats in the flooded forests. Data were collected in 20 plots distributed in unflooded forest and 20 plots from flooded forest, totalling 40 plots (Fig. 1). Each plot covered an area of 250 × 10 m and was positioned along the topographic contour lines, minimizing altitude

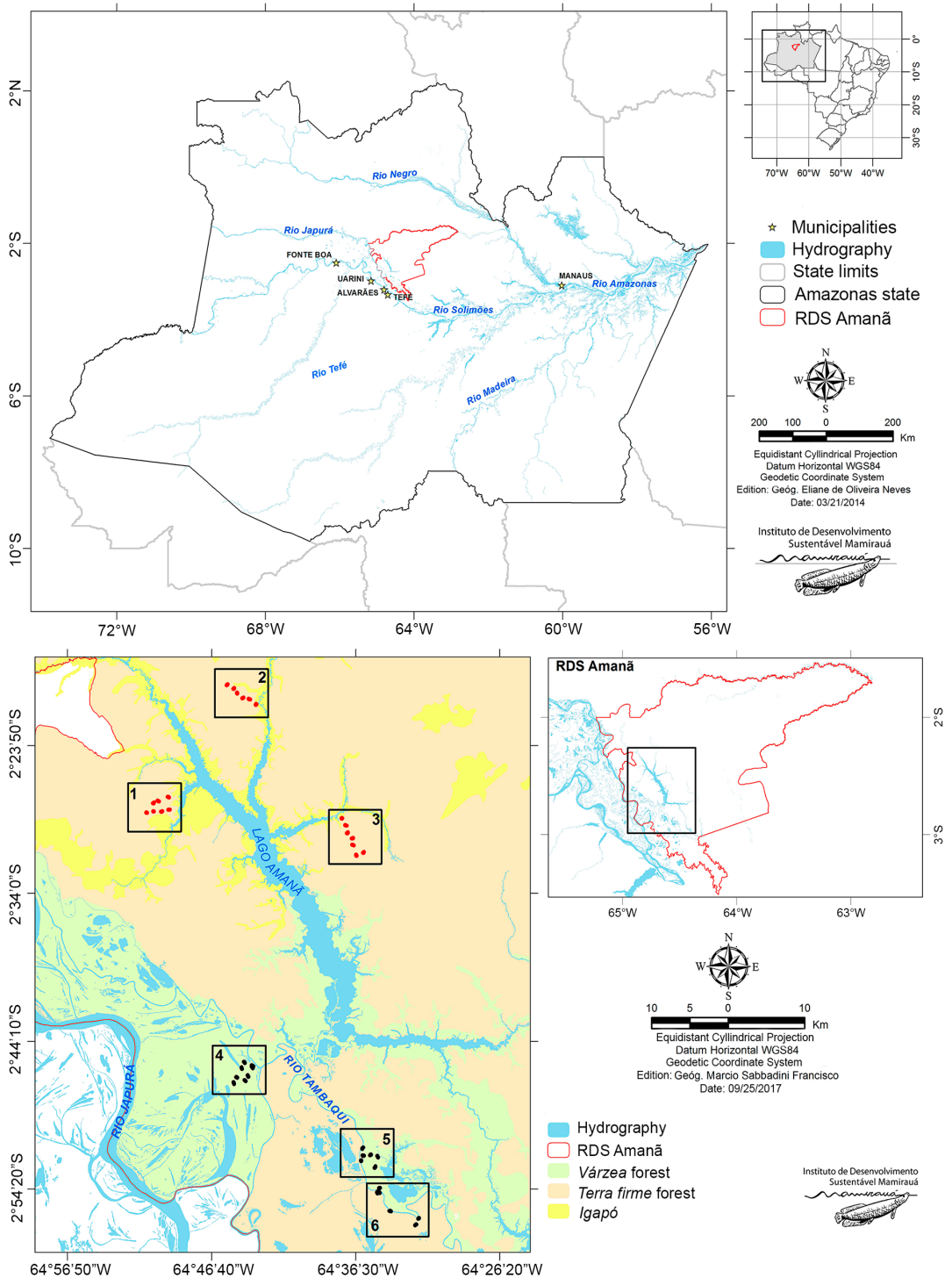


Figure 1. Geographical location of the study area, Amanã Sustainable Development Reserve, central Amazonia, Brazil. Red dots indicate the plots in unflooded forest and black dots indicate the plots in flooded forest. Site number and name and coordinates of each area are indicated in the Table 1.

Table 1. Sites of sampling in the Amanã Sustainable Development Reserve, central Amazonia, Brazil.

Site number	Site Name	Habitat type	Latitude, Longitude
1	Jaquirana	Unflooded forest	-2.47083, -64.82775
2	Capoeirinha	Unflooded forest	-2.35062, -64.72570
3	Ubin	Unflooded forest	-2.51108, -64.61138
4	Poção	Flooded forest	-2.76421, -64.72972
5	Furo da Paca	Flooded forest	-2.85864, -64.60023
6	Repartimento	Flooded forest	-2.93025, -64.56761

and soil variation within plots (Magnusson *et al.*, 2005). A complementary trail of 40 m was attached to each plot to installation of pitfall traps with drift fences. The distance between plots varied from 700 m to 75 km. For each sampling event, we performed two methods: (1) pitfall traps with drift fences and (2) time constrained visual search.

One pitfall station consisting of three buckets (100 L; 51 cm mouth diameter and 69 cm height) arranged in line (Cechin and Martins, 2000), was installed in each plot. Distance between buckets was 10 m and they were connected by drift fences (1 m high, 0.20 m buried in the ground). The stations were set 30 days before the first sampling event and remained closed until the beginning of the second event. Traps remained open for 5 days in each sampling event (totalling 10 days) and specimens were collected daily from buckets, totalling 117 pitfall traps per day (39 plots \times 3 buckets by plot). A total effort was 1,170 pitfall-days (one pitfall trap station was discarded due the incorrect installation). During this study, data of one pitfall trap station in flooded forest was discarded due to the lack of soil drainage affecting the use of this method.

We performed time constrained visual searches for 1.5 h in each plot by five people (senior author and four fieldwork assistants) by walking in line and searching for squamate reptiles in the leaf litter, trunks, tree holes and vegetation at a maximum distance of 5 m left and right of the main trail of the plot, and up to a height of 5 m on vegetation (adapted from Crump and Scott, 1994; Fraga *et al.*, 2011). The total sampling effort of time constrained visual searches was 600 h (1.5 hour/plot \times 5 observers \times 40 plots \times 2 sampling events). Specimens obtained from occasional encounters (Sawaya *et al.*, 2008) by other researchers and assistants involved were not included in the analysis, but they were included in the species list.

Species were identified based on Peters and Orejas-Miranda (1970), Avila-Pires (1995), Vitt *et al.* (2008) and Fraga *et al.* (2013). Voucher specimens were killed using intravenous or intramuscular injection (Mader, 2006) of ketamine hydrochloride (50 mg/kg) associated with xylazine (2 mg/kg). Posteriorly, potassium chloride was injected intracardially or intravenously (2 mg/kg). Specimens were preserved in 10% formalin, transferred to 70% alcohol and deposited in the Herpetological Collection of the Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), municipality of Tefé, state of Amazonas (collection numbers: IDSM 01220 to IDSM 01346; Appendix 1). Capture and collection of the specimens was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade / Sisbio (# 12927169) and the protocol for killing the specimens was approved by the Ethics Committee of the IDSM (007/2013).

Data analysis.—We performed all the following analyses using the total number of species recorded in the two sampling events. We constructed rarefaction curves of the species richness based on the on number of plots (*sensu* Gotelli and Colwell, 2001) in each forest type (flooded and unflooded forests) and animal group (lizards and snakes), using the program EstimateS 9.1, and the Mao Tau Sobs index (Colwell, 2013). According to Gotelli and Colwell (2001), rarefaction methods are suitable for estimating species richness and comparing data sets with different number of specimens. We conducted nested analysis of variance (ANOVA) in order to compare i) the differences in the total species richness of lizards and snakes between habitats (unflooded and flooded forests) and among sampling areas and ii) the differences in the total abundance of the most recorded species of lizards between flooded and unflooded forests and among sampling areas.

The lizard species composition in flooded and unflooded forests was reduced by multivariate analysis in two dimensions based on a non-metric multidimensional scaling (NMDS). We do not make multivariate analysis using snake species composition due the small number of reported individuals (26 individuals in 40 plots; see Results). We estimated ordination for quantitative data (abundance) using Bray-Curtis dissimilarity index while for qualitative data (presence/absence), ordination was estimated using the Jaccard index. We run a new NMDS based on one dimension and we tested the

scores produced for differences between the two types of forests using a Kruskal-Wallis chi-squared test.

Results

A total of 512 individuals were recorded (461 lizards, one amphisbaenian and 50 snakes) (Table 2). Lizards were classified in 30 species belonging to 11 families. The most diverse families were Teiidae (n = 6 species) and Gymnophthalmidae (n = 5 species). *Kentropyx altamazonica* and *Gonatodes humeralis* were the most abundant species (Fig. 2; Table 2). Snakes comprised

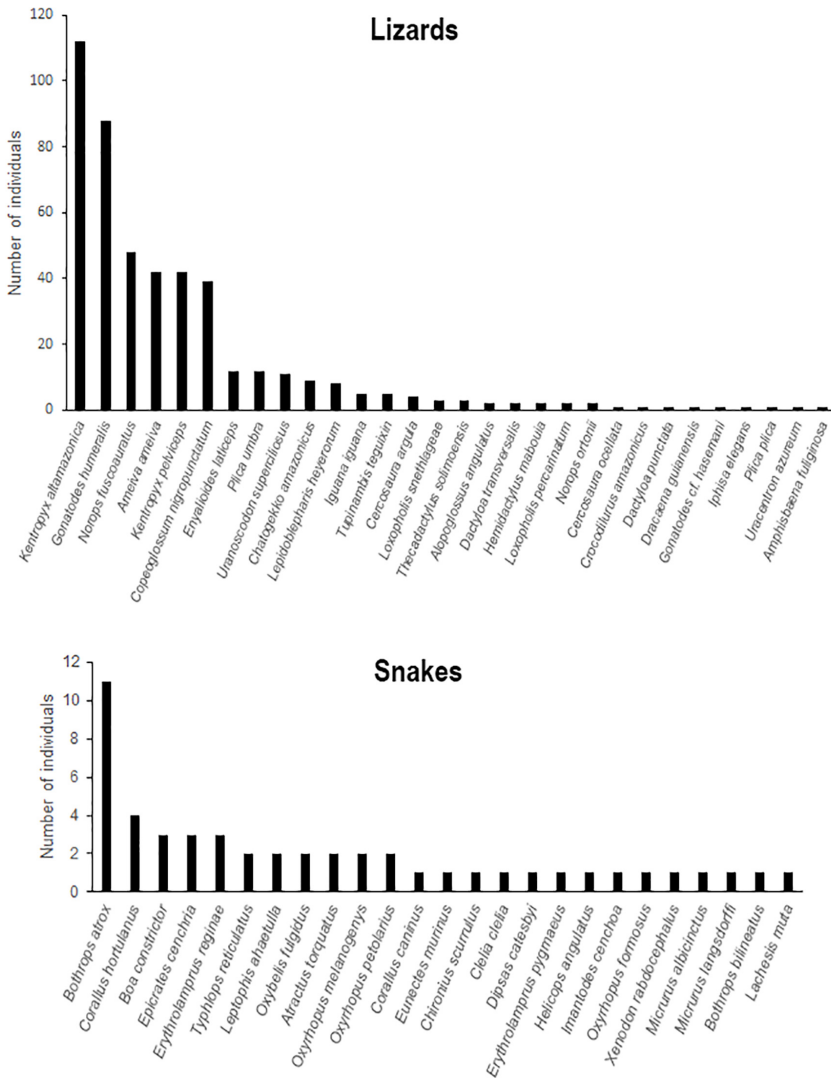


Figure 2. Total number of individuals per species of Squamate reptiles (lizards + amphisbaenian and snakes) recorded in the Amanã Sustainable Development Reserve, central Amazonia, Brazil.

Table 2. Species of Squamate reptiles found in the Amanã Sustainable Development Reserve, central Amazonia, Brazil. The numbers of individuals are indicated according to: type of forests habitat (flooded and unflooded forests), number of plots - NP and sampling method (pitfall traps with drift fence - PT, time constrained visual search - TC and occasional encounters - OE).

Family/Species	Flooded forest (N=20 plots)			Unflooded forest (N=20 plots)			OE	Total
	NP	PT	TC	NP	PT	TC		
Suborder Sauria								
Amphisbaenidae (1 species)								
<i>Amphisbaena fuliginosa</i> Linnaeus, 1758	0	0	0	0	0	0	1	1
Iguanidae (1 species)								
<i>Iguana iguana</i> (Linnaeus, 1758)	0	0	0	0	0	0	5	5
Tropiduridae (4 species)								
<i>Plica plica</i> (Linnaeus, 1758)	0	0	0	0	0	0	1	1
<i>Plica umbra</i> (Linnaeus, 1758)	3	3	3	6	6	0	0	12
<i>Uracentron azureum</i> (Linnaeus, 1758)	0	0	0	0	0	0	1	1
<i>Uranoscodon superciliosus</i> (Linnaeus, 1758)	5	5	4	2	2	0	0	11
Gekkonidae (1 species)								
<i>Hemidactylus mabouia</i> (Moreau de Jonnès, 1818)	0	0	0	0	0	0	2	2
Phyllodactylidae (1 species)								
<i>Thecadactylus solimoensis</i> Bergmann and Russell, 2007	0	0	0	0	0	0	3	3
Sphaerodactylidae (4 species)								
<i>Chatogekko amazonicus</i> (Andersson, 1918)	0	0	0	5	1	8	0	9
<i>Gonatodes cf. hasemani</i> Griffin, 1917	0	0	0	1	1	0	0	1
<i>Gonatodes humeralis</i> (Guichenot, 1855)	16	3	85	0	0	0	0	88
<i>Lepidoblepharis heyerorum</i> Vanzolini, 1978	6	4	4	0	0	0	0	8
Teiidae (6 species)								
<i>Ameiva ameiva</i> (Linnaeus, 1758)	1	0	1	13	7	34	0	42
<i>Crocodilurus amazonicus</i> Spix, 1825	0	0	0	1	1	0	0	1
<i>Dracaena guianensis</i> Daudin, 1802	1	0	1	0	0	0	0	1
<i>Kentropyx altamazonica</i> (Cope, 1876)	15	10	79	12	6	17	0	112
<i>Kentropyx pelviceps</i> (Cope, 1868)	4	3	7	15	21	11	0	42
<i>Tupinambis teguixin</i> (Linnaeus, 1758)	5	1	4	0	0	0	0	5
Dactyloidae (4 species)								
<i>Dactyloa punctata</i> (Daudin, 1802)	0	0	0	0	0	0	1	1
<i>Dactyloa transversalis</i> (Duméril, 1851)	0	0	0	2	1	1	0	2
<i>Norops fuscoauratus</i> (D'Orbigny, 1837)	15	2	29	5	0	6	11	48
<i>Norops ortonii</i> (Cope, 1868)	0	0	0	0	0	0	2	2
Hoplocercidae (1 species)								
<i>Enyalioides laticeps</i> (Guichenot, 1855)	0	0	0	9	7	5	0	12
Alopoglossidae (1 species)								
<i>Alopoglossus angulatus</i> (Linnaeus, 1758)	0	0	0	2	2	0	0	2
Gymnophthalmidae (5 species)								
<i>Cercosaura argula</i> Peters, 1863	3	0	4	0	0	0	0	4
<i>Cercosaura ocellata</i> Wagler, 1830	0	0	0	1	1	0	0	1
<i>Iphisa elegans</i> Gray, 1851	0	0	0	1	1	0	0	1
<i>Loxopholis percarinatum</i> (Müller, 1923)	0	0	0	2	2	0	0	2
<i>Loxopholis snethlageae</i> (Ávila-Pires, 1995)	2	1	1	1	1	0	0	3

Table 2. Continued.

Family/Species	Flooded forest (N=20 plots)			Unflooded forest (N=20 plots)			OE	Total
	NP	PT	TC	NP	PT	TC		
Mabuyidae (1 species)								
<i>Copeoglossum nigropunctatum</i> (Spix, 1825)	7	3	9	9	1	11	15	39
Number of species	10		13	16		8	10	30
Number of individuals	35		231	61		93	42	462
Suborder Ophidia								
Typhlopidae (1 species)								
<i>Typhlops reticulatus</i> (Linnaeus, 1758)	0	0	0	1	0	1	1	2
Boidae (5 species)								
<i>Boa constrictor</i> Linnaeus, 1758	1	0	1	0	0	0	2	3
<i>Corallus caninus</i> (Linnaeus, 1758)	0	0	0	0	0	0	1	1
<i>Corallus hortulanus</i> (Linnaeus, 1758)	0	0	0	1	0	1	3	4
<i>Epicrates cenchria</i> (Linnaeus, 1758)	0	0	0	2	1	1	1	3
<i>Eunectes murinus</i> (Linnaeus, 1758)	0	0	0	0	0	0	1	1
Colubridae (3 species)								
<i>Chironius scurrulus</i> (Wagler, 1824)	0	0	0	0	0	0	1	1
<i>Leptophis ahaetulla</i> (Linnaeus, 1758)	1	0	1	0	0	0	1	2
<i>Oxybelis fulgidus</i> (Daudin, 1803)	0	0	0	0	0	0	2	2
Dipsadidae (11 species)								
<i>Atractus torquatus</i> (Duméril, Bibron and Duméril, 1854)	0	0	0	2	1	1	0	2
<i>Clelia clelia</i> (Daudin, 1803)	0	0	0	1	0	1	0	1
<i>Dipsas catesbyi</i> (Santzen, 1796)	1	0	1	0	0	0	0	1
<i>Erythrolamprus pygmaeus</i> (Cope, 1868)	0	0	0	1	0	1	0	1
<i>Erythrolamprus reginae</i> (Linnaeus, 1758)	1	0	1	1	0	1	1	3
<i>Helicops angulatus</i> (Linnaeus, 1758)	0	0	0	1	1	0	0	1
<i>Imantodes cenchoa</i> (Linnaeus, 1758)	1	0	1	0	0	0	0	1
<i>Oxyrhopus formosus</i> (Wied-Neuwied, 1820)	0	0	0	1	1	0	0	1
<i>Oxyrhopus melanogenys</i> (Tschudi, 1845)	0	0	0	1	0	1	1	2
<i>Oxyrhopus petolaris</i> (Linnaeus, 1758)	2	0	2	0	0	0	0	2
<i>Xenodon rabdocephalus</i> (Wied, 1824)	0	0	0	1	0	1	0	1
Elapidae (2 species)								
<i>Micrurus albicinctus</i> Amaral, 1925	0	0	0	0	0	0	1	1
<i>Micrurus langsdorffi</i> (Wagler, 1824)	0	0	0	1	1	0	0	1
Viperidae (3 species)								
<i>Bothrops atrox</i> (Linnaeus, 1758)	4	0	6	1	0	1	4	11
<i>Bothrops bilineatus</i> (Wied-Neuwied, 1821)	0	0	0	0	0	0	1	1
<i>Lachesis muta</i> (Linnaeus, 1766)	0	0	0	0	0	0	1	1
Number of species	0		7	5		10	15	25
Number of individuals	0		13	5		10	22	50

25 species belonging to six families, with Dipsadidae family being the most diverse (n = 11 species), and *Bothrops atrox* was the most abundant species (Fig. 2;

Table 2). The only species of amphisbaenian recorded was found outside of sampling plots. Photos of some species reported in this study are shown in Figure 3.



Figure 3. Species of Squamate reptiles recorded in the Amanã Sustainable Development Reserve, central Amazonia, Brazil: 1) *Eunectes murinus*; 2) *Erythrolamprus reginae*; 3) *Lepidoblepharis heyerorum*; 4) *Typhlops reticulatus*; 5) *Alopoglossus angulatus*; 6) *Norops fuscoauratus*; 7) *Dactyloa transversalis*; 8) *Chironius scurrulus*; 9) *Corallus hortulanus* 10) *Dipsas catesbyi*; 11) *Leptophis ahaetulla*; 12) *Gonatodes humeralis*; 13) *Ameiva ameiva*; 14) *Enyalioides laticeps*; 15) *Bothrops atrox*. (Photos: IVD).

The number of species detected in each sampling method varied (10 to 21 species in pitfall traps and 18 to 20 species in time constrained visual search) in both types of forests (Table 2). The use of pitfall traps in flooded and unflooded forests allowed the recording of six species of lizards and three species of snakes exclusively using this method. During time constrained visual search in flooded and unflooded forests two species of lizards and nine species of snakes were detected exclusively using this method. Moreover, during occasional encounters, we were able to detect 10 lizard species (seven species exclusively using this method) and 15 snake species (seven species exclusively using this method) (Table 2). The largest number of lizards (324 individuals, 16 species), was observed during time constrained visual search while 96 (20 species) and 42 (10 species) individuals were recorded from pitfall traps and occasional encounters, respectively. The number of snakes observed in each sampling method was 23 individuals (15 species) during time constrained visual search, 22 individuals (15 species) during occasional encounters and five individuals (five species) in pitfall traps (Table 2).

Using the standardized sampling methods of pitfalls traps with drift fences and time constrained visual search, 13 species of lizards and seven species of snakes were found distributed in one and up to 16 plots in flooded forests. *Gonatodes humeralis* and *Kentropyx altamazonica* accounted for 66.5% of the lizards recorded in this type of forest. These species were found in a larger number of plots along with *Norops fuscoauratus*. The number of snakes recorded in plots in flooded forests varied from one to six individuals. *Bothrops atrox* was the most abundant snake species, representing 46.1% of the total number of recorded snakes. The lizards *Cercosaura argula*, *Dracaena guianensis*, *G. humeralis*, *Lepidoblepharis heyerorum*, *Tupinambis teguixin* and the snakes *Boa constrictor*, *Dipsas catesbyi*, *Imantodes cenchoa*, *Leptophis ahaetulla*, *Oxyrhopus petolarius* were found exclusively in flooded forest (Table 2).

In unflooded forests, 17 lizard species and 13 species of snakes were found distributed in one and up to 15 plots. *Kentropyx pelviceps* and *Ameiva ameiva* were the most abundant species, accounting for 47.4% of the total number of recorded lizards. These two species and *K. altamazonica* were found each in at least 12 plots. The number of snakes recorded in plots in unflooded forests varied from one to two individuals. Nine species of lizards (*Alopoglossus angulatus*, *Cercosaura*

ocellata, *Chatogecko amazonicus*, *Crocodilurus amazonicus*, *Dactyloa transversalis*, *Enyalioides laticeps*, *Gonatodes cf. hasemani*, *Iphysa elegans* and *Loxopholis percarinatum*) and 11 species of snakes (*Atractus torquatus*, *Clelia clelia*, *Corallus hortulanus*, *Epicrates cenchria*, *Erythrolamprus pygmaeus*, *Helicops angulatus*, *Micrurus langsdorffi*, *Oxyrhopus formosus*, *Oxyrhopus melanogenys*, *Typhlops reticulatus* and *Xenodon rabdocephalus*) were found exclusively in unflooded forest (Table 2).

Eight species of lizards and the snakes *B. atrox* and *Erythrolamprus reginae* were found in both flooded and unflooded forests (Table 2). Species richness of lizards and snakes did not differ between the two types of forests ($F_{1,38} = 0.174$, $p = 0.678$ and $F_{1,38} = 0.495$, $p = 0.485$, respectively). Sampling-based rarefaction curves showed a tendency toward stabilization for lizard species (Fig. 4A, B) in both flooded and unflooded forests while for snake species in the same habitats, this pattern was not observed (Fig. 4C, D).

The two axes of the NMDS captured 66% and 69% of the variation in lizard composition between flooded and unflooded forests based on both qualitative and quantitative data, respectively (Fig. 5). Species composition was significantly different between flooded and unflooded forests for both qualitative (Kruskal-Wallis = 194.88, $df = 21$, $p < 0.001$) and quantitative (Kruskal-Wallis = 210.42, $df = 21$, $p < 0.001$) data.

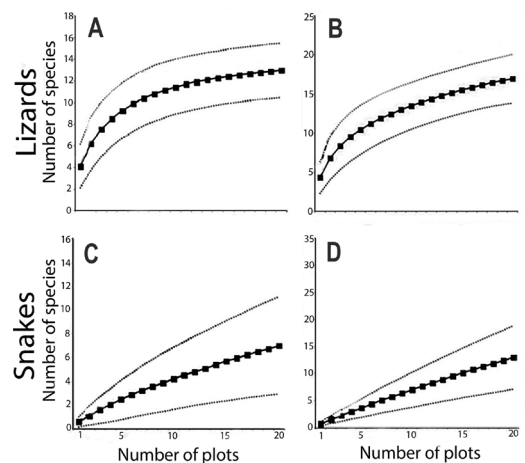


Figure 4. Rarefaction curves based on the number of plots (closed squares) to lizards (A and B) and snakes (C and D) at Amanã Sustainable Development Reserve, central Amazonia, Brazil. A and C: flooded forest. B and D: unflooded forest. Dotted lines: 95% confidence intervals.

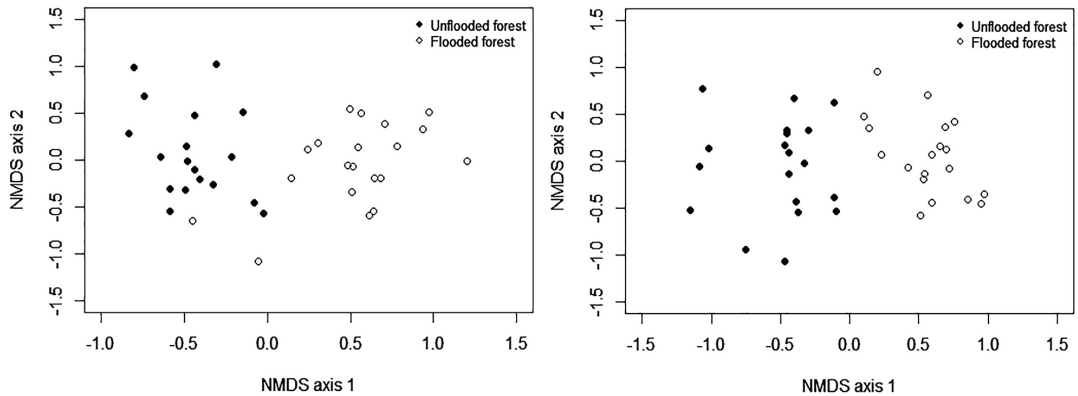


Figure 5. Non-metric multidimensional scaling (NMDS) based on abundance (left) and presence/absence (right) of lizard species to flooded and unflooded forests at Amanã Sustainable Development Reserve, central Amazonia, Brazil.

The abundance of the species *K. altamazonica* ($F_{5,34} = 6.123$, $p < 0.001$) and *N. fuscoauratus* ($F_{5,34} = 4.514$, $p = 0.003$) were significantly higher in flooded forest. The abundance of *K. pelviceps* was not different ($F_{5,34} = 1.442$, $p = 0.235$) between the two types of forests.

Discussion

Despite applying the same sampling effort, we not observed significant difference in the species richness between the two forest types. Similar results were observed by Pantoja and Fraga (2012) in flooded and unflooded forests in a reserve at Juruá River basin. However, species composition of lizards varied between both types of forests indicating a high beta-diversity in response to differences in the habitat type. Analysing only the taxonomic dimension of the biodiversity, the local pool of species in our study was determined by the turnover of species from both habitats. On the other hand, conservation planning should consider analysis based in complementarity that is structured in taxonomic, phylogenetic and functional dimensions of the biodiversity (Brum *et al.*, 2017).

Species composition generally is determined by ecological and historical characteristics of each type of habitat. Unflooded forests are characterized by a higher plant diversity and soils with lower concentrations of macronutrients when compared to flooded forests (Haugaasen and Peres, 2006). Edaphic characteristics, leaf-litter depth and vegetation structure are factors known to affect the species composition and the species richness of anurans and lizards in unflooded forests (e.g.,

Pinto, 2006; Menin *et al.*, 2007, 2011; Faria *et al.*, 2019). On the other hand, in flooded forests, the habitat varies between seasons due to the annual cycle of drought and flood (Junk *et al.*, 1989). According to Haugaasen and Peres (2005), flooded forests are simplified considerably in terms of forest structure because their understory and ground layers remain completely submerged during flood season and this characteristic prevent the survival of only some species in this environment. In our study, the lizards *K. altamazonica*, *N. fuscoauratus* and *G. humeralis* were found commonly in flooded forests. These species have morphological and behavioural characteristics that allow them to survive in this type of forest such as adaptations for locomotion across vegetation (Vitt *et al.*, 2001). Anuran communities also are affected by frequency of floods, permitting only adapted species to survive and resilient species to recolonize this environment during the periods of low water (Ramalho *et al.*, 2018). In our study, the presence of terrestrial medium- to large-sized lizards both in flooded and unflooded forest might be related to migratory processes during seasons, as observed by Adis (1997) in invertebrate organisms.

The survey of lizard species indicated (1) a tendency towards an asymptote only in the flooded forest suggesting that the number of species was underestimated in unflooded forest and differs from estimates reported in the lower Purus River by Waldez *et al.* (2013); (2) the absence of some terrestrial and arboreal lizard species in the flooded forest (*C. amazonicus*, *G. cf. hasemani*, *D. transversalis*, *E. laticeps*, *A. angulatus*, *C. ocellata*, *I. elegans*); (3) the greater number of species

in the Teiidae family in the flooded forest. These last results were also reported in the lower Purus River (Waldez et al., 2013), showing a congruency in species occurrences. Gymnophthalmidae and Dactyloidae were the family with the greatest number of species in different sites in Amazonia biome (e.g., Avila-Pires et al., 2010; Pantoja and Fraga, 2012; Prudente et al., 2013; Waldez et al., 2013; Fonseca et al., 2019; Peixoto et al., 2019). Additionally, the occurrence of the most abundant species in our study varied between forest types. *Kentropyx altamazonica* was more abundant in flooded forest while *K. pelviceps* was more abundant in unflooded forest, as Waldez et al. (2013) also reported previously. *Kentropyx altamazonica* is commonly associated with edges of watercourses, spending much of their time climbing in vegetation (Vitt et al., 2001). Moreover, species of *Kentropyx* have some morphological characteristics (keeled ventral scales and rectangular fringes on their toes) that are considered adaptations for locomotion across water and vegetation (Vitt et al., 2001). The lizard *N. fuscoauratus* was more abundant in flooded forest during our study while they more common in both unflooded and flooded forests in the lower Purus River (Waldez et al., 2013). According to Pinto (2006), this species is associated with areas of closed canopy and can also be found in different types of forests (Vitt et al., 2003). *Gonatodes humeralis* was present in great abundance only in flooded forest, contrasting the reports of being also present in unflooded forests from previous studies (Neckel-Oliveira and Gordo, 2004; Pinto, 2006; Waldez et al., 2013). Our study was conducted from the end of the dry season – October and November – to the beginning of rainy season – December to February. However, we cannot ignore the possibility of variations in species detection due to the gradual increase of water levels in the flooded forests. This fact may have generated the differences in the abundance and occurrence of lizard species when compared with other studies (e.g., Pantoja and Fraga, 2012; Waldez et al., 2013) performed in flooded and unflooded forests in Amazonia.

Snake species were found in low abundance (one to three individuals of 23 species from a total of 25 species recorded) and only two species, *E. reginae* and *B. atrox*, were recorded in both types of forest. These two species are widely distributed in Amazonia (Cole et al., 2013; Fenker et al., 2014). Dipsadidae was the most representative family of snakes, as also reported in other studies (e.g., Pantoja and Fraga, 2012). Snake species rarefaction curves for both forests did not show asymptotic tendency suggesting that additional sampling

effort should be applied in order to detect more species. The small number of snake species in our study could be related to (1) difficulties in detecting snakes in the forests causing the low detectability of most species (Fraga et al., 2014) and (2) the period (diurnal) when the time constrained visual search was performed (snakes are commonly sampled at night; Fraga et al., 2014). Despite of the use of pitfall traps as complementary sampling methods (Ribeiro-Júnior et al., 2008), fossorial species were poorly represented in our study. Additionally, the development of long-term studies with intense sampling effort (Vitt et al., 2008; Fraga et al., 2013, 2014) is important for a more accurate estimate of the number of squamate reptile species in Amazonia.

The RDS Amanã is located in the Jaú area of endemism (Borges and Silva, 2012). The only herpetofaunal studies in this area recorded 26 species of lizards and 43 species of snakes in the Jaú National Park (Neckel-Oliveira and Gordo, 2004), and 15 species of lizards and 10 species of snakes in the RDS Mamirauá (Avila-Pires and Hoogmoed, 1994), both regions being continuous to the RDS Amanã. Some lizard species and many snake species reported in Neckel-Oliveira and Gordo (2004) were not observed in the present study [for example, *Bachia flavescens* (Bonnaterre, 1789), *Arthrosaura reticulata* (O'Shaughnessy, 1881) (Gymnophthalmidae), *Norops tandai* (Avila-Pires, 1995) (Dactyloidae), *Polychrus marmoratus* (Linnaeus, 1758) (Polychrotidae) and *Varzea bistriata* (Spix, 1825) (Mabuyidae), *Anilius scytale* (Linnaeus, 1758) (Aniliidae), *Dendrophidion dendrophis* (Schlegel, 1837), *Tantilla melanocephala* (Linnaeus, 1758) (Colubridae) and many other species of Colubridae and Dipsadidae, *Micrurus spixii* Wagler, 1824, *M. lemniscatus* (Linnaeus, 1758) (Elapidae) and *Bothrops taeniatus* Wagler, 1824 (Viperidae)]. Many of these species are widely distributed in Amazonia (Neckel-Oliveira and Gordo, 2004; Fraga et al., 2011; Waldez et al., 2013; Fonseca et al., 2019; Peixoto et al., 2019) and the lack of their records in our study might be related to insufficient sampling periods for the pitfall traps (Pantoja and Fraga, 2012). In contrast, we observed 12 individuals of *E. laticeps* in nine plots of unflooded forest, this species was not reported at Jaú National Park (Neckel-Oliveira and Gordo, 2004). Due to the small number of studies in the Jaú area of endemism, the sampling biases and the wide distribution of many species found in our study and by Neckel-Oliveira and Gordo (2004), we cannot provide a detailed analysis of this area of endemism. Avila-Pires et al. (2009) recognized with lizards only Napo, Inambari, and Guiana areas of endemism, and found little or no

evidence of other areas of endemism, suggesting that the limits of the areas of endemism should be better defined by other terrestrial vertebrates than amphibians and squamate reptiles.

Considering the sampling methods applied in our study, the time constrained visual search was the most efficient method for detecting squamate reptiles ($n = 31$ species and 347 individuals; versus 25 species and 101 individuals for pitfall traps with drift fence). This efficiency was also observed in other studies developed in Amazonia (Neckel-Oliveira and Gordo, 2004; Pinto, 2006; Prudente *et al.*, 2013; Waldez *et al.*, 2013). However, the method of pitfall traps with drift fences provided better sampling of lizards in unflooded forests. Although some studies have discussed the efficiency of pitfall traps due to its high installation costs in forest and low number of sampled species (Pinto, 2006; Waldez *et al.*, 2013), we were able to detect nine species of lizards and three species of snakes in unflooded forest exclusively by using this method (Table 2). In flooded forests, no species were exclusively detected by pitfall traps. Moreover, the difficulties of installing pitfall traps in flooded forests where the soil is saturated impede the application of the same sampling effort in both flooded and unflooded forests (Doan, 2003; Neckel-Oliveira and Gordo, 2004; Waldez *et al.*, 2013).

This study compared the differences in species composition of flooded and unflooded forests in the Amanã Sustainable Development Reserve. Our results indicate that the local pool of species in this region is determined by the complementarity of species between the two types of forests. Differences in species composition between the two types of forests could be explained by both ecological and historical factors, indicating that the maintenance of both habitats is needed in order to protect the biodiversity of this region. Additionally, the flooding pulse might be the main factor determining the presence of species with adaptations to survive in this type of forest due to the restriction in the access to terrestrial environment during flood season (Adis, 1997; Haugaasen and Peres, 2005; Waldez *et al.*, 2013).

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Appendix 1

Voucher specimens collected at the study sites at Amanã Sustainable Development Reserve, Middle Solimões River, central Amazonia.

Plica umbra (IDSM 01320-01326), *Uracentron azureum* (IDSM 01340), *Uranoscodon superciliosus* (IDSM 01330-01338), *Thecadactylus solimoensis* (IDSM01341), *Chatogekko amazonicus* (IDSM01240), *Gonatodes* cf. *hasemani* (IDSM 01263), *Gonatodes humeralis* (IDSM 01264-01270), *Lepidoblepharis heyerorum* (IDSM 01290-01296), *Ameiva ameiva* (IDSM 01223-01226), *Crocodylurus amazonicus* (IDSM 01248), *Dracaena guianensis* (IDSM 01342), *Kentropyx altamazonica* (IDSM 01274-01277), *Kentropyx pelviceps* (IDSM 01278-01289), *Tupinambis teguixin* (IDSM 01327), *Dactyloa transversalis* (IDSM 01249), *Norops fuscoauratus* (IDSM 01303-01316), *Norops ortonii* (IDSM 01343), *Enyalioides laticeps* (IDSM 01251-01259), *Alopoglossus angulatus* (IDSM 01220, 01222), *Cercosaura argula* (IDSM 01237-01239), *Cercosaura ocellata* (IDSM 01236), *Iphisa elegans* (IDSM 01272), *Loxopholis percarinatum* (IDSM 01297-01298), *Loxopholis snethlageae* (IDSM 01299-01301), *Copeoglossum nigropunctatum* (IDSM 01241-01247), *Typhlops reticulatus* (IDSM01328), *Boa constrictor* (IDSM 01229), *Corallus hortulanus* (IDSM 01221), *Epicrates cenchria* (IDSM 01260-01261), *Eunectes murinus* (IDSM 01344), *Chironius scurrulus* (IDSM 01345), *Oxybelis fulgidus* (IDSM 01346), *Atractus torquatus* (IDSM 01227-01228), *Dipsas catesbyi* (IDSM 01250), *Erythrolamprus pygmaeus* (IDSM 01329), *Erythrolamprus reginae* (IDSM 01262), *Helicops angulatus* (IDSM 01271), *Imantodes cenchoa* (IDSM 01273), *Oxyrhopus formosus* (IDSM 01317), *Oxyrhopus melanogenys* (IDSM 01319), *Oxyrhopus petolarius* (IDSM 01318), *Xenodon rabdocephalus* (IDSM 01339), *Micrurus langsdorffi* (IDSM 01302), *Bothrops atrox* (IDSM 01230-01235).