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Amphibians from Santa Isabel do Rio Negro, Brazilian Amazonia

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Abstract

Amphibians from Santa Isabel do Rio Negro, Brazilian Amazonia. A species list of amphibians from Santa Isabel do Rio Negro in Brazilian Amazonia is provided. Collections were made from March–April 2012 along each of two 3-km trails with the following sampling methods: (1) pitfall traps with drift fences; (2) visual and auditory surveys; and (3) chance encounters. The trail at Daraá is north of the Rio Negro, whereas the other in Ayuanã is south of the river. Forty species of anurans and one salamander species representing 20 genera and nine families were recorded. The species composition was compared with those of 16 other studies conducted in the Guiana, Imeri, and Jaú areas of endemism, where species richness varies from 21–63, and similarity indices range from 23–100%. The anuran fauna at our sites resembles that of Flota Faro in eastern Amazonia more than it does that of the nearest site in the Departamento del Guainía of Colombia. The index of similarity is extremely variable between sites of the same and distinct areas of endemism. This pattern also was observed in the cluster analysis. As expected, geographically close areas have similar faunal compositions. However, the anuran fauna of

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Parque Nacional do Jaú (Jaú area of endemism) resembles that of Manaus (Guiana area of endemism) more closely than it does that of the Ayuanã River, which belongs to the same area of endemism as Parque Nacional do Jaú. The limits of the areas of endemism are better defined by the presence / absence of other terrestrial vertebrates, such as birds and mammals, than by the assemblage of amphibians and squamate reptiles.

Keywords: Anura, areas of endemism, Caudata, similarity index, species richness, western Amazonia.

Resumo

Anfíbios de Santa Isabel do Rio Negro, Amazônia Brasileira. No presente estudo fornecemos uma lista de espécies de anfíbios de Santa Isabel do Rio Negro na Amazônia Brasileira. As amostragens foram realizadas de março a abril de 2012 em dois conjuntos de trilhas de 3 km de extensão, usando os seguintes métodos: (1) armadilhas de interceptação e queda com cerca direcionadora; (2) amostragens visuais e auditivas simultâneas; (3) encontros ocasionais. As trilhas foram instaladas ao norte (rio Daraá) e ao sul (rio Ayuanã) do rio Negro. Registramos 40 espécies de anuros e uma espécie de salamandra, pertencentes a 20 gêneros e nove famílias. A composição de espécies foi comparada com as de 16 outros estudos desenvolvidos nas áreas de endemismo Guiana, Imeri e Jaú, onde a riqueza de espécies variou de 21 a 63, e a similaridade, de 23 a 100%. A anurofauna das duas áreas estudadas foi mais similar à de Flota Faro, localizada na Amazônia Oriental, do que à de um sítio mais próximo, Departamento del Guainía, Colômbia. O índice de similaridade foi extremamente variável entre os sítios da mesma ou de distintas áreas de endemismo. Esse padrão também foi observado nas análises de agrupamento. Como esperado, áreas geograficamente mais próximas foram mais similares na composição da anurofauna. No entanto, a anurofauna do Parque Nacional do Jaú (área de endemismo Jaú) foi mais similar à de Manaus (área de endemismo Guiana) do que à do rio Ayuanã, que pretence à mesma área de endemismo que o Parque Nacional do Jaú. Os limites das áreas de endemismo podem ser melhor definidos para outros vertebrados terrestres, como aves e mamíferos, do que para anfíbios e répteis Squamata.

Palavras-chave: Amazônia Ocidental, Anura, áreas de endemismo, Caudata, índice de similaridade, riqueza de espécies.

Introduction

The amphibian diversity of Amazonia is estimated to exceed 550 species (WWF 2010, Funk *et al.* 2012). However, some authors (Fouquet *et al.* 2007, Angulo and Reichle 2008, Funk *et al.* 2012) have suggested that undescribed cryptic diversity may increase this number markedly. Minimally 332 amphibian species occur in Amazonian Brazil; these include 309 anurans (Hoogmoed and Galatti 2017), five salamanders (Brcko *et al.* 2013, Hoogmoed 2016a), and 18 caecilians (Hoogmoed 2016b).

There are several inventories of amphibians from the northern (e.g., Hoogmoed and Ávila-Pires 1991, Reynolds and MacCulloch 2012) and western Amazonian regions (e.g., Duellman 1978, 2005, Bernarde 2007). In contrast, less is known about amphibian assemblages in Amazonian Brazil. Although more reports have been published during the last decade (e.g., Bernarde 2007, Ávila-Pires *et al.* 2010, Ilha and Dixo 2010, Prudente *et al.* 2013), the amphibian inventories from Amazonian Brazil are scarce, fragmented, and frequently published in "gray" literature (fide Azevedo-Ramos and Galatti 2002). Published species inventories and field guides for Amazonian Brazil (e.g., Crump 1971, Ilha and Dixo 2010, Lima *et al.* 2012) traditionally are concentrated along the main tributaries of the Amazon River or the few regions that could be accessed by roads (Azevedo-Ramos and Galatti 2002). More recently, difficult-to-access areas have been inventoried (e.g., Lima 2008, Ávila-Pires *et al.* 2010). Based on the results of published and unpublished studies since 2002, Azevedo-Ramos and Galatti (2002) concluded that there are distinct assemblages of anurans in different localities in Amazonian Brazil. This information is crucial for the formulation of conservation strategies in this region, but the conservation statuses of amphibians in this biome have yet to be determined (Peloso 2010).

There are distinct areas of endemism separated by the major rivers in Amazonia (Cracraft 1985, Ron 2000, Silva *et al.* 2005, Borges and Silva 2012). Most are described on the basis of terrestrial vertebrates (e.g., birds and primates) and have played an important role in understanding the evolution of the Amazonian biota (Silva *et al.* 2005). In the only study involving anurans, Ron's (2000) results are coincident with the areas of endemism found for terrestrial vertebrates.

Anurans are sensitive to environmental degradation and considered to be among the most vulnerable vertebrate groups (Navas and Otani 2007). In Brazil, 41 anuran species (ca. 4% of Brazilian amphibians) are threatened with extinction (Ministério do Meio Ambiente 2014). However, basic data (e.g., distribution) for the species are lacking. Therefore, species inventories are critical to obtain information on distributions and to discover undescribed species—data indispensable to formulation of reasonable conservation measures (Verdade *et al.* 2012).

Herein, we provide a list of species of anurans and salamander from the region of Santa Isabel do Rio Negro in Amazonas, Brazil, based on collections by three different sampling methods. The observed species diversity is compared with those of other studies of lowland forests located in the Imeri, Jaú, and Guiana areas of endemism.

Materials and Methods

Study site

We conducted our study at two sites in the region of Santa Isabel do Rio Negro, Amazonas state, Brazil: (1) the right margin of the Rio Daraá (0°23'57" S; 64°47'12" W), and (2) the right margin of the Rio Ayuanã (0°35'15" S; 64°53'30" W) (Figure 1). Both rivers are black-water (as defined by Sioli 1991) tributaries of the Rio Negro. Situated in the Guiana area of endemism, the Rio Daraá is a left margin tributary has a high-velocity current and a complex of cataracts near its mouth; our collecting site is located at the base of the cataracts. Situated in the Imeri and Jaú areas of endemism, the Rio Ayuanã is a right margin tributary that has an almost imperceptible current. Along the edges of both rivers, we laid out a standardized grid composed of three, parallel 3-km-long trails, 1 km apart.

The region of Santa Isabel do Rio Negro is a tropical rainforest that lacks a dry season; precipitation in the driest month exceeds 60 mm (climate symbol "Af") according to the Köppen-Geiger system (Peel *et al.* 2007). The annual mean air temperature is 27.5°C (range: 21.5–32.6°C). The rainiest season usually is between May and July, and the annual rainfall is 2800 mm.

Data Collection

We used three methods to sample amphibians between 28 March and 17 April 2012, as follow: (1) pitfall traps with drift fences; (2) visual and auditory surveys; and (3) chance encounters. The pitfall traps remained open for 20 days. Four trapping stations 500 m apart were set along each trail. Each array contained four bins (~ 100 L; 51-cm mouth diameter × 69 cm deep) in a Y-formation (Corn 1994, Cechin and Martins 2000, Ribeiro-Junior *et al.* 2008). The bins were separated by 10 m and linked by a polyethylene fence guide (10 m long × 1 m high, with the bottom 0.10 m of the fence buried in the

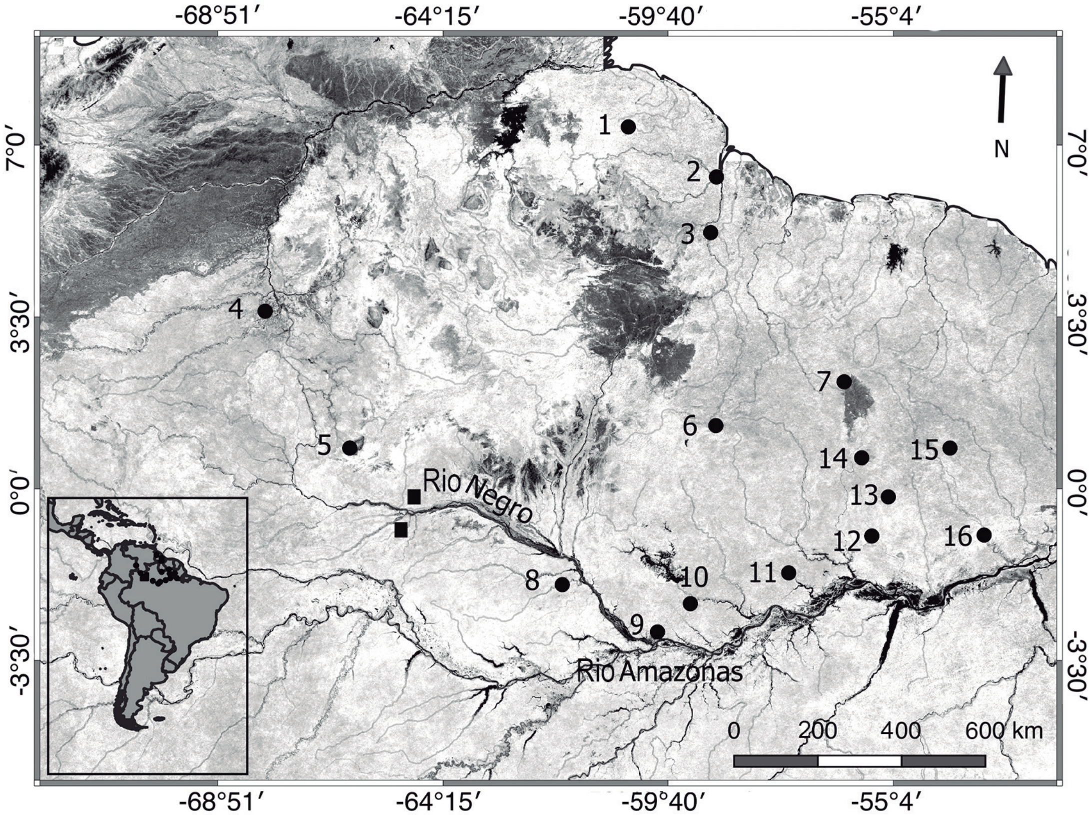

Figure 1. Geographic location of the study sites (Rio Daraá and Rio Ayuanã) in Santa Isabel do Rio Negro, Amazonas state, Brazil, and other sites used for comparisons. Squares: Rio Daraá (North) and Rio Ayuanã (South). Dots: 1. Baramita, Guyana; 2. Kartabo, Guyana; 3. Mabura, Guyana; 4. Comunidad La Ceiba, Departamento del Guainía, Colombia; 5. Cerro de la Neblina, Venezuela; 6. Estação Ecológica (ESEC) Grão-Pará North; 7. Sipaliwini, Suriname; 8. Parque Nacional do Jaú; 9. Manaus; 10. Rio Preto da Eva; 11. Floresta Estadual (FLOTA) Faro; 12. FLOTA Trombetas; 13. ESEC Grão-Pará South; 14. ESEC Grão-Pará Center; 15. Reserva Biológica Maicuru; 16. FLOTA Paru.

ground). Specimens were recovered from the buckets daily. Thus, a total of 24 stations of pitfall traps was checked each day to yield a total effort of 480 pitfall-days.

We sampled the nocturnal anuran assemblage by standardized and simultaneous visual-encounter and auditory surveys (Crump and Scott Jr. 1994, Zimmerman 1994). These methods are complementary and adequate for surveying the distribution and abundance of anurans in long and short-term studies (Doan 2003). We sampled each trail 10 times between 18:30 and 22:00 h. Two observers stopped every 5 m and recorded the species in call activity and searched the litter and vegetation for anurans. Vocalizations were not recorded.

Amphibians also were collected by other researchers and assistants who were sampling other taxonomic groups on the same expedition (chance encounter method; Sawaya *et al.* 2008).

Species Identification and Preservation

Species were identified based on their morphology based on the information provided by Duellman (1978, 2005) and Lima *et al.* (2012), or by their call based in the previous knowledge of the researchers along with the taxonomic expertise of the team. Only one species was identified exclusively by its vocalizations and no voucher was collected. The nomenclature in this study follows the classification of *Amphibian Species of the World* (Frost 2017). If we could not determine the identity of an individual anuran, we applied the follow conventions: *confer* (cf.) indicates that the determination is uncertain and specimen closely resembles the nominal; species (sp.) indicates that the individuals could not be related to any nominal species; *affinis* (aff.) indicates that the specimen is considered probably a new undescribed species (Bengtson 1988). Specimens were euthanized with an overdose of 2% lidocaine hydrochloride, and a muscle-tissue sample was removed from the thigh of each specimen. Tissue samples are deposited in the tissue collections at the Universidade Federal do Amazonas (CTGA-UFAM) and Instituto Nacional de Pesquisas da Amazônia (INPA). The voucher specimens were fixed in 10% formalin and later transferred to 70% alcohol. Vouchers were deposited in the Amphibians and Reptiles Collection of the INPA (INPA-H), Paulo Bürhnheim Zoological Collection of the Universidade Federal do Amazonas, Section Amphibians (CZPB-AA), and in the Herpetological Collection of the Universidade Regional do Cariri (URCA-H) (Appendix I). Collection of the material was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade / SISBIO (# 11323).

Data Analysis

There are many inventories of amphibian faunas in Amazonia. We compared our results with those of studies made (1) in the same area of endemism of our sampling sites (fide Ron 2000); (2) in unflooded, lowland forest (below 500 m a.s.l.); (3) at a comparable spatial scale to our study; (4) with taxonomic resolution (i.e., most of the frogs listed in the study are identified to species); and (5) using similar sampling methods and / or sampling effort. Reports with a complete list of species from a country were not considered. Given these criteria, the following published lists of other survey sites in the Guiana area of endemism were consulted: Suriname (Sipaliwini, Fouquet *et al.* 2015); Guyana (Baramita and Kartabo, Cole *et al.* 2013) (Mabura Hill, Ernst *et al.* 2005); Venezuela (Cerro de la Neblina, only lowland areas, Brewer-Carías 1988); Brazil (Rio Preto da Eva, Ilha and Dixo 2010) (Manaus, Tocher *et al.* 2001, Lima *et al.* 2012) [Floresta Estadual (FLOTA) Faro, FLOTA Trombetas, FLOTA Paru, Reserva Biológica (ReBio) Maicuru, Estação Ecológica Grão-Pará (sections North, Center and South), Ávila-Pires *et al.* 2010] and Jaú [Brazil: Parque Nacional do Jaú, Neckel-Oliveira and Gordo 2004]. In addition, we included studies from nearby areas for a better represention of the fauna of the Imeri area of endemism: Colombia (Comunidad La Ceiba, Departamento del Guainía, Lynch and Vargas-Ramírez 2000, Lynch and Suárez-Mayorga 2011). Moreover, given the large (> 1.7 million km^2, Silva *et al.* 2005) size of the Guiana area of endemism, the aforementioned sites are distributed across this region (i.e., Guiana, Suriname, Venezuela, and Brazil). The sampling techniques and sizes of study sites are not equivalent among the study sites.

To calculate faunal similarity, we used two indices: (1) Simpson's (1960) index is appropriate for incomplete sampling [$(C/N_1) \times 100$], where C = the number of species found in common at both sites and N_1 = the number of species at the most depauperate site or presumably, the most incompletely sampled site (Cole *et al.* 2013); (2) we also used the Jaccard similarity coefficient and the clustering method UPGMA (Primer software 6.0). We performed three cluster analyses using—(1) all the species found in all the areas; (2) only the identified species (i.e., excluding "sp.," "cf.," and "aff."; and (3) only the species identified and excluding typical diurnal species.

Results

A total of 41 species of amphibians (40 anurans; one salamander) was collected at both sites. These taxa represent 20 genera and nine families (Table 1; Figures 2, 3). In the Rio Daraá site, 33 species of anurans were recorded whereas in the Rio Ayuanã site, 30 species of anurans and one species of salamander were recorded. The number of species collected is correlated with the sampling methods. Thus, 34 species were found by visual encounter surveys (eight species only by this method), 28 species by chance encounters (two only by this method), and 17 species in pitfall traps (one species only by this method). In addition, five species were encountered auditory surveys, but only one was detected exclusively by this method—*Phyllomedusa bicolor* (Boddaert, 1772), which was not collected; the other four species were collected) (Table 1). Twenty-nine species were recovered with two or more sampling methods, and 23 species were collected at both sampling sites (i.e., Rio Daraá and Rio Ayuanã; Table 1). At a locality farther up the river, near the Rio Ayuanã site, additional anuran species not represented in this study were reported in fieldwork in 2013 by a team from the Museu Paraense Emílio Goeldi (Pará state). These are, as follow: Bufonidae: *Amazophrynella minuta* (Melin, 1941); *Rhinella* sp. (*R. margaritifera* Group); Hylidae: *Boana boans* (Linnaeus, 1758), *Scinax garbei* (Miranda-Ribeiro, 1926); and Phyllomedusidae: *Phyllomedusa vaillantii* Boulenger, 1882 (M.S. Hoogmoed pers. comm.).

Species richness values vary from 21–63 in the studies conducted in the Guiana, Imeri, and Jaú areas of endemism (Table 2; Figure 1). The numbers of species shared range between 5 (among Rio Preto da Eva and FLOTA Paru and ReBio Maicuru; Rio Daraá and ESEC Grão-Pará section North; Baramita and FLOTA Faro) and 29 (Parque Nacional do Jaú and Manaus; Table 2). Based on Simpson's index, the similarity of amphibian species among our sites and the other survey sites varies from 23–74% (Table 2). If all sites surveyed are included, the similarity value varies from 22% (Rio Preto da Eva and FLOTA Paru and ReBio Maicuru) to 100% (Manaus and Rio Preto da Eva; Table 2).

The three cluster analyses reveal a similar pattern. The anuran faunas of the Rio Daraá and Rio Ayuanã sites resemble those of FOTA Faro in the Pará state, Brazil, more than those from the Departamento del Guainía in Colombia (Figure 4). In contrast, the species assemblages from the sites closer to ours (i.e., Manaus, Rio Preto da Eva, and Parque Nacional do Jaú in Brazil, and Cerro de la Neblina in Venezuela) were less similar than our sites, but they group with our study sites plus the FLOTA Faro site (Figure 4). As expected, geographically close sites (Figure 1) have similar anuran species compositions [Brazil, Pará state: FLOTA Trombetas, Estação Ecológica Grão-Pará (Center and South sections), ReBio Maicuru, FLOTA Paru; Guyana: Baramita, Kartabo; Brazil, Amazonas state: Manaus, Parque Nacional do Jaú, Rio Preto da Eva] (Figure 4).

Discussion

Visual encounter surveys were the most efficient method for sampling amphibians in our survey and also in studies conducted in forested areas elsewhere in the Amazonian Brazil (Neckel-Oliveira and Gordo 2004, Vogt *et al.* 2007, Menin *et al.* 2008, Turci and Bernarde 2008, Waldez *et al.* 2013). Although pitfall traps are considered useful for sampling herpetofaunas in tropical forests (Cechin and Martins 2000, Ribeiro-Júnior *et al.* 2008), the method is most effective for capturing squamates (Oliveira *et al.* 2014), or for use in biomes such as Cerrado and open areas in the Amazonia. In our study, pitfall traps yielded only one species of anuran that was not recovered by the other sampling methods.

Table 1. Amphibian species recorded in the Santa Isabel do Rio Negro region, Amazonas state, Brazil. Sites of sampling: DR = Rio Daraá; AR = Rio Ayuanã. Sampling methods: AS = auditory survey; OE = occasional encounter; PT = pitfall traps with drift fence; VES = visual encounter survey.

Order / Family / Species	Sampling sites		Sampling methods
	DR	AR	
ANURA			
Aromobatidae			
Allobates femoralis (Boulenger, 1884)		X	OE
Allobates paleovarzensis Lima, Caldwell, Biavati and Montanarin, 2010	X	X	PT, VES, OE
Allobates sp.	X		VES, OE
Bufonidae			
Rhaebo guttatus (Schneider, 1799)	X		PT, OE
Rhinella cf. *margaritifera* (Laurenti, 1768)	X	X	PT, OE, VES, AS
Rhinella marina (Linnaeus, 1758)	X	X	PT, VES
Craugastoridae			
Pristimantis cf. *ockendeni* (Boulenger, 1912)		X	VES, OE
Pristimantis zeuctotylus (Lynch and Hoogmoed, 1977)	X	X	VES
Hylidae			
Boana cf. *cinerascens* (Spix, 1824)	X	X	VES, OE
Boana cf. *geographica* (Spix, 1824)	X	X	VES, OE
Boana wavrini (Parker, 1936)	X	X	VES, OE
Dendropsophus minusculus (Rivero, 1971)	X		VES
Dendropsophus cf. *minutus* (Peters, 1872)	X	X	PT, VES
Dendropsophus parviceps (Boulenger, 1882)	X	X	VES, OE, AS
Dendropsophus sarayacuensis (Shreve, 1935)		X	VES, OE, AS
Osteocephalus leprieurii (Duméril and Bibron, 1841)	X	X	VES
Osteocephalus oophagus Jungfer and Schiesari, 1995	X	X	VES, OE
Osteocephalus planiceps Cope, 1874		X	VES
Osteocephalus taurinus Steindachner, 1862	X	X	VES, OE
Osteocephalus vilarsi (Melin, 1941)	X	X	VES, OE
Scinax sp. 1	X		VES

Table 1. *Continued.*

Order / Family / Species	**Sampling sites**		**Sampling methods**
	DR	**AR**	
Scinax sp. 2		X	VES, OE
Trachycephalus coriaceus (Peters, 1867)	X		VES
Trachycephalus cunauaru Gordo, Toledo, Suárez, Kawashita-Ribeiro, Ávila, Morais and Nunes, 2013	X		VES, OE, AS
Leptodactylidae			
Adenomera andreae (Müller, 1923)	X	X	PT, VES, OE
Leptodactylus knudseni Heyer, 1972	X	X	PT, VES, OE
Leptodactylus mystaceus (Spix, 1824)	X	X	PT, VES, OE
Leptodactylus pentadactylus (Laurenti, 1768)	X	X	PT, VES, OE
Leptodactylus petersii (Steindachner, 1864)	X	X	PT, OE
Leptodactylus rhodomystax Boulenger, 1884	X	X	PT, VES, OE
Leptodactylus riveroi Heyer and Pyburn, 1983	X	X	PT, OE
Lithodytes lineatus (Schneider, 1799)		X	PT
Physalaemus ephippifer (Steindachner, 1864)	X		PT, VES
Microhylidae			
Adelastes hylonomos Zweifel, 1986	X		VES
Chiasmocleis hudsoni Parker, 1940	X		PT, VES, OE
Chiasmocleis ventrimaculata (Andersson, 1945)		X	PT, VES, OE
Ctenophryne geayi Mocquard, 1904	X	X	PT, VES, OE
Phyllomedusidae			
Callimedusa tomopterna (Cope, 1868)	X	X	VES, OE
Phyllomedusa bicolor (Boddaert, 1772)	X		AS
Pipidae			
Pipa pipa (Linnaeus, 1758)	X	X	OE
CAUDATA			
Plethodontidae			
Bolitoglossa sp.		X	VES
Total number of species	**33**	**31**	

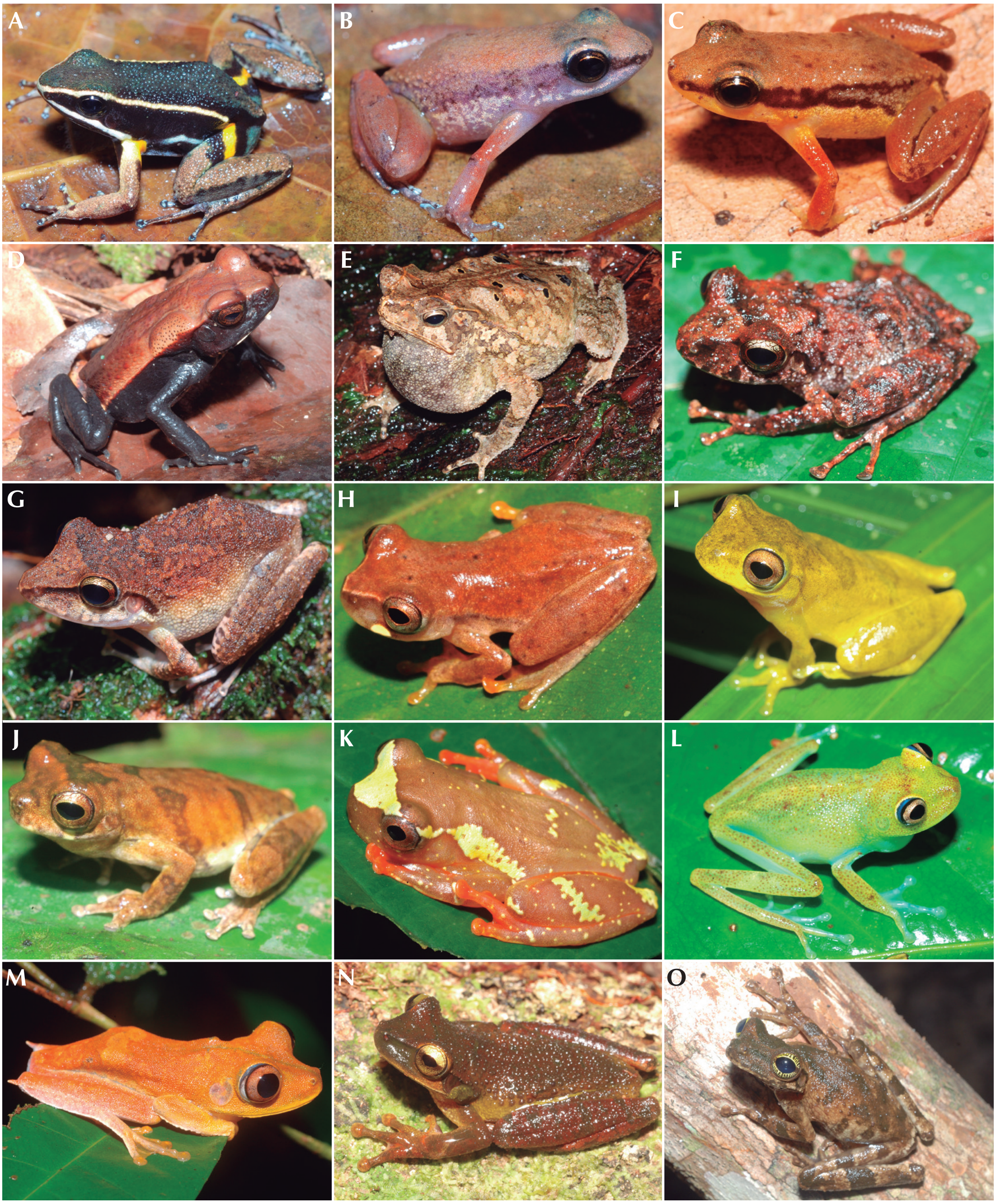

Figure 2. Amphibians found in the Santa Isabel do Rio Negro region, Amazonas state, Brazil: (**A**) *Allobates femoralis;* (**B**) *Allobates paleovarzensis;* (**C**) *Allobates* sp.; (**D**) *Rhaebo guttatus;* (**E**) *Rhinella* cf. *margaritifera;* (**F**) *Pristimantis* cf. *ockendeni;* (**G**) *Pristimantis zeuctotylus;* (**H**) *Dendropsophus minusculus;* (**I**) *Dendropsophus* cf. *minutus;* (**J**) *Dendropsophus parviceps;* (**K**) *Dendropsophus sarayacuensis;* (**L**) *Boana* cf. *cinerascens;* (**M**) *Boana* cf. *geographica;* (**N**) *Osteocephalus leprieurii;* (**O**) *Osteocephalus oophagus* (Photos by VTC).

Figure 3. Amphibians found in the Santa Isabel do Rio Negro region, Amazonas state, Brazil: (**A**) *Osteocephalus taurinus;* (**B**) *Callimedusa tomopterna;* (**C**) *Scinax* sp. 1; (**D**) *Trahycephalus cunauaru;* (**E**) *Leptodactylus knudseni;* (**F**) *Leptodactylus mystaceus;* (**G**) *Leptodactylus rhodomystax;* (**H**) *Leptodactylus riveroi;* (**I**) *Lithodytes lineatus;* (**J**) *Adelastes hylonomos;* (**K**) *Chiasmocleis hudsoni;* (**L**) *Chiasmocleis ventrimaculata;* (**M**) *Ctenophryne geayi;* (**N**) *Pipa pipa;* (**O**) *Bolitoglossa* sp. (Photos A–I and K–O by VTC; photo J by M. Gordo.)

Table 2. Number of species found in 18 sites in Guiana, Imeri, and Jaú areas of endemism. Numbers on the diagonal represent the total number of species at each site (all species included). Above the diagonal are the numbers of species shared between each pair of sites. Bellow the diagonal are the values of Simpson's index. DR = Rio Daraá; AR = Rio Ayuanã; Sip = Sipaliwini, Suriname; Bar = Baramita, Guyana; Kar = Kartabo, Guyana; Mab = Mabura, Guyana; CN = Cerro de la Neblina, Venezuela; RPE = Rio Preto da Eva, Brazil; Man = Manaus, Brazil; Far = Foresta Estadual (FLOTA) Faro; Tro = FLOTA Trombetas; Par = FLOTA Paru; Mai = Reserva Biológica Maicuru; GPN = Estação Ecológica (ESEC) Grão-Pará North; GPC = ESEC Grão-Pará Centre; GPS= ESEC Grão-Pará South; Gua = Comunidad La Ceiba, Departamento del Guainía, Colombia; and Jaú = Parque Nacional do Jaú, Brazil.

	DR	AR	Sip	Bar	Kar	Mab	CN	RPE	Man	Far	Tro	Par	Mai	GPN	GPC	GPS	Gua	Jaú
DR	**33**	23	14	6	11	13	15	8	17	12	12	8	7	5	12	13	8	14
AR	74	**31**	13	7	11	13	13	8	17	11	12	9	7	7	11	12	8	17
Sip	42	42	**63**	15	19	23	17	12	26	10	19	13	18	15	18	26	9	20
Bar	24	28	60	**25**	21	15	13	9	16	5	10	9	7	6	11	12	8	12
Kar	33	35	44	84	**43**	18	19	10	25	9	13	13	12	7	15	16	12	15
Mab	39	42	66	60	51	**35**	17	10	22	12	14	15	16	12	17	19	10	17
CN	45	42	34	52	44	49	**50**	13	24	10	12	12	10	7	14	15	12	18
RPE	35	35	52	39	43	43	57	**23**	23	9	9	5	5	8	10	11	11	12
Man	52	55	43	64	58	63	48	100	**61**	13	15	11	13	13	16	23	13	29
Far	57	52	48	24	43	57	48	43	62	**21**	11	9	8	9	12	13	8	10
Tro	43	43	68	40	46	50	43	39	54	52	**28**	15	15	11	18	19	8	13
Par	33	38	54	36	54	63	50	22	46	43	63	**24**	16	8	14	17	8	11
Mai	23	23	58	28	39	52	32	22	42	38	54	67	**31**	9	13	17	7	11
GPN	23	32	68	27	32	55	32	36	59	43	50	36	41	**22**	8	10	6	10
GPC	39	35	58	44	48	55	45	43	52	57	64	58	42	36	**31**	19	10	12
GPS	39	39	74	48	46	54	43	48	66	62	68	71	55	45	61	**35**	9	18
Gua	29	29	32	32	43	36	43	48	46	38	29	33	25	27	36	32	**28**	10
Jaú	42	55	48	48	36	49	43	52	69	48	46	46	35	45	39	51	36	**42**

The abundance of species of Hylidae and Leptodactylidae is typical of studies from other different regions of Amazonia (Gordo 2003, Neckel-Oliveira and Gordo 2004, Ilha and Dixo 2010, Lima *et al.* 2012, Waldez *et al.* 2013) and other biomes in South America (Duellman 1988). The numbers of anurans and salamander species that we report represent about 13% of the total number of species known to occur in Amazonian Brazil (Hoogmoed 2016a, Hoogmoed and Galatti 2017). Given the great diversity of cryptic anuran species in Amazonia revealed by molecular evidence (SISBIOTA project, unpubl. data), it is possible that undescribed species may be represented in our samples.

The species of *Bolitoglossa* that we found probably is undescribed. This is the first record of a salamander north of the Rio Solimões. Our data corroborate the suggestion of Brcko *et al.* (2013) that the distribution of *Bolitoglossa* includes the western and southern parts of the Guiana Region and the conclusion that the genus is not restricted to the area south of the Rio Amazonas. The rare microhylid anuran *Adelastes hylonomus* Zweifel, 1986, has been recorded recently in our study area; this is the first record of this species outside Venezuela (Almeida *et al.* 2014).

Our study was located in two areas of endemism: Guiana (Rio Daraá) and Imeri / Jaú (Rio Ayuanã) (Silva *et al.* 2005, Borges and Silva 2012). The lower part of Imeri area has been called Jaú, but the geographical limits of this area are uncertain (Borges and Silva 2012). There are many species inventories for the Guiana area of endemism as a result of surveys in Guyana, Suriname, and French Guiana (e.g., Hoogmoed and Ávila-Pires 1991, MacCulloch and Reynolds 2012, Reynolds and MacCulloch 2012). In addition, Molina *et al.* (2009) provided a complete list of species occurring Venezuela and Lescure and Marty (2000) in French Guiana. However, the amphibian assemblages reported in these studies cannot be directly compared to the results of our study because anurans were sampled in highland areas (MacCulloch and Reynolds 2012) and in disturbed forest areas during the dry season (Reynolds and MacCulloch 2012) or over greater spatial scales (Lescure and Marty 2000, Molina *et al.* 2009). Species inventories in the Imeri and Jaú areas of endemism are scarce and include studies conducted in the Departamento del Guainía in Colombia, the Colombian lowlands east of the Andes (Lynch and Vargas-Ramírez 2000, Lynch and Suárez-Mayorga 2011), and the Parque Nacional do Jaú (Neckel-Oliveira and Gordo 2004), respectively. Some species descriptions and incomplete species lists emerged from expeditions in the first half of the 20th century in areas near our study sites [São Gabriel da Cachoeira, Uaupés, Cucuí (Guiana area of endemism) and Taracuá / Marabitana / Pari /

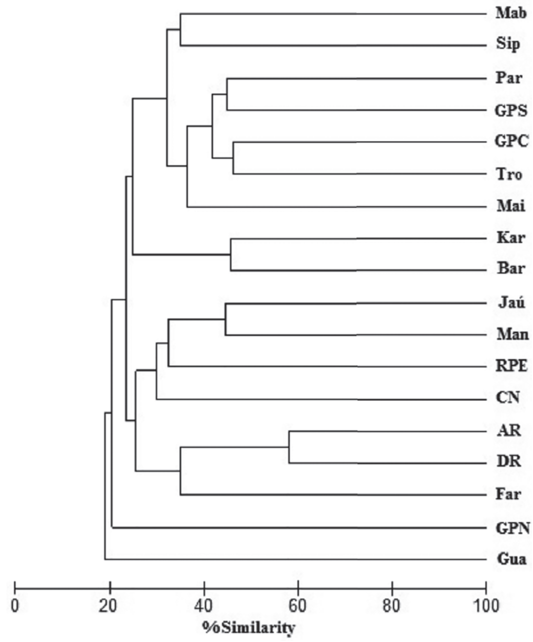

Figure 4. Dendrogram for the coefficient of Jaccard and UPGMA cluster analysis of 18 amphibian assemblages from lowland Amazonia forests. The cluster analyses were performed using only the species identified (excluding "sp.," "cf.," and "aff."). Abbreviations of the site names as in Table 2.

Iauaretê (Imeri area of endemism); Melin 1941, Lutz and Kloss 1952] but they cannot be compared with our results in detail.

Study sites located relatively near our sites share more species in common with our sites: Manaus (17 species at both Rio Daraá and Rio Ayuanã; indices 52 and 55%, respectively) and Parque Nacional do Jaú (17 species at Rio Ayuanã; index 55%) (Table 2, Figure 1). The sites located in Manaus were studied during the 1990s and later (Zimmerman and Rodrigues 1990, Lima *et al.* 2012). In contrast, at more distant sampling sites, (e.g., sites in Pará state), the similarity varies from 23% (Rio Ayuanã and ReBio Maicuru; Rio Daraá and ReBio Maicuru and Estação Ecológica Grão-Pará section North) to 57% (Rio Daraá and FLOTA Faro). Comparing all pairs of sites, the highest Simpson's index (100%) occurs between the closest geographically sites such as Manaus and Rio Preto da Eva. The closest site to ours is Cerro de la Neblina, which shares 15 species (45%) and 13 species (42%) with the Rio Daraá and Rio Ayuanã sites, respectively.

The index of similarity is extremely variable between sites of the same and distinct areas of endemism—a pattern that also characterizes the cluster analysis and reflects contradictions. As anticipated, geographically close areas have similar anuran faunas (Figure 4). Therefore, the similarity among our study sites and those from the Departamento del Guainía in Colombia are low because they belong to different area of endemism (Rio Daraá: Guiana; Rio Ayuanã: Imeri/Jaú; Guainía, Colombia: Imeri). However, the anuran assemblage of Parque Nacional do Jaú (Jaú area of endemism) is more similar to that of Manaus (Guiana area of endemism) than to the Rio Ayuanã, which belongs to the same area of endemism as Jaú. With respect to lizards, Ávila-Pires *et al.* (2009) recognized only Napo, Inambari, and Guiana areas of endemism, finding little or no evidence of other areas of endemism. The limits of the areas of endemism are better defined by other terrestrial vertebrates (birds and mammals) than amphibians and perhaps squamate reptiles, and in the case of the Jaú area of endemism, the geographical limits can be defined only partially (Borges and Silva 2012).

The differences in species richness, number of species shared, and the faunal similarities among the Amazonian sites may reflect differences in sampling efforts, the season during which sampling was conducted (Azevedo-Ramos and Galatti 2002), the total area sampled (e.g., Ilha and Dixo 2010), and the sampling methods employed (e.g., double-ended funnel traps with drift fences; Waldez *et al.* 2013). Each of the latter directly affects the numbers of individuals and species collected; thus, the observed species richness may be artificial. Differences in habitat also affect faunal composition (e.g., Cole *et al.* 2013 on the herpetofauna of Guyana); highland areas, savannas, and lowland forest sites in Amazonia have distinct faunas (Duellman 1999).

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Appendix I. *Voucher specimens collected at the study sites at Rio Daraá (D) and Rio Ayuanã (A).*

Allobates femoralis (A: CZPB-AA 238), *Allobates paleovarzensis* (A: CZPB-AA 266-270; D: CTGA-N-487), *Allobates* sp. (D: CZPB-AA 215-219), *Rhaebo guttatus* (D: CZPB-AA 161-163), *Rhinella* cf. *margaritifera* (A: URCA-H 12732; D: URCA-H 12731), *Rhinella marina* (A: CZPB-AA 254; D: CZPB-AA 255), *Pristimantis* cf. *ockendeni* (A: CZPB-AA 275-277), *Pristimantis zeuctotylus* (A: no voucher; D: CZPB-AA 125, 220), *Boana* cf. *cinerascens* (A: INPA-H 31680; D: INPA-H 31681), *Boana* cf. *geographica* (A: CZPB-AA 865, 871, 872, 874, 875, 877–882; D: CZPB-AA 160, 863, 864, 866–870, 873, 876, 883, 884), *Boana wavrini* (A: CZPB-AA 200; D: CZPB-AA 199), *Dendropsophus minusculus* (D: CZPB-AA 221, 823–826), *Dendropsophus* cf. *minutus* (A: CZPB-AA 110, 115, 121; D: CZPB-AA 103–109, 111–114, 116–120; 122–124, 159), *Dendropsophus parviceps* (A: CZPB-AA 224, 228, 231–233; D: CZPB-AA 222, 223, 225, 226, 229, 230, 234), *Dendropsophus sarayacuensis* (A: CZPB-AA 271–274), *Osteocephalus leprieurii* (A: CZPB-AA 95, 96, 98; D: CZPB-AA 97, 129), *Osteocephalus oophagus* (A: CZPB-AA 241, 242, 244; D: CZPB-AA 2343), *Osteocephalus planiceps* (A: CZPB-AA 239–240), *Osteocephalus taurinus* (A: CZPB-AA 246, 248, 250, 251, 853; D: CZPB-AA 245, 247, 249), *Osteocephalus vilarsi* (A: CZPB-AA 857; D: CZPB-AA 126–128; 854–856), *Scinax* sp. 1 (D: CTGA-N- 303–309), *Scinax* sp. 2 (A: CTGA-N-342–342), *Trachycephalus coriaceus* (D: CZPB-AA 130–136), *Trachycephalus cunauaru* (D: CZPB-AA 235–236), *Adenomera andreae* (A: CZPB-AA 185, 186, 190; D: CZPB-AA 184, 187–189, 191), *Leptodactylus knudseni* (A: CZPB-AA 337–344; D: CZPB-AA 237, 336), *Leptodactylus mystaceus* (A: CZPB-AA 172, 176, 178, 180; D: CZPB-AA 171, 173–175, 177, 179, 181–183), *Leptodactylus pentadactylus* (A: CZPB-AA 253, 347–349, 351–353; D: CZPB-AA 350), *Leptodactylus petersii* (A: CZPB-AA 205; D: CZPB-AA 204), *Leptodactylus rhodomystax* (A: CZPB-AA 256, 260–262, 265; D: CZPB-AA 257–259, 263, 264), *Leptodactylus riveroi* (A: CZPB-AA 208–212, 214; D: CZPB-AA 206, 207, 213), *Lithodytes lineatus* (A: CZPB-AA 1001), *Physalaemus ephippifer* (D: CZPB-AA 201–203), *Callimedusa tomopterna* (A: CTGA-N-492; D: CZPB-AA 155–158), *Phyllomedusa bicolor* (D: no voucher), *Adelastes hylonomos* (D: INPA-H 32510, CZPB-AA 605), *Chiasmocleis hudsoni* (D: CZPB-AA 137–154), *Chiasmocleis ventrimaculata* (A: CZPB-AA 99–102, 252), *Ctenophryne geayi* (A: CZPB-AA 168; D: CZPB-AA 164–167, 169, 170), *Pipa pipa* (A: CZPB-AA 193–195; D: CZPB-AA 192, 196–198), *Bolitoglossa* sp. (A: CZPB-AA 227).