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On the Geographic Distribution of the Bald Uakaris (*Cacajao calvus* ssp.) in Brazilian Amazonia

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Abstract: An understanding of a species' geographic distribution is essential to assess, plan, and develop strategies for its conservation. The geographic distribution of the bald uakari, *Cacajao calvus*, and its component subspecies has been poorly investigated, with disjunct distributions being reported in Brazil and Peru. In this study, we reveal new records of bald uakari occurrence based on multi-year surveys, a literature review, and an examination of vouchers available in six zoological collections, clarifying the geographic distribution of all subspecies. We confirm that *C. c. calvus* has a disjunct distribution with populations along the rios Tarauacá and Pauini, 250 km away from those on the left bank of middle Rio Juruá and lower Rio Jutaí; and 650 km from the population of the Mamirauá Sustainable Development Reserve (Mamirauá SDR). *Cacajao c. rubicundus* has a disjunct distribution with three isolated populations 1) inhabiting the flooded forests of the Rio Solimões and the Paraná (channel) Jacurapá, 2) the left bank of the lower Rio Jutaí; and 3) in the Auati-Paraná. *Cacajao c. novaesi* has the smallest geographic distribution of the bald uakaris, occurring only in the Gregório-Tarauacá interfluvium. *Cacajao c. novaesi* and *C. c. calvus* are separated by the Rio Tarauacá, which is also a significant geographic barrier for other primates, including titi and saki monkeys. We also confirm the occurrence of *Cacajao c. ucayalii* in Brazil in the Serra do Divisor National Park. This Peruvian subspecies has the most extensive range, with isolated populations found in areas completely separated from the lowlands. The patchy distribution of *Cacajao calvus* provides a unique opportunity to understand how local environmental variation may have promoted ecological flexibility for the successful establishment of isolated populations.

Keywords: Disjunct distribution, Extent of Occurrence, Neotropical primates, Pitheciinae, Amazonian rainforest.

Introduction

The bald uakaris, genus *Cacajao*, are endemic to western Amazonia, occurring in the forests of the Ucayali, Solimões and Juruá river basins (Silva Jr *et al.* 2013). These primates have a complex facial vascular system that confers a singular bare red face (Mayor *et al*. 2015). Four subspecies were recognized by Hershkovitz (1987): *C. calvus calvus*, *C. c. rubicundus*, *C. c. ucayalii*, and *C. c. novaesi* (Fig. 1). All available data suggest that they have a patchy distribution, largely along rivers, rarely occupying unflooded (upland) forests in the most central regions of the interfluvia (Silva Jr. *et al.* 2013)—at least not regularly, as is the case for other Amazonian primates (but see Peres 1997). Their geographic distributions have been updated in Peru (Ward and Chism 2003; Bowler *et al*. 2009; Vermeer *et al*. 2013) and Brazil (Vieira *et al*. 2008; Cardoso *et al*. 2014), but their range-wide occurrence remains poorly known.

In the 1980s, the white uakari, *C. c. calvus*, was the first to be the focus of a long-term study on its ecology and behavior (Ayres 1986; Ayres and Johns 1987). At the time, this subspecies was thought to occur only in the flooded forests of the Mamirauá Sustainable Development Reserve (Mamirauá SDR) but primate surveys confirmed its occurrence along the middle Rio Juruá (Peres 1988, 1997), and further surveys provided new evidence of white uakaris along the south bank of the Rio Solimões, well-separated from the Mamirauá SDR. The population of white uakaris recorded in the region of the Rio Jurupari, a right-bank tributary of the Rio Envira in the upper Rio Juruá basin, is about 700 km from the white uakaris of the Mamirauá SDR (Silva Jr. and Martins 1999). New reports on the presence of white uakaris between these two areas were presented more recently (Cardoso *et al.* 2014; Silva *et al.* 2017; Sampaio *et al.* 2018) but did not provide a specific hypothesis for their geographic distribution. Surveys in the region of the lower Rio Jutaí (Cardoso *et al.* 2014; Silva *et al.* 2017), for example, confirmed the presence of white uakaris only on the right bank, with *C. c. rubicundus* being recorded on the left bank. The Rio Jutaí is a south bank tributary of the Rio Solimões about 100 km to the southwest of the populations of white uakaris in the Mamirauá SDR. A new population of was also reported in the Pauini basin, a left-bank tributary of the Rio Purus (Sampaio *et al.* 2018). The populations of Jurupari and Pauini are about 250 km apart from the middle Rio Juruá and about 650 km from the Mamirauá SDR. If these populations are in fact completely separated is unclear, however.

Silva Jr. and Martins (1999) mentioned that the population from the Rio Jurupari is completely isolated from that of Mamirauá SDR, but "with *C. c. novaesi* enclaved between them". The report of Novaes' uakari, *C. c. novaesi*, in the middle Rio Juruá, however, was based on a previous misidentification. One of the main diagnostic characters of *C. c. novaesi*, as indicated by Hershkovitz (1987), is its "General coloration orange with dorsum from nape to tail tip contrastingly paler orange, buffy or whitish…" (Hershkovitz 1987; p.42). With limited data available, the subspecies' range was described by Hershkovitz (1987) as follows: "Known only from between the Rio Tarauacá and Rio Eiru, south bank upper Rio Juruá, Amazonas, Brazil; the range may extend west from the Tarauacá to the Rio Gregório or beyond to occupy the entire basin between the Tarauacá and right bank of the Rio Juruá; the genus is unknown to the south in Acre" (Hershkovitz 1987; p.38).

Cacajao c. novaesi was supposedly recorded at the Lago da Fortuna, left bank of the Rio Juruá, upriver of the town of Carauari, which would extend its range by about 500 km to the northeast (Peres 1988). Peres (1988; p.84) referred to the uakaris of that region as the "recently described subspecies of white uakari (*Cacajao calvus novaesi*)"—an apparent reference to the subspecies *C. c. calvus* from the Rio Juruá basin (see Silva Jr. and Martins 1999) and not to the orange-buff uakari (*C. c. novaesi*) described by Hershkovitz

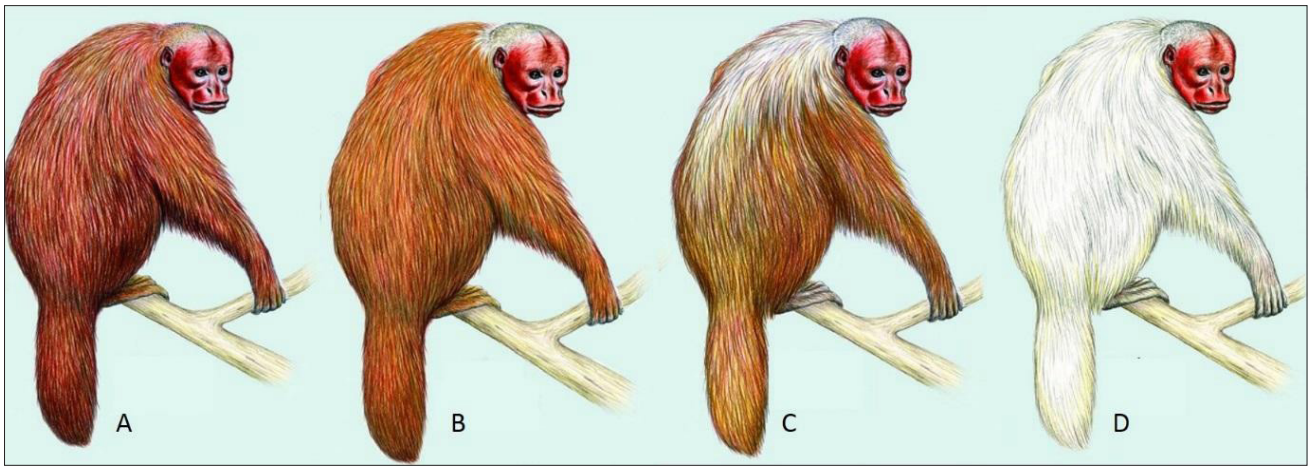

Figure 1. The four subspecies of bald uakaris, *Cacajao calvus*, according to Hershkovitz (1987). **A** – *C. c. ucayalii*; **B** – *C. c. rubicundus*; **C** – *C. c. novaesi*; **D** – *C. c. calvus*. Illustrations courtesy of Stephen D. Nash.

a year before. This misidentification of *C. c. novaesi* in the middle Rio Juruá, however, has since underpinned the geographic distribution of this taxon, with its inclusion in species checklists of protected areas and other publications (Peres 1990; Bowler and Bodmer 2009; Barnett *et al.* 2013; Figueiredo-Ready *et al.* 2013; Silva Jr *et al.* 2013; Veiga *et al.* 2020, Aquino *et al.* 2021).

Another subspecies with inaccurate information on its occurrence in Brazil is *C. c. ucayalii*. This taxon occurs mostly in Peruvian forests, in the Ucayali-Yavarí interfluvium (Silva Jr. *et al.* 2013), but additional records have been published beyond this range (Bowler *et al.* 2009; Vermeer *et al.* 2013; McHugh *et al.* 2019). Bowler *et al.* (2009) reported *C. c. ucayalii* on the right bank of the Río Yanayacu, a small tributary of the Río Marañon, in the Pacaya-Samiria National Reserve. Prior to this record, the taxon had been listed in just one protected area: the Tamshiyacu-Tahuayo Communal Reserve (Bowler *et al.* 2009). The second report is from montane forests in the Cordillera Cahuapanas, San Martín, northeastern Peru, where Vermeer *et al.* (2013) found a new isolated population more than 365 km to the west of the locality reported by Bowler *et al.* (2009). McHugh *et al.* (2019) recorded an isolated population of reddish uakaris in montane areas of southwest Peru, district of Pampa Hermosa, Región Junin (approximately1287–2015 m above sea level). Hershkovitz (1987) mentioned the presence of *C. c. ucayalii* in Brazil based on voucher specimens held in the Museu Paraense Emílio Goeldi: "Four males (1 juv.) and 3 females labelled Estirão do Equador, east bank of lower Rio Javari, Amazonas, Brazil, agree with *C. c. ucayalii* from the opposite bank of the same river but their backs average slightly paler. These specimens of *ucayalii* are the only ones known to occur east of the Rio Javari. They almost certainly represent an enclave population cut off from parental stock on the west or Peruvian bank of the Rio Javari (Yavari)" Hershkovitz (1987; p.35).

There are no field data, however, from the right bank of the Río Yavari to confirm *C. c. ucayalii* in Brazil. Bald uakaris were recorded in the Serra do Divisor National Park (SDNP) – Acre State, Brazil, but their identification in that region is controversial (Calouro 1999; Silva Jr. and Martins 1999; Lopes and Rehg 2003). Calouro (1999), for example, reported the occurrence of red uakaris—identified as *Cacajao calvus rubicundus*—in a montane region (about 600 m above sea level) in the northern sector of the Serra do Divisor National Park that is drained by the Rio Moa, a left-bank tributary of the Rio Juruá. Some years later, Lopes and Rehg (2003) presented a species list of the primates recorded in the Rio Ouro Preto basin, a left-bank tributary of the Rio Juruá in the southern sector of the Serra do Divisor National Park and listed *Cacajao calvus*. The presence of *C. c. ucayalii* in Brazilian territory, therefore, remained uncertain.

Although Calouro (1999) identified the red uakaris of the Serra do Divisor as *C. c. rubicundus*, this taxon is only known from a few localities along the middle Rio Solimões. Its type locality is the mouth of Rio Içá, a left (north) bank tributary of the Rio Solimões, opposite the town of São Paulo de Olivença, state of Amazonas (Hershkovitz 1987). The subspecies has a disjunct distribution, also occurring in the Auati-Paraná, in a contact zone with *C. c. calvus* (Vieira *et al.*, 2008). *Cacajao c. rubicundus* also occurs in the Rio Jutaí basin, in the Jutaí-Solimões Ecological Station (Silva *et al.* 2017), southern bank of the Rio Solimões.

The occurrence and distribution of bald uakari populations in Brazil have been overlooked and in some key areas the subspecies have been misidentified, and some reports of *C. calvus* entirely omitted infraspecific taxonomy. Here, we elucidate the geographic distribution of bald uakaris in Brazil based on new information on the occurrence of each subspecies from numerous surveys. We provide new hypotheses for the geographic distributions of the bald uakari subspecies and estimate their range and the Extent of Occurrence.

Methods

The study area is the floodplains of western Amazonia, but we also present data from upland forests. The marked seasonal variation in annual rainfall influences the flood pulse of Amazonian rivers, which in western Amazonia have their origin in the Andes, and transport large amounts of nutrient rich sediments (Sioli, 1956; Junk *et al.* 2011). The soils are composed of sedimentary units from the Miocene known as the Solimões formation (Rossetti *et al.* 2005).

The locality data presented here include literature records, zoological collection vouchers, and unpublished information from fieldwork. The field data are from mammal surveys, including inventories performed in protected areas and Indigenous land as contributions to their management plans and long-term monitoring (for example, Peres 1988, 1997, see also <www.institutojurua.org>), and any authoritative sightings or mentions on the presence and absence of bald uakaris. Surveys were conducted from 2008 to 2018 in the Rio Solimões basin (Fig. 2, Table 1). We used preexisting trails and paths to survey the terra firma forest, and small canoes for the flooded forests (Campbell *et al.* 2016; Barnett *et al.* 2019). The surveys were done mostly during the morning and afternoon, but we also recorded any occasional sightings of uakaris. We include records based only on sightings, although reports on the presence or absence of uakaris are considered as additional evidence.

We identified the bald uakari subspecies following the descriptions of the pelage coloration provided by Hershkovitz (1987). During the surveys, occasional specimen collections were made to support the accurate identification of bald uakaris at the subspecies level (SISBio permits 55777-2, 42111-1, 42111-2, 42111-3; see also Sikes and The Animal Care & Use Committee of the American Society of Mammalogists, 2016). The material collected was deposited in the specimen collections of the Mamirauá Institute for Sustainable Development (IDSM) and the National Institute of

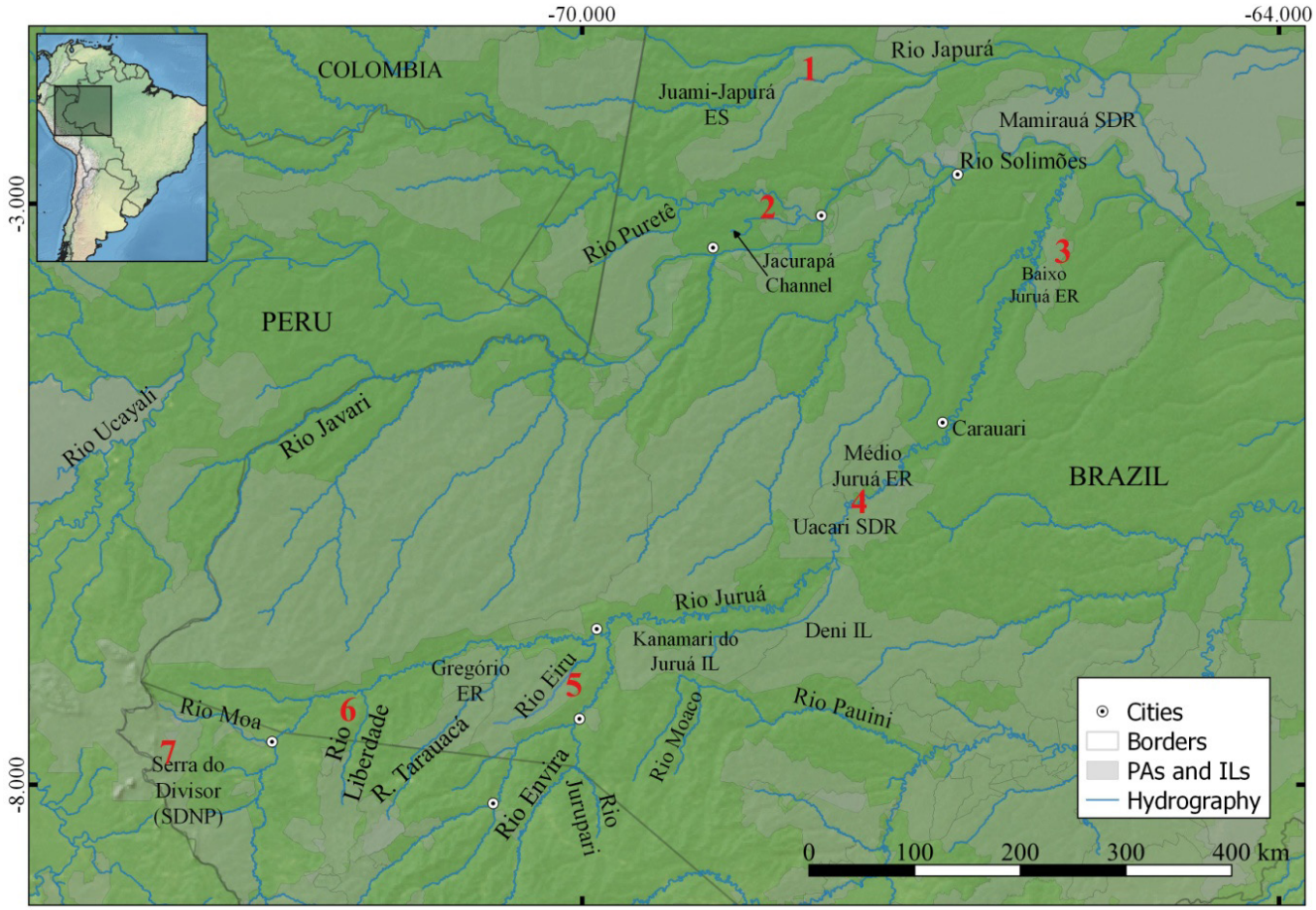

Figure 2. The study area: 1 – Juami-Japurá Ecological Station; 2 – Içá–Solimões interfluve; 3 – Baixo Juruá Extractive Reserve; 4 – the middle Rio Juruá; 5 – Gregório-Tarauacá interfluvium; 6 – Rio Liberdade; 7 – Serra do Divisor National Park (SDNP). ES – Ecological Station, ET – Extractive Reserve, SDR – State Development Reserve, NP – National Park, IL – Indigenous Land.

Amazonian Research (INPA). We also examined voucher specimens in four other scientific collections (Appendix 1), those of the Museu de Zoologia of the Universidade de São Paulo (MUZUSP), the Museu Paraense Emílio Goeldi (MPEG), the Museu Nacional of the Universidade Federal do Rio de Janeiro (MNRJ), and the Field Museum of Natural History (FMNH).

We estimated the Extent of Occurrence (EOO) of each taxon using the minimum convex polygon based on the set of occurrence records obtained from field surveys, literature, and scientific collections (Joppa *et al.* 2016; IUCN Standards and Petitions Committee 2019). We also recorded the absence of uakaris in the survey areas, which allowed us to estimate the geographic distribution considering the disjunct distribution of each subspecies. We plotted all records and created polygon layers for each taxon using the geographic information system in the software QGIS version 3.14.16 (QGIS Development Team 2019), and considered the field evidence for the presence or absence of uakaris to identify the limits of the species' distribution, producing a more accurate measurement of the total area potentially occupied by the species.

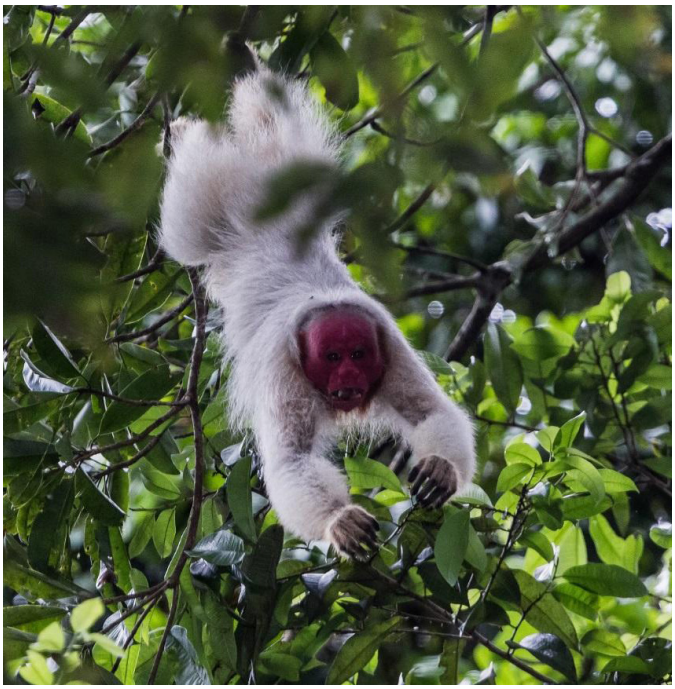

Figure 3. *Cacajao c. calvus* from the right bank of the Rio Tarauacá. Photograph by Marcelo I. Santana.

Table 1. Areas surveyed in the basins of the rios Solimões and Juruá. JJES – Juami-Japurá Ecological Station; BJER – Baixo Juruá Extractive Reserve; USDR – Uacari Sustainable Development Reserve; MJER – Médio Juruá Extractive Reserve; DIL – Deni Indigenous Land; KJIL – Kanamari do Juruá Indigenous Land; RGER – Rio Gregório Extractive Reserve; RLER Riozinho da Liberdade Extractive Reserve; SDNP – Serra do Divisor National Park; N/A – Not applicable (unprotected area).

Area	River	Year	Legally protected land	Locality	Latitude	Longitude	Effort (days)
1	Japurá	2017	JJES	-	-2.1798	-68.3547	14
2	Içá	2015	N/A	Jacurapá channel	-3.2369	-68.6181	5
				Cachoeira & Monte Tabor (Cuiaoá) villages	-2.8895	-68.3681	5
				Lago Mapuru	-2.9543	-68.4239	5
				São Pedro village	-3.0294	-68.8823	5
				Pauiri & Nova Esperança villages (Igarapé Tapuru, Rio Puretê)	-3.0415	-69.1057	5
3	Juruá	2018	BJER	-	-3.5649	-65.9690	17
4	Juruá	2008-2010	USDR	Left bank Rio Juruá - Anaxiqui, Baúna, Eré, Marari	-5.6243	-67.6504	209
				Right bank Rio Juruá -Anaxiqui, Baúna, Eré, Marari	-5.6243	-67.6504	195
			MJER	Riozinho, left bank tributary of Rio Juruá	-4.4007	-66.8369	347
		2015	USDR	Left bank Rio Juruá, Lago Pupunha	-5.6243	-67.6504	14
		2011-2012	DIL	Rio Xeruã, right bank tributary of Rio Juruá	-6.7048	-68.4572	54
			KJIL	Rio Xeruã, right bank tributary of Rio Juruá	-6.7485	-68.6881	40
5	Gregório	2015	RGER	Igarapé do Coatá	-7.1577	-70.7670	14
	Tarauacá	2017	N/A	Igarapé São Romão	-6.7531	-69.9248	6
	Eiru	2017	N/A	Igarapé Preto	-6.8643	-70.1958	14
6	Liberdade	2018	RLER	Comunidade Periquito	-8.0667	-72.0642	8
				Comunidade Alegria	-7.8911	-72.2670	4
				Comunidade Bom Futuro	-7.9037	-72.0654	2
				Comunidade Morro da Pedra	-7.8440	-72.0545	4
				Comunidade Mauício Mapes	-7.7989	-72.0223	4
				Comunidade Santa Rita	-7.7059	-71.9980	4
				Comunidade São João	-7.6322	-71.9606	6
				Comunidade São José	-7.6039	-71.9512	6
				Comunidade São Luiz	-7.5652	-71.9416	6
7	Moa	2018	SDNP	Comunidade Pé da Serra	-7.4614	-73.6680	10

Results

Cacajao c. calvus

Cacajao c. calvus (Fig. 3) has an EOO of 154,252 km² but occurs in three separate areas (Figs. 4 and 5). The first, the Mamirauá SDR, an area of 11,240 km² of *várzea* (flooded forest) and *chavascal* (dense and species-poor shrub/tree communities in old depressions, abandoned channels, and shallow lakes) (Ferreira-Ferreira *et al.* 2014), encompasses the populations delimited by the rios Solimões and Japurá, and by the Auati-Paraná to the west (Fig. 5). There is also an isolated population in the Amanã Sustainable Development Reserve on the left bank of the Rio Japurá (see locality 2, Fig. 5, Table 2).

The second area is the middle Rio Juruá and lower Rio Jutaí (Fig. 5). There, we recorded the subspecies on the left bank of the middle Rio Juruá, in the Médio-Juruá Extractive Reserve and the Uacari Sustainable Development Reserve, which have flooded and terra firma forests. We recorded *C. c. calvus* on only two occasions on the right bank of the middle Rio Juruá (in *várzea*, localities 8 and 15, Table 2, Fig. 5), despite a prolonged survey (289 days, see Table 1). The populations of white uakaris, *C. c. calvus*, from the Mamirauá SDR and the right bank of the Rio Jutaí, occur on opposite banks of the Rio Solimões, and there is a considerable distance (about 100 km) between them without any record of bald uakaris. We estimated the range of the populations from the left bank of middle Juruá and the lower bank of Rio Jutaí to cover 16,780 km² (Fig. 5).

The third area where we recorded white uakaris was on the right bank of the Rio Tarauacá (Figs. 3 and 5), close to the records presented by Sampaio *et al.* (2018) along the

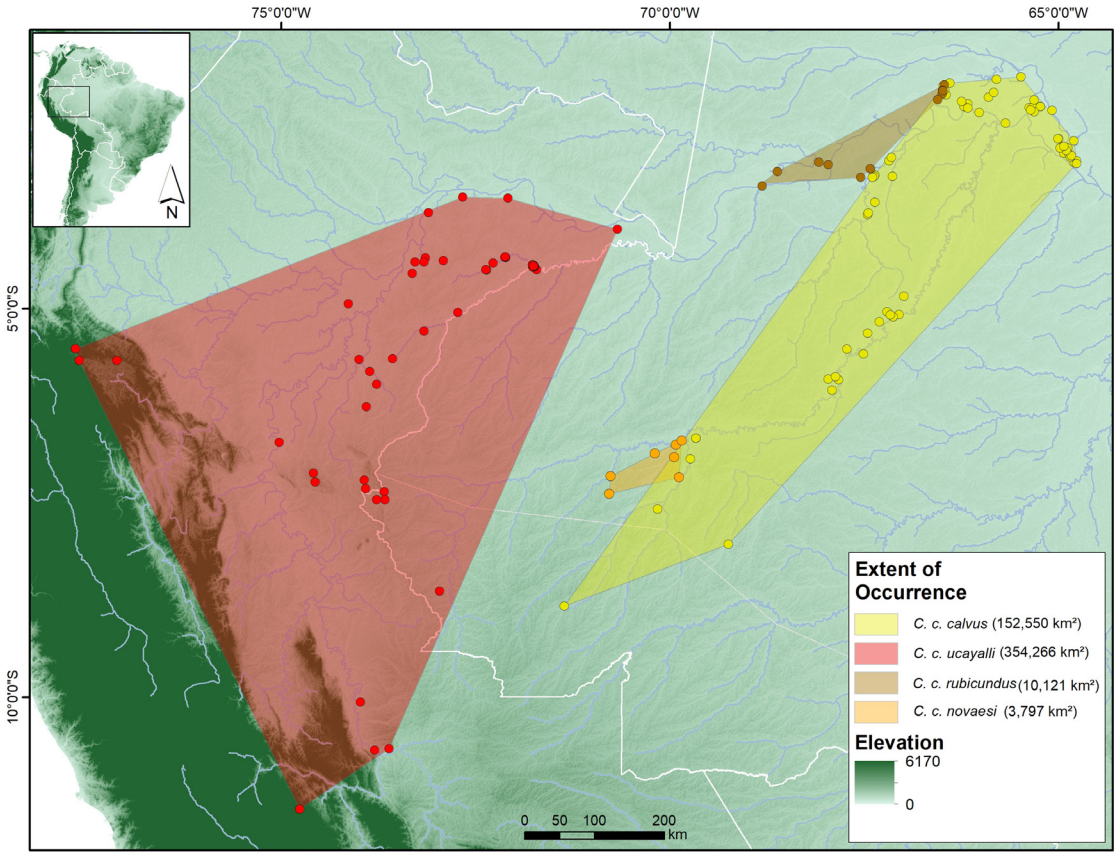

Figure 4. The Extent of Occurrence of the bald uakaris, *Cacajao calvus* ssp.

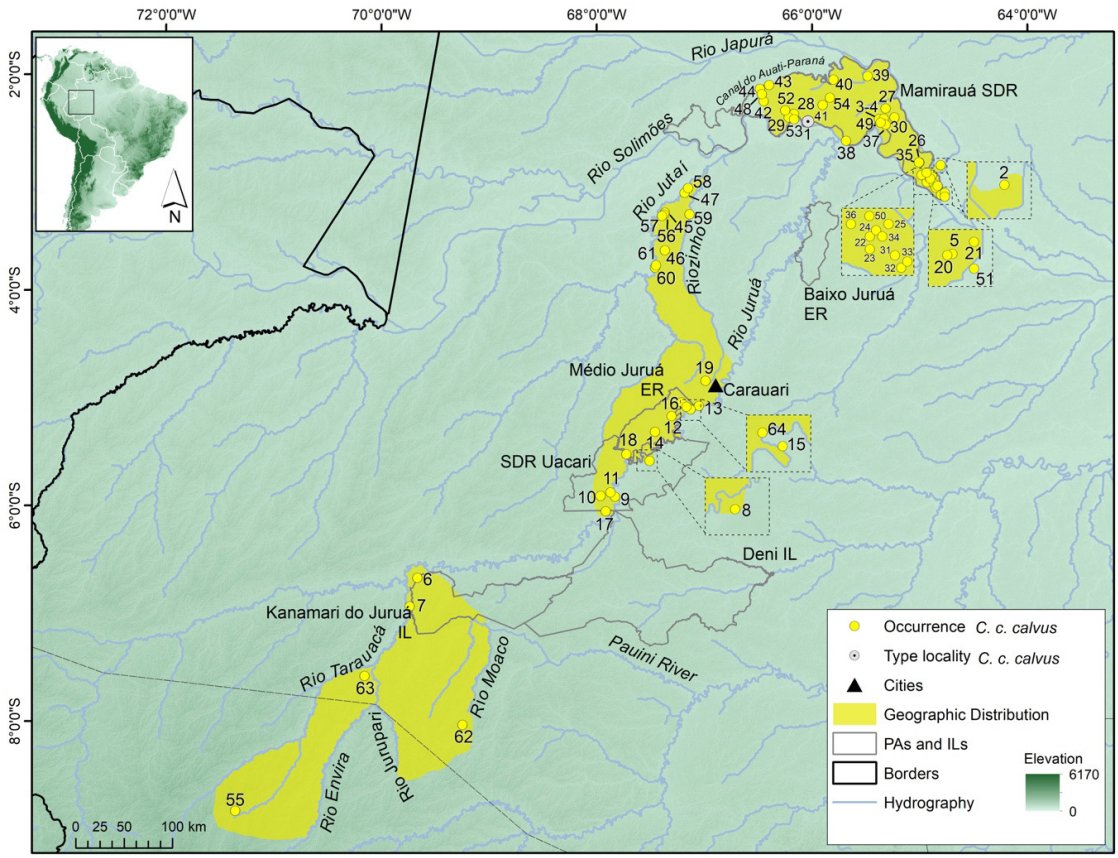

Figure 5. The geographic distribution of *Cacajao c calvus*. PAs: Protected Areas; ILs: Indigenous lands. The localities are listed in Table 2.

Table 2. The occurrence records of *Cacajao c. calvus*. In bold, the type locality, no.1. The localities are shown in Figure 5.

	Taxon	Latitude	Longitude	Locality	Reference
1	***C. c. calvus***	**-2.4360**	**-66.0330**	**Rio Solimões (left bank), opposite Fonte Boa, Amazonas, Brazil**	**Hershkovitz (1987)**
2	*C. c. calvus*	-2.8414	-64.8048	Lago Pantaleão, Low Rio Japurá, Amanã Reserve, Amazonas, Brazil	This study
3	*C. c. calvus*	-2.4156	-65.3781	Comunidade Bate Papo, Paraná do Aranapú, Amazonas, Brazil	This study
4	*C. c. calvus*	-2.4113	-65.3337	Comunidade Bate Papo, Paraná do Aranapú, Amazonas, Brazil	This study
5	*C. c. calvus*	-3.1150	-64.7936	Comunidade Boca do Mamirauá, Amazonas, Brazil	This study
6	*C. c. calvus*	-6.6706	-69.6673	Comunidade São Romão, Igarapé Grande, Rio Tarauacá (right bank), Amazonas, Brazil	This study
7	*C. c. calvus*	-6.9351	-69.7379	Lago Tucumã, Rio Tarauacá (right bank), Amazonas, Brazil	This study
8	*C. c. calvus*	-5.5857	-67.5098	Comunidade Santo Antônio do Brito, Uacari SDR (right bank Rio Juruá), Amazonas, Brazil	This study
9	*C. c. calvus*	-5.9170	-67.8309	Comunidade Mandioca, Uacari SDR, Amazonas, Brazil	This study
10	*C. c. calvus*	-5.9095	-67.9654	Comunidade Sorocaba, Uacari SDR, Amazonas, Brazil	This study
11	*C. c. calvus*	-5.8767	-67.8731	Comunidade Xibaua, Uacari SDR, Amazonas, Brazil	This study
12	*C. c. calvus*	-5.1695	-67.3061	Comunidade Fortuna, Médio Juruá Extractive Reserve, Amazonas, Brazil	This study
13	*C. c. calvus*	-5.0760	-67.0518	Comunidade Goiabal, Médio Juruá Extractive Reserve, Amazonas, Brazil	This study
14	*C. c. calvus*	-5.3162	-67.4598	Comunidade Nova União, Médio Juruá Extractive Reserve, Amazonas, Brazil	This study
15	*C. c. calvus*	-5.1082	-67.1287	Comunidade Novo Horizonte, Rio Juruá (right bank), Amazonas, Brazil	This study
16	*C. c. calvus*	-5.0422	-67.2107	Comunidade Roque, Médio Juruá Extractive Reserve, Amazonas, Brazil	This study
17	*C. c. calvus*	-6.0526	-67.9170	Comunidade São Sebastião, Médio Juruá Extractive Reserve, Amazonas, Brazil	This study
18	*C. c. calvus*	-5.5228	-67.7245	Comunidade Tabuleiro, Uacari SDR, Amazonas, Brazil	This study
19	*C. c. calvus*	-4.8428	-66.9905	Rio Riozinho, Amazonas, Brazil	This study
20	*C. c. calvus*	-3.1167	-64.8000	Vila Alencar, Amazonas, Brazil	Ayres (1986), MZUSP 17536, 17537, 17542
21	*C. c. calvus*	-3.1000	-64.7667	Lago Tracajá, Amazonas, Brazil	Ayres (1986), MZUSP 17535, 17539
22	*C. c. calvus*	-2.9667	-64.9333	Lago Acácio, Amazonas, Brazil	Ayres (1986)
23	*C. c. calvus*	-3.0000	-64.9333	Lago Mamirauá, Amazonas, Brazil	Ayres (1986); IDSM/ FES102
24	*C. c. calvus*	-2.9500	-64.9167	Lago Teiú, Amazonas, Brazil	Ayres (1986)
25	*C. c. calvus*	-2.9333	-64.8833	Lago Jacitara, Amazonas, Brazil	Ayres (1986)
26	*C. c. calvus*	-2.8167	-65.0000	Lago da Campina, Paraná do Jarauá, Amazonas, Brazil	Ayres (1986)
27	*C. c. calvus*	-2.3167	-65.3167	Lago Viola, Paraná do Panauã, Amazonas, Brazil	Ayres (1986)
28	*C. c. calvus*	-2.3667	-66.1667	São José, opposite Fonte Boa, Amazonas, Brazil	Ayres (1986)
29	*C. c. calvus*	-2.4000	-66.2167	Paraná do Maiana, opposite Fonte Boa, Amazonas, Brazil	Ayres (1986)
30	*C. c. calvus*	-2.4000	-65.2333	Lago Fortuna, Paraná do Aranapú, Amazonas, Brazil	Cardoso *et al.* (2014), Ayres (1986)
31	*C. c. calvus*	-3.0167	-64.8667	Setor Mamirauá, Amazonas, Brazil	Cardoso *et al.* (2014)
32	*C. c. calvus*	-3.0500	-64.8500	Setor Mamirauá, Amazonas, Brazil	Cardoso *et al.* (2014)
33	*C. c. calvus*	-3.0333	-64.8333	Setor Mamirauá, Amazonas, Brazil	Cardoso *et al.* (2014)
34	*C. c. calvus*	-2.9667	-64.9000	Setor Mamirauá, Amazonas, Brazil	Cardoso *et al.* (2014)
35	*C. c. calvus*	-2.8167	-65.0067	São Raimundo do Jarauá, Amazonas, Brazil	Cardoso *et al.* (2014)
36	*C. c. calvus*	-2.9333	-64.9833	Cauaçú, Amazonas, Brazil	Cardoso *et al.* (2014)
37	*C. c. calvus*	-2.4667	-65.3167	Comunidade Barroso, Paraná do Aranapu, Amazonas, Brazil	Cardoso *et al.* (2014)
38	*C. c. calvus*	-2.6167	-65.6833	Comunidade Batalha de Baixo, Amazonas, Brazil	Cardoso *et al.* (2014)

Table 2. *Cont'd.*

39	*C. c. calvus*	-2.0167	-65.4833	Paraná Itaúba, Amazonas, Brazil	Cardoso *et al.* (2014)
40	*C. c. calvus*	-2.0500	-65.8000	Paraná Itaúba, Amazonas, Brazil	Cardoso *et al.* (2014)
41	*C. c. calvus*	-2.2833	-65.9000	Santa Maria da Agua Branca, Paraná do Panauã, Rio Japurá, Amazonas, Brazil	Cardoso *et al.* (2014)
42	*C. c. calvus*	-2.2500	-66.4500	Lago Coatá, Paraná Maiana, Amazonas, Brazil	Cardoso *et al.* (2014)
43	*C. c. calvus*	-2.1000	-66.4000	Igarapé Lua, Paraná Maiana, Amazonas, Brazil	Cardoso *et al.* (2014)
44	*C. c. calvus*	-2.1333	-66.4833	Igarapé Zefinha, Paraná Aiupiá, Amazonas, Brazil	Cardoso *et al.* (2014)
45	*C. c. calvus*	-3.2833	-67.3667	Comunidade Cazuza, Paraná do Acural, Rio Jutaí, Amazonas, Brazil	Cardoso *et al.* (2014)
46	*C. c. calvus*	-3.6333	-67.3667	Paraná Oitero, Rio Jutaí, Amazonas, Brazil	Cardoso *et al.* (2014)
47	*C. c. calvus*	-3.1000	-67.1833	Comunidade Bordalé, Rio Jutaí, Amazonas, Brazil	Cardoso *et al.* (2014)
48	*C. c. calvus*	-2.1833	-66.4667	Igarapé Matias, Paraná do Aiupiá, Amazonas, Brazil	Vieira *et al.* (2008); Cardoso *et al.* (2014)
49	*C. c. calvus*	-2.4473	-65.3620	Comunidade Bate Papo, Paraná do Aranapú, Amazonas, Brazil	IDSM/Masto (1383)
50	*C. c. calvus*	-2.9118	-64.9346	Lago Mamirauá, Amazonas, Brazil	IDSM/Masto (283)
51	*C. c. calvus*	-3.1333	-64.7667	Rio Japurá (mouth), Amazonas, Brazil	Hershkovitz (1987)
52	*C. c. calvus*	-2.3333	-66.2500	Paraná Maiana, Series Lako – MNRJ, Amazonas, Brazil	Hershkovitz (1987)
53	*C. c. calvus*	-2.4167	-66.1667	Sitio São José, Paraná do Maraui, Amazonas, Brazil	Hershkovitz (1987)
54	*C. c. calvus*	-2.2167	-65.8333	Panauã (Refuge), Amazonas, Brazil	Rylands & Mittermeier (1983)
55	*C. c. calvus*	-8.8300	-71.3600	Sacado do Tarauacá, Acre, Brazil	INPA5241/CCM112
56	*C. c. calvus*	-3.2995	-67.3739	Rio Jutaí Extractive Reserve, Amazonas, Brazil	Silva *et al.* (2017)
57	*C. c. calvus*	-3.3130	-67.3946	Rio Jutaí Extractive Reserve, Amazonas, Brazil	Silva *et al.* (2017)
58	*C. c. calvus*	-3.0561	-67.1506	Left bank of Riozinho (right-bank tributary of Rio Jutaí)	Silva *et al.* (2017)
59	*C. c. calvus*	-3.2981	-67.1371	Left bank of Riozinho (right-bank tributary of Rio Jutaí)	Silva *et al.* (2017)
60	*C. c. calvus*	-3.7919	-67.4583	Rio Jutaí Extractive Reserve, Amazonas, Brazil	Silva *et al.* (2017)
61	*C. c. calvus*	-3.7713	-67.4502	Rio Jutaí Extractive Reserve, Amazonas, Brazil	Silva *et al.* (2017)
62	*C. c. calvus*	-8.0339	-69.2481	Rio Moaco (right bank tributary of Rio Pauini), Amazonas, Brazil	Sampaio *et al.* (2018)
63	*C. c. calvus*	-7.5792	-70.1588	Rio Jurupari (right bank tributary of Rio Envira, Acre, Brazil	Silva Jr. & Martins (1999)
64	*C. c. calvus*	-5.0833	-67.1667	Lago Fortuna (left bank of Rio Juruá), Carauari, Amazonas, Brazil	Peres (1988, 1993, 1997)

upper Rio Moaco, a right-bank tributary of the Rio Pauini (Fig. 5). They were found throughout the right (east) bank of the Rio Tarauacá up to its confluence with the Rio Juruá (Fig. 5). Although the precise limits of the geographic range of these populations are not clear, we estimated an area of about 30,028 km².

Cacajao c. rubicundus

The geographic distribution of *Cacajao c. rubicundus* is delimited by the flooded forests of the Rio Solimões. The EOO is estimated to be 10,291 km² (Fig. 4), although this subspecies occurs in three restricted and disjunct populations (Fig. 6). The first is in the flooded forests delimited by the Jacurapá channel (*paraná*) and the Rio Solimões (Fig. 6), estimated to be 2,328 km². The Jacurapá channel is a right-bank tributary of the lower Rio Içá that extends about 150 km to the west. During our surveys in the Içá-Solimões interfluvia, we recorded *C. c. rubicundus* only along the Jacuarapá channel, even though we surveyed from the mouth of the Rio Içá to the Rio Puretê, near the Brazil-Colombia border. We did not register bald uakaris during surveys in the Juamí-Japurá Ecological Station (Fig. 2, Area 1, see also Fig. 6), on the north bank of the Rio Içá. Local people reported emphatically that the Jacurapá channel was the only place where uakaris occur in that region, on the north bank of the Rio Solimões, opposite the town of São Paulo de Olivença, which is the type locality of the subspecies (see Table 3, locality 1).

There is another *C. c. rubicundus* population on the left bank of the Rio Jutaí, about 40 km from the Jacurapá channel on the south bank of the Rio Solimões. We estimated the range of this population to be 1,396 km², although further surveys are needed on the right bank of the Solimões to confirm their range to the south. A third population of *C. c. rubicundus* occurs along the Auati-Paraná, a channel that connects the Rio Solimões to the Rio Japurá. This region is about 100 km northeast of the population on the left bank of the Rio Jutaí, and about 270 km east of that of the Jacurapá

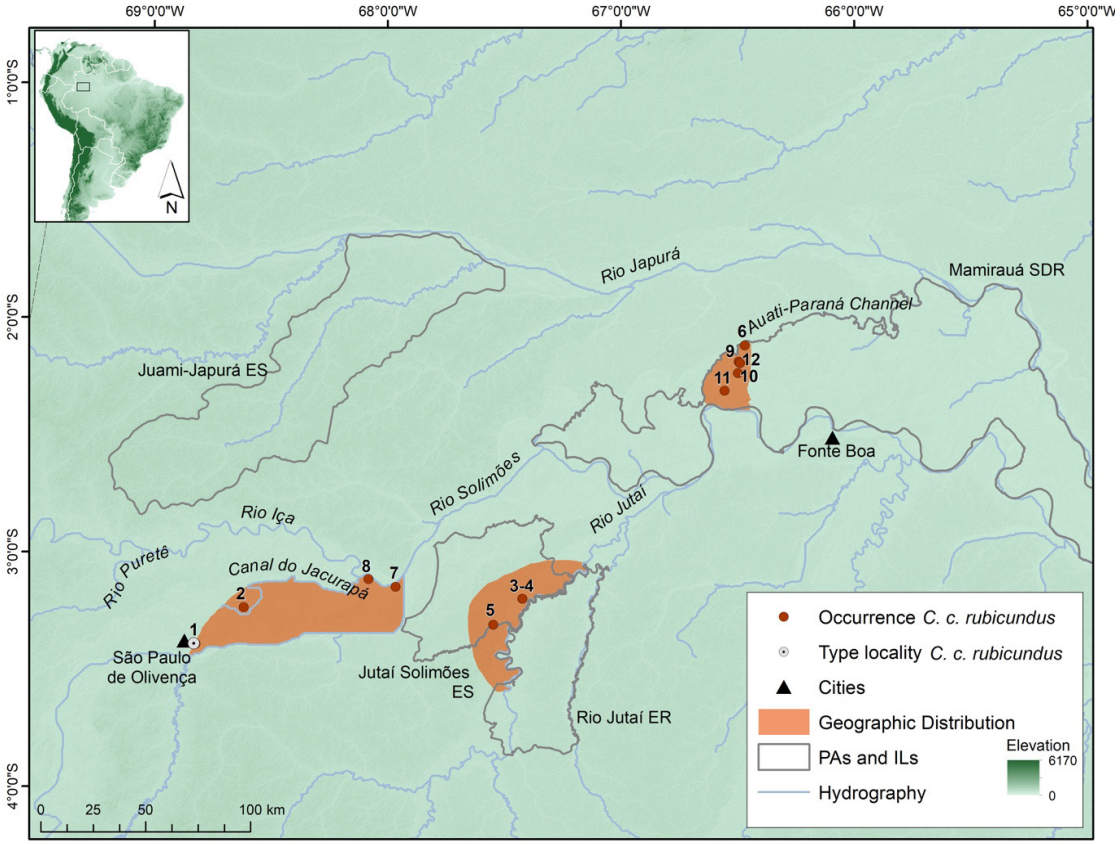

Figure 6. The geographic distribution of *Cacajao c. rubicundus*. PAs: Protected Areas; ILs: Indigenous lands. The localities are listed in Table 3.

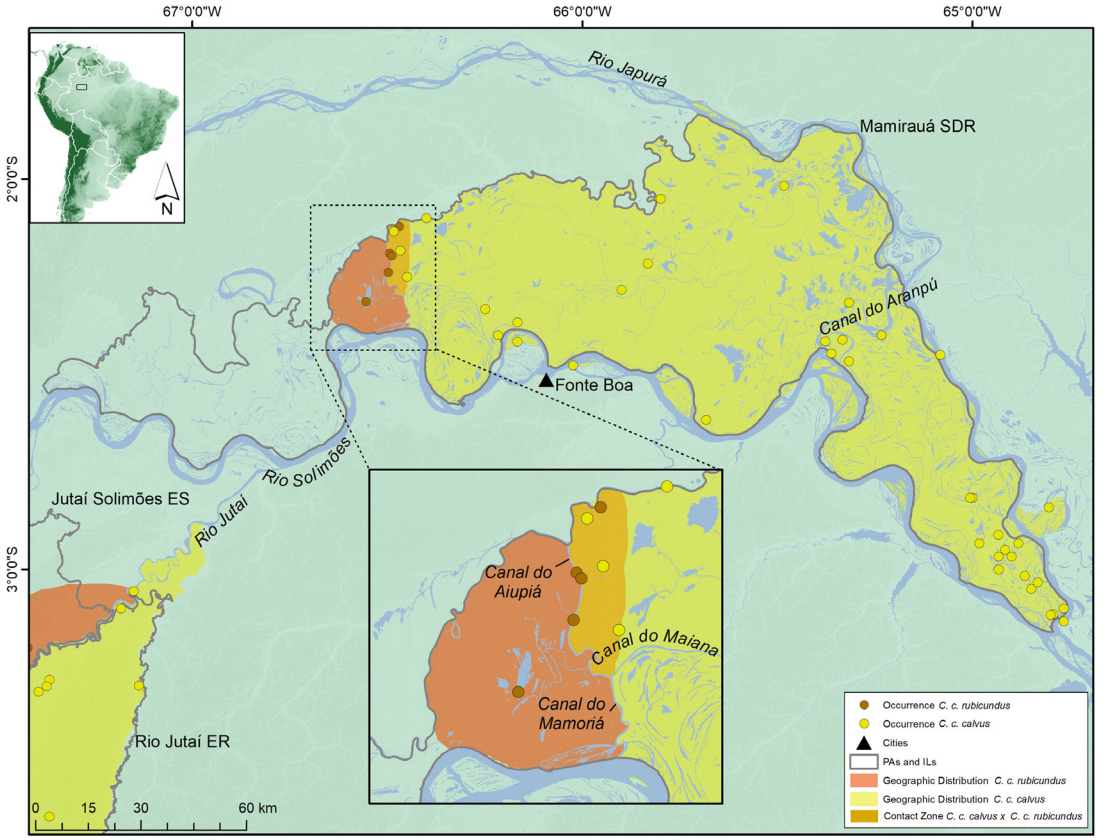

Figure 7. Contact zone between *C. c. calvus* and *C. c. rubicundus*. PAs: Protected Areas; ILs: Indigenous lands.

Table 3. The occurrence records of *Cacajao c. rubicundus*. In bold, the type locality, no. 1. The localities are shown in Figure 6.

	Taxon	Latitude	Longitude	Locality	Reference
1	***C. c. rubicundus***	**-3.3920**	**-68.8250**	**São Paulo de Olivença, opposite, north bank Rio Solimões, Amazonas, Brazil**	**Hershkovitz (1987)**
2	*C. c. rubicundus*	-3.2369	-68.6181	Jacurapá channel (right-bank tributary of Rio Içá), Amazonas, Brazil	This study
3	*C. c. rubicundus*	-3.2009	-67.4227	Jutaí-Solimões Ecological Station, Amazonas, Brazil	Silva *et al.* (2017)
4	*C. c. rubicundus*	-3.2008	-67.4226	Jutaí-Solimões Ecological Station, Amazonas, Brazil	Silva *et al.* (2017)
5	*C. c. rubicundus*	-3.3116	-67.5476	Rio Pati (left bank) Jutaí-Solimões Ecological Station, Amazonas, Brazil	Silva *et al.* (2017)
6	*C. c. rubicundus*	-2.1216	-66.4693	Buiussú, Auati-Paraná, Amazonas, Brazil	Ayres (1986); MU-ZUSP 17552 17553
7	*C. c. rubicundus*	-3.1500	-67.9667	Jacurapá channel (right-bank tributary of Rio Içá), Amazonas, Brazil	Hershkovitz (1987)
8	*C. c. rubicundus*	-3.1167	-68.0833	Jacurapá channel (right-bank tributary of Rio Içá), Amazonas, Brazil	Hershkovitz (1987)
9	*C. c. rubicundus*	-2.1900	-66.4942	Igarapé Preto, Paraná do Aiupiá, Amazonas, Brazil	Vieira *et al.* (2008)
10	*C. c. rubicundus*	-2.2392	-66.4975	Igarapé do Itaúba, Paraná do Aiupiá, Amazonas, Brazil	Vieira *et al.* (2008)
11	*C. c. rubicundus*	-2.3142	-66.5550	Lago do Sapateiro, Paraná do Aiupiá, Amazonas, Brazil	Vieira *et al.* (2008)
12	*C. c. rubicundus*	-2.1961	-66.4892	Igarapé Matias, Paraná do Aiupiá, Amazonas, Brazil	Vieira *et al.* (2008)

channel. This is the most restricted population of bald uakaris, occurring in an area estimated at 546 km². *Cacajao c. rubicundus* and *C. c. calvus* have a contact zone along the Aiupiá channel, a south bank tributary of the Auati-Paraná (Vieira *et al.* 2008) (Fig. 7).

Cacajao c. ucayalii

Cacajao c. ucayalii has an estimated EOO of 356,019 km², but also has a disjunct distribution with isolated populations occurring at higher elevations. Most of its range is in the Ucayali-Javari interfluvium, in an area of about 122,611 km². It occurs in an irregular pattern, being absent over large areas (for example, the region between the rios Javari-Mirim and Javari; see Fig. 8).

In Brazil, we recorded a group of more than 30 individuals in terra firma forest at an elevation of 350 m above sea level, on the right back of the upper Rio Moa (Fig. 8, Table 4). This locality is in the Serra do Divisor National Park on the border with Peru. The uakaris there have the reddish pattern described by Hershkovitz (1987) for *C. c. ucayalii*: a "general coloration entirely reddish orange or reddish golden without sharply contrastingly-colored nape or midback" (p.34). This "contrastingly-colored" buffy or whitish nape and mid-back is present only in *C. c. rubicundus* and *C. c. novaesi* (Fig. 9).

Cacajao c. novaesi

The range of *Cacajao c. novaesi* is delimited by the rios Gregório and Tarauacá, occurring in flooded and terra firma forests, in an estimated geographic range of 13,650 km² (Fig. 10). We have only a few records from a handful of localities for this taxon and the EOO may well be underestimated (3,126 km²). There is no evidence, however, of uakaris occurring along the upper rios Gregório and Tarauacá, supporting our geographic range estimate. In the Rio Gregório Extractive Reserve, we registered *C. c. novaesi* on the right bank of the Rio Gregório. We carried out surveys along the Rio Liberdade for 44 days but failed to record any bald uakaris there. We conclude, therefore, that the Rio Gregório is the western limit of the range of *C. c. novaesi*—a finding also supported by reports from local people in both areas. We recorded *C. c. novaesi* on the left bank of the Rio Tarauacá and the Igarapé Preto, a small tributary on the right bank of the Rio Juruá, near its type locality (Rio Eiru) (Figs. 10 and 11; Table 5). We did not record this taxon on the right bank of the Rio Tarauacá, but we did record white uakaris, indicating that the Rio Tarauacá is a significant geographic barrier for bald uakaris.

Discussion

Bald uakaris have a patchy geographic distribution, with isolated and disjunct populations found in all subspecies except *C. c. novaesi*. *Cacajao c. calvus* occurs in flooded and terra firma forests. It has a linear range along the middle Rio Juruá and the lower Rio Jutaí, and our extensive surveys support the absence of this taxon over large areas between the three ranges we identified. White uakaris, *C. c. calvus*, are parapatric with *C. c. novaesi*, along the Rio Tarauacá; and have a contact zone with *C. c. rubicundus* in the Mamirauá SDR (see also Vieira *et al.* 2008). *Cacajao c. rubicundus* is restricted to the flooded forests of the Rio Solimões, occurring in three disjunct populations over a relatively small range. *Cacajao c. ucayalii* has the largest geographic distribution, mostly in Peruvian forests, but we have confirmed this subspecies in Brazilian territory in the Serra

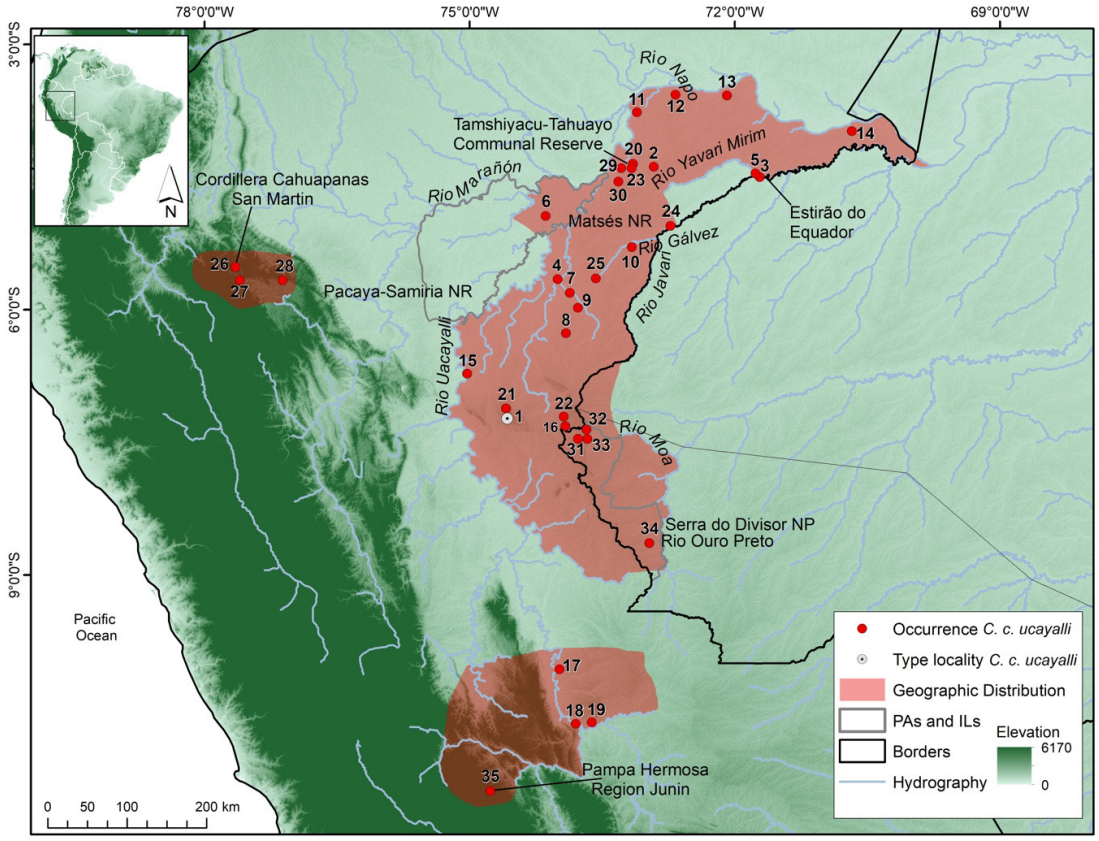

Figure 8. The geographic distribution of *Cacajao c. ucayalii*. PAs: Protected Areas; ILs: Indigenous lands. The localities are listed in Table 4.

Figure 9. The red bald uakaris, adult males, A – *Cacajao c. ucayalii* from the Serra do Divisor National Park (IDSM03678), dorsal; B – *Cacajao c. rubicundus* from the left bank of Rio Jutaí (IDSM00082), dorsal; C – *Cacajao c. novaesi* from the Rio Eiru (MUZUSP 4333), ventral.

do Divisor National Park. It is entirely allopatric and occupies a broad range of habitats, including flooded and terra firma forests (see Heymann and Aquino 2010). *Cacajao c. novaesi* is restricted to the Gregório-Tarauacá interfluvium and has the smallest range among the bald uakaris.

Table 4. The occurrence records of *Cacajao c. ucayalii*. In bold, the type locality, no. 1. The localities are shown in Figure 8.

	Taxon	Latitude	Longitude	Locality	Reference
1	***C. c. ucayalii***	**-7.2333**	**-74.5667**	**Cerro Azul, Contamana, Río Ucayali, Peru**	**Hershkovitz (1987)**
2	*C. c. ucayalii*	-4.3833	-72.9167	Quebrada Blanco, Peru	Aquino & Encarnación (1999)
3	*C. c. ucayalii*	-4.5000	-71.7167	Agua Negra-Carolina, Río Yavarí, Peru	Aquino (1998); Aquino and Encarnación (1999)
4	*C. c. ucayalii*	-5.6550	-74.0036	Río Tapiche, Peru	Bennett *et al.* (2001)
5	*C. c. ucayalii*	-4.4583	-71.7650	Lago Preto Conservation Concession, Peru	Bowler & Bodmer (2009)
6	*C. c. ucayalii*	-4.9389	-74.1406	Quebrada Ahuara, Río Yanayacu, Pacaya-Samiria National Reserve, Peru	Bowler *et al.* (2009)
7	*C. c. ucayalii*	-5.8100	-73.8656	Wiswincho, Río Blanco, Peru	Escobedo Torres (2005)
8	*C. c. ucayalii*	-6.2650	-73.9100	Anguila, Trapiche-Blanco interfluvium, Peru	Escobedo Torres (2005)
9	*C. c. ucayalii*	-5.9767	-73.7736	Quebrada Pobreza, Trapiche-Blanco interfluvium, Peru	Escobedo Torres (2005)
10	*C. c. ucayalii*	-5.2917	-73.1639	Matsés village of Nuevo San Juan, Río Galvez, Peru	Fleck & Harder (2000)
11	*C. c. ucayalii*	-3.7670	-73.1060	Iquitos (opposite), Río Amazonas, Peru	Hershkovitz (1987)
12	*C. c. ucayalii*	-3.5678	-72.6692	Río Napo, opposite mouth at Río Amazonas, Peru	Hershkovitz (1987)
13	*C. c. ucayalii*	-3.5776	-72.0867	Río Orosa, Río Amazonas, Peru	Hershkovitz (1987)
14	*C. c. ucayalii*	-3.9802	-70.6743	Chimbote, Río Amazonas, Peru	Hershkovitz (1987)
15	*C. c. ucayalii*	-6.7225	-75.0289	Sarayacu, opposite, right bank, Río Ucayali, Peru	Hershkovitz (1987)
16	*C. c. ucayalii*	-7.3167	-73.9167	Río Bambo, mouth of Río Tapiche, Peru	Hershkovitz (1987)
17	*C. c. ucayalii*	-10.0667	-73.9833	Río Tahuania, Río Ucayali, Peru	Hershkovitz (1987)
18	*C. c. ucayalii*	-10.6833	-73.8000	Lagarto, Alto Río Ucayali, Peru	Hershkovitz (1987)
19	*C. c. ucayalii*	-10.6667	-73.6167	Río Inuya, Río Urubamba, Peru	Hershkovitz (1987)
20	*C. c. ucayalii*	-4.3500	-73.1500	Reserva Comunal Tamshiyacu-Tahuayo (RCTT), Peru	Heymann & Aquino (1994)
21	*C. c. ucayalii*	-7.1160	-74.5885	Ojo de Contaya, Serra del Divisor, Peru	Jorge & Velazco (2006)
22	*C. c. ucayalii*	-7.2085	-73.9345	Tapiche, Serra del Divisor, Peru	Jorge & Velazco (2006)
23	*C. c. ucayalii*	-4.4000	-73.1667	Communal Reserve Tamshiyacu-Tahuayo, Quebrada Cuchara, Peru	Leonard & Bennett (1996); Aquino (1998)
24	*C. c. ucayalii*	-5.0514	-72.7283	Quebrada Curacinha, Río Yavari, Peru	Salovaara *et al.* (2003)
25	*C. c. ucayalii*	-5.6464	-73.5707	Reserva Nacional Matsés, Alto Río Gálvez, Peru	Torres-Oyarce *et al.* (2017)
26	*C. c. ucayalii*	-5.5167	-77.6500	Candamo, Cordillera Cahuapanas, Peru	Vermeer *et al.* (2013)
27	*C. c. ucayalii*	-5.6667	-77.6000	Aguas Verdes Cordillera Cahuapanas, Peru	Vermeer *et al.* (2013)
28	*C. c. ucayalii*	-5.6667	-77.1167	Kusu Cordillera Cahuapanas, Peru	Vermeer *et al.* (2013)
29	*C. c. ucayalii*	-4.4000	-73.2833	Quebrada Tangarana, Río Tahuayo, Peru	Ward & Chism (2003)
30	*C. c. ucayalii*	-4.5500	-73.3167	Quebrada Tahuaillo, Río Tahuayo, Peru	Ward & Chism (2003)
31	*C. c. ucayalii*	-7.4589	-73.7744	SDNP - Sítio Norte 5, Brazil	Calouro (1999)
32	*C. c. ucayalii*	-7.3564	-73.6781	SDNP - Sítio Norte 6, Brazil	Calouro (1999)
33	*C. c. ucayalii*	-7.4614	-73.6679	SDNP - Rio Moa, Brazil	This study
34	*C. c. ucayalii*	-8.6398	-72.9660	SDNP - Rio Ouro Preto, Brazil	Lopes & Rehg (2003)
35	*C. c. ucayalii*	-11.4415	-74.7649	San Antonio village, Región Junín, Peru	McHugh *et al.* (2019)

The only subspecies of bald uakari that occurs at higher-elevations is *C. c. ucayalii*, being recorded in the Sierras de Contamana at 600–700 m above sea level (Aquino *et al.* 2005; Heymann and Aquino 2010), the mountains of the Cordillera Cahuapanas at about 1,400 m above sea level) (Vermeer *et al.* 2013) and the Sierra del Divisor in Peru and Brazil (Jorge and Velazco 2006; Heymann and Aquino 2010). The reported flexibility in their habitat requirements (Peres 1997; Heymann and Aquino, 2010) may be the key to their maintaining isolated populations in these areas.

Although our record for the Serra do Divisor confirms the occurrence of *C. c. ucayalii* in Brazil, we did not survey the region of Estirão do Equador, on the right bank of the Rio Javari where specimens were collected in 1960s (MPEG 1848-1854). Reports from local people indicate that uakaris occur only on the left bank of the Rio Javari (Peruvian

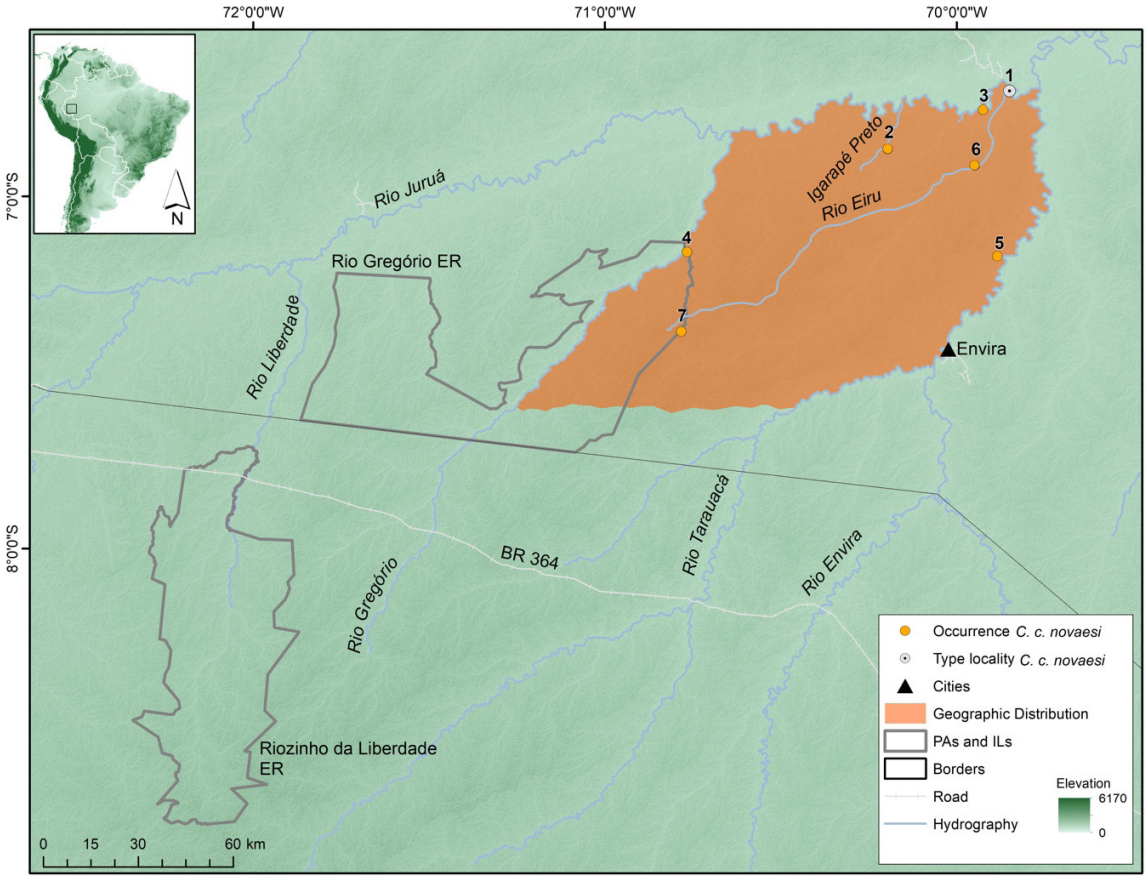

Figure 10. The geographic distribution of *Cacajao c. novaesi*. PAs: Protected Areas; ILs: Indigenous Land. The localities are listed in Table 5.

Table 5. The occurrence records of *Cacajao c. novaesi*. In bold, the type locality, no. 1. The localities are shown in Figure 10.

	Taxon	Latitude	Longitude	Locality	Reference
1	***C. c. novaesi***	**-6.7000**	**-69.8500**	**Santo Antonio, Rio Eiru, Amazonas, Brazil**	**Hershkovitz (1987)**
2	*C. c. novaesi*	-6.8643	-70.1958	Igarapé Preto, Rio Juruá (right bank), Amazonas, Brazil	This study
3	*C. c. novaesi*	-6.7532	-69.9248	Igarapé Lontra, Rio Juruá (right bank), Amazonas, Brazil	This study
4	*C. c. novaesi*	-7.1577	-70.7670	Igarapé Coatá, Rio Gregório (right bank), Amazonas, Brazil	This study
5	*C. c. novaesi*	-7.1699	-69.8858	Comunidade Sobral, Rio Tarauacá (right bank)	This study
6	*C. c. novaesi*	-6.9109	-69.9488	Santa Cruz, Rio Eiru, Amazonas, Brazil	MUZUSP series
7	*C. c. novaesi*	-7.3833	-70.7833	Santa Cruz, Rio Eiru, Amazonas, Brazil	Hershkovitz (1987)

territory). It is possible, therefore, that these specimens were collected there and brought to Estirão do Equador – in the Brazilian territory (Mark Bowler, pers. comm.). Surveys throughout the Río Yavarí are still needed to confirm if this subspecies occurs on the right bank of this river in Brazil.

Our field survey in the Baixo Juruá Extractive Reserve and reports of local people indicate that uakaris do not occur along the lower Rio Juruá, from Carauari to its confluence with the Rio Solimões (see Fig. 4) (see also Cardoso *et al.* 2014). The populations of white uakaris from the rios Tarauacá and Pauini are more than 250 km from those of the middle Rio Juruá and lower Rio Jutaí, and about 650 km from the Mamirauá SDR. The two records of white uakaris (localities 8 and 15, Table 2, Fig. 5) on the right bank of Rio Juruá may be explained by the meandering characteristic of this river, which can promote the isolation of subpopulations on opposite riverbanks. Indeed, these were the only two records of white uakaris after 289 days of sampling effort on the right bank of the middle Rio Juruá. The meander cut off may also have isolated a population of white uakaris on the left bank of the Rio Japurá (locality 2, Table 2, Fig. 5), in the Amanã Sustainable Development Reserve.

Figure 11. *Cacajao c. novaesi* from the Igarapé Preto, state of Amazonas (see Fig. 10). Photograph by Marcelo I. Santana.

Another point, particularly relevant to the Rio Juruá, is that the dynamic geological and sedimentary activity in the western Amazon rainforest has caused an ongoing change in the river network (Ruokolainen *et al.* 2019; Pupim *et al.* 2019). The meandering water course and intense sedimentary activity of this river are noticeable by the avulsions identified in that region, which mark changes in the routes of the rivers over the last 50,000 yrs (Ruokolainen *et al.* 2019). One of these avulsions marks the course of the Rio Juruá toward the lower Rio Jutaí during the Quaternary (Fig. 13, see also Ruokolainen *et al.* 2019). The available evidence, therefore, points to an occurrence of *C. c. calvus* from the Riozinho-Jutaí interfluvium to the left bank of the middle Rio Juruá following this avulsion (Fig. 13).

Problems of taxon identification and inaccurate information on the occurrence and distribution of uakaris imply erroneous species' lists for protected areas, misinforming as such assessments of conservation status, and besides confusing interpretations of species diversity. For example, Figueiredo-Ready *et al.* (2013) carried their phylogenetic and phylogeographic analysis of *Cacajao* with just the few samples available in scientific collections at the time. In their analysis, however, two were misidentified as "*Cacajao calvus novaesi*" (i.e., INPA5241 and UFPA-Ccn1). The INPA5241 specimen is a white uakari, *C. c. calvus*, collected on the right bank of the Rio Tarauacá (Fig. 12). The UFPA-Ccn1 sample is not represented in any material in a scientific collection but the locality assigned for the sample UFPA-Ccn1 is the left bank of the Rio Juruá, near the town of Carauari (Fig. 2), the region where white uakaris were misidentified as *C. c. novaesi* years before, as already mentioned. This perhaps resulted in the authors' conclusion that the phylogeny of bald uakaris "is consistent with geographic but not morphological patterns" (Figueiredo-Ready *et al*. 2013; p.26).

Our data show that disjunct distributions are common in bald uakaris. Some possibilities have been raised to explain this pattern, but without any specific research. Limited sampling, especially in remote areas, was thought to be an explanation of the discontinuities in the geographic distribution of bald uakaris (Cardoso *et al.* 2014), which is reasonable considering the paucity of studies on *Cacajao* in only a handful of field sites. Nevertheless, we found evidence

Figure 12. *Cacajao calvus calvus*. A – The specimen INPA5241, an immature male from the upper Rio Tarauacá misidentified as *novaesi* by Figueiredo-Ready *et al*. (2013). B – An adult male from the Mamirauá SDR (MNRJ 1705). C – An adult male from the Rio Jurupari, reported by Silva Jr and Martins (1999).

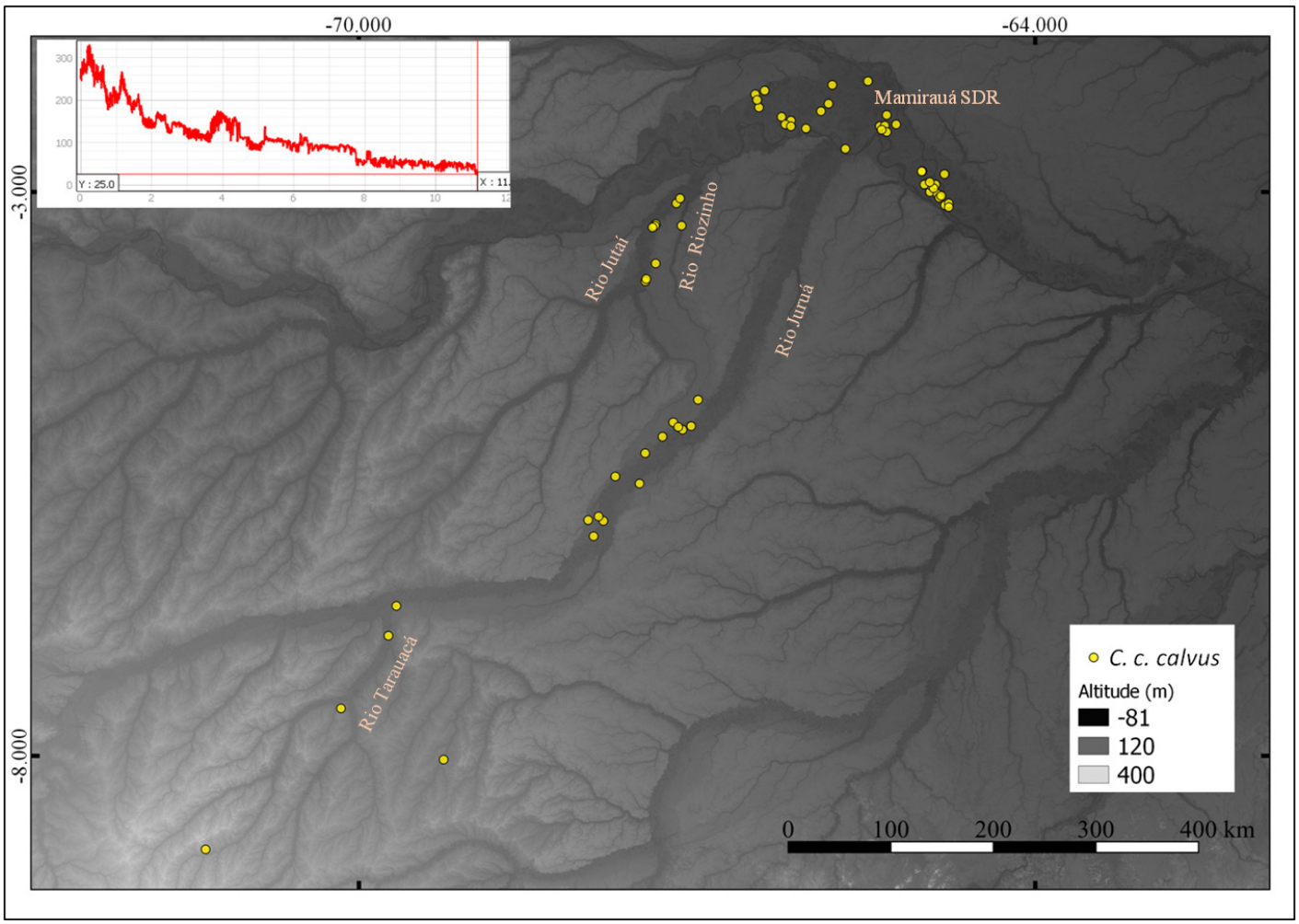

Figure 13. The topographic profile of the geographic distribution of *Cacajao c. calvus*. While the southern populations occur in unflooded forests (terra firma) of 300 m above sea level, the northern populations are restricted to seasonal flooded forests (*várzeas*).

from the field surveys that bald uakari populations can be found hundreds of kilometers apart from each other (also see, for example, Vermeer *et al.*, 2013).

Now that the disjunct distributions of bald uakaris have been found to be real, studies on their ecology and behavior are essential to shed light on the key resources maintaining them in the different floristic communities where they occur. One essential plant family in the feeding ecology of the genus *Cacajao* is the Lecythidaceae (Ayres and Prance 2013). These plants produce fruits with hard husks, and the immature fruits are available to these seed predator specialists in periods of fruit scarcity (especially the dry season) (Ayres and Prance 2013). Monitoring of the potential effects of climate change and habitat degradation on the productivity, phenology, and mortality of members of the Lecythidaceae could shed light on the extent to which uakaris will be affected. The disjunct distribution and the isolation of some populations provide a unique opportunity to understand which ecological singularities of each field site may have influenced the evolution of adaptations to the different climatic patterns of the past and which may be essential for future scenarios.

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Appendix

Material examined (Total 103 vouchers) in the following zoological collections: Instituto de Desenvolvimento Sustentável Mamirauá (**IDSM**); Instituto Nacional de Pesquisas da Amazônia (**INPA**); Museu de Zoologia, Universidade de São Paulo (**MUZUSP**); Museu Paraense Emílio Goeldi (**MPEG**); Museu Nacional, Universidade Federal do Rio de Janeiro (**MNRJ**); and the Field Museum of Natural History (**FMNH**).

Cacajao calvus calvus *(N = 43):*

- ✓ Mamirauá Sustainable Development Reserve, Amazonas, Brazil: IDSM_03174, IDSM_0519, MNRJ_1706, MNRJ_1591, MNRJ_1595, MNRJ_1599, MNRJ_1703, MNRJ_1704, MNRJ_1705, MNRJ_2441, MNRJ_2442, MNRJ_2444, MNRJ_2445, MNRJ_2447, MNRJ_2452, MUZUSP_17535, MUZUSP_17539, MUZUSP_17536, MUZUSP_17537, MUZUSP_17542;
- ✓ Rio Jutaí Extractive Reserve, Amazonas, Brazil: IDSM_0003, IDSM_0040, IDSM_0784, IDSM_0785, IDSM_0786, IDSM_0787;
- ✓ Rio Juruá, Brazil: MPEG_0576; São Pedro, Rio Japurá, Amazonas, Brazil: MUZUSP_17545, MUZUSP_17538; INPA_0212;
- ✓ Igarapé Grande, São Romão, right bank of the Rio Tarauacá, Amazonas, Brazil: IDSM_03668, IDSM_03674, IDSM_03675;
- ✓ Lago Tucumã, right bank of the Rio Tarauacá, Amazonas, Brazil: IDSM_03676;
- ✓ Sacado do Tarauacá, Acre, Brazil: INPA_05241;
- ✓ Rio Pauini, Amazonas, Brazil: INPA_07276, INPA_07279, INPA_07280;
- ✓ Rio Jurupari, right bank, Amazonas, Brazil: MPEG_21861, MPEG_21862, MPEG_21863;
- ✓ Unknown locality: INPA_0212, MUZUSP_03734.

Cacajao rubicundus rubicundus (N = 8):

- ✓ Jutaí-Solimões Ecological Station, Amazonas, Brazil: IDSM_0082, IDSM_0083, IDSM_0788;
- ✓ Jacurapá channel, right bank tributary of Rio Içá, Amazonas, Brazil: IDSM_03665, IDSM_03666, IDSM_03667;
- ✓ Buiuçu, Auatí-Paraná, Amazonas, Brazil: MUZUSP_17552, MUZUSP_17553.

Cacajao calvus ucayalii *(N = 32):*

- ✓ Alto Yavari Mirim, Loreto, Peru: FMNH_88810, FMNH_88811, FMNH_88812, FMNH_88813, FMNH_88814, FMNH_88815, FMNH_88816, FMNH_88817, FMNH_88818, FMNH_88819, FMNH_88820, FMNH_88821, FMNH_88822, FMNH_88823, FMNH_88824, FMNH_88825;
- ✓ Chimbotes, Peru: MPEG_0461, MPEG_0468;
- ✓ Río Napo, Peru: MPEG_0462, MPEG_0049, MPEG_0499, MPEG_0506, MPEG_0511, MPEG_0512;
- ✓ Serra do Divisor National Park, Acre, Brazil: IDSM_03678, IDSM_03679;
- ✓ Rio Javari, Estirão do Ecuador, Amazonas, Brazil(?): MPEG_1848, MPEG_1849, MPEG_1850, MPEG_1852, MPEG_1853, MPEG_1854.

Cacajao calvus novaesi *(N = 20):*

- ✓ Igarapé Preto, right bank of the Rio Juruá, Amazonas, Brazil: IDSM_03669, IDSM_03670, IDSM_03671;
- ✓ Igarapé Lontra, right bank of the Rio Juruá, Amazonas, Brazil: IDSM_03672, IDSM_03673;
- ✓ Santa Cruz, Rio Eiru: MUZUSP_04149, MUZUSP_04150, MUZUSP_04151, MUZUSP_04330, MUZUSP_04331, MUZUSP_04332, MUZUSP_04333, MUZUSP_04334, MUZUSP_04335, MUZUSP_04336, MUZUSP_04337, MUZUSP_04338, MUZUSP_04339, MUZUSP_05496, MUZUSP_9701.