

# Relationships between food shortages, endoparasite loads and health status of golden-headed lion tamarins (*Leontopithecus chrysomelas*)

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Abstract: Both anthropogenic actions and abiotic parameters, such as rainfall, temperature and photoperiod, can affect fruit and flower availability for animals, which consequently affects nutritional status and thus animals' health. Herein, we investigated whether abiotic factors are related to changes in fruit availability that can lead to changes in feeding behavior and, consequently, in endoparasite load and general health status in two groups of goldenheaded lion tamarins (Leontopithecus chrysomelas) living in degraded fragments of Atlantic forest in Southern Bahia, Brazil. We detected that there was a high variation in availability of ripe fruits throughout the year, with lower availability occurring at the end of spring and beginning of summer. Despite this, there was no difference in tamarins' general health status, body mass and blood counts between seasons. This is probably because during native fruit scarcity, the tamarins eat cultivated species, such as banana (Musa spp.) and jackfruit (Artocarpus heterophyllus). Temperature and daylength were negatively correlated with golden-headed lion tamarin endoparasite loads. Contrary to our expectations, endoparasite loads are not linked to fruit scarcity and consequent changes in feeding behavior. Nevertheless, we found higher parasite diversity in the group of golden-headed lion tamarins that occupied the smallest home range. The smaller the area available, the greater the contact with parasites the animal will have, as they are forced to travel constantly along the same routes in the forest, increasing infection risk and re-infection rates. Our results highlight how animals' health is associated with environmental health as well as the need for constant monitoring to ensure the effective conservation of endangered species, such as the golden-headed lion tamarin.

Keywords: biodiversity loss; conservation; fruit availability; one health; parasites; primates.

# Relações entre escassez alimentar, carga endoparasitária e estado de saúde do mico-leão-de-cara-dourada (*Leontopithecus chrysomelas*)

**Resumo:** Parâmetros abióticos, como precipitação, temperatura e fotoperíodo, podem afetar a disponibilidade de frutos e flores para os animais, o que consequentemente afeta o estado nutricional e a saúde dos animais. Neste estudo, investigamos se fatores abióticos estão relacionados com alterações na disponibilidade de frutos, o que pode levar a mudanças no comportamento alimentar e, consequentemente, na carga de endoparasitas e estado de saúde geral em dois grupos de mico-leão-de-cara-dourada (*Leontopithecus chrysomelas*) que vivem em fragmentos degradados de Floresta Atlântica no sul da Bahia, Brasil. Detectamos que houve grande variação na disponibilidade de frutos maduros ao longo do ano, com menor disponibilidade no final da primavera e início do verão. Apesar disto, não houve diferenças no estado geral de saúde, na massa corporal ou nas contagens de células sanguíneas dos animais entre as estações do ano. Isto provavelmente ocorreu porque durante a escassez de frutos nativos, os micos comem espécies cultivadas, tais como a banana (*Musa* spp.) e jaca (*Artocarpus heterophyllus*). A temperatura e a duração do dia foram negativamente correlacionadas com a carga de endoparasitas de mico-leão-de-cara-dourada. Contrário ao previsto, a carga de endoparasitas não está ligada à escassez sazonal de frutos e consequentes mudanças no comportamento alimentar. Entretanto, encontramos maior diversidade de endoparasitas

no grupo de mico-leão-de-cara-dourada que usou uma área de vida menor. Quanto menor a área disponível, maior o contato com parasitas, porque os micos são forçados a se deslocar constantemente pelas mesmas rotas na floresta, aumentando o risco de infecção e as taxas de reinfecção. Nossos resultados destacam como a saúde dos animais está associada à saúde ambiental, bem como a necessidade de monitoramento constante para a conservação eficaz das espécies ameaçadas de extinção, como o mico-leão-de-cara-dourada.

Palavras-chave: perda de biodiversidade; conservação; disponibilidade de frutos; saúde única; parasitas; primatas.

#### Introduction

Abiotic factors, such as rainfall (Opler et al. 1976), temperature (Williams-Linera 1997), photoperiod (Rivera et al. 2002) and soil moisture (Lobo et al. 2003), influence phenological processes in plants, causing fluctuations in fruit and flower availability for animals (Mendoza et al. 2017). Anthropogenic actions, which cause habitat fragmentation, also impact abiotic parameters and fruit availability (Mendoza et al. 2017). Some non-human primate species can change their feeding behavior as a result of food shortage periods caused by both abiotic factors and anthropogenic impact. Howler monkeys (Alouatta palliata mexicana), for example, change their diet, including items with lower nutritional and energy value, increasing the intake of leaves as a strategy to counterbalance the decreased availability of ripe fruits (Asensio et al. 2007). On the other hand, black howler monkeys (Alouatta pigra) increase the time spent foraging on the ground rather than in trees, due to food scarcity in small forest fragments due to human action, exposing themselves to terrestrial predators (Pozo-Montuy & Serio-Silva 2007).

The nutritional alternatives may lead to immunosuppression, resulting in increased susceptibility to parasites (Chapman et al. 2006). When western gorillas (Gorilla gorilla) experience a scarcity of food during the dry season, they usually show higher parasitic load compared to the rainy season and more food availability (Masi et al. 2012). Changes in environmental temperature and rainfall may intensify parasite infection due to increased host biomass or increased exposure to parasite infection stages (Behie et al. 2013). Moreover, environmental changes can influence the ecological balance between vector, parasite and host as well (Daszak et al. 2000, Masi et al. 2012). Chimpanzees (Pan troglodytes schweinferthii) living in degraded forest fragments show increased infection by Oesophagostomun sp., which was associated with intensification of rainfall and decrease in temperature (McLennan et al. 2017). In this regard, efforts should be made to ensure the interpretation of 'animal health' within the One Health concept (Thompson 2013) for wild animals, monitoring deleterious effects of food shortages and investigating the effects on endoparasite load.

The golden-headed lion tamarin (*Leontopithecus chrysomelas*) is endemic to the Atlantic Forest of Southern Bahia, Brazil, and it is classified as an endangered (EN category) species, mainly due to deforestation (Kierulff et al. 2008). Most populations of *L. chrysomelas* are found in degraded areas or in cocoa agroforestry systems, known as *cabruca* (Raboy et al. 2004, Oliveira et al. 2011, Catenacci et al. 2016a). Costa et al. (2020) reported endoparasite infection in groups of golden-headed lion tamarins living in degraded areas, named Degraded Forest fragments embedded within an Agricultural Matrix of pastures (DFAM), but not in populations living in *cabruca*. These authors associate these findings with individual behavioral traits and endoparasite infection, possibly caused both by the intake of infected

insects during food scarcity and by social grooming. Nevertheless, the intake of insects may be associated with abiotic factors, which alter food availability and consequently parasitological cycles, causing increased infection of animals by parasites (Masi et al. 2012). Thus, we will test the hypothesis that reduced fruit availability caused by abiotic factors affects the general health status of golden-headed lion tamarin. Therefore, herein, we aimed to investigate whether abiotic factors (rainfall, temperature and daylength) and fruit availability were related to changes in feeding behavior (exploratory and food intake), general health status and, specifically, endoparasite loads in golden-headed lion tamarins living in degraded areas of Atlantic forest in Southern Bahia, Brazil. If abiotic factors indeed influence fruit availability, we predict greater availability of ripe fruits in the months with higher rainfall, lower temperatures and shorter daylength, as observed in the southeast of Bahia (Pessoa 2008, Pessoa et al. 2012, Catenacci et al. 2016a). Moreover, if fruit availability indirectly influences endoparasite load, as suggested by Costa et al. (2020), we expect that during lower availability of ripe fruits, tamarins will show higher endoparasite infection, because they increase their substrate exploration to supplement feeding with insects, as observed by Guidorizzi (2008). Furthermore, if our previous predictions are confirmed, and if higher endoparasite load results in detrimental effects on general health status of tamarins, as verified by Monteiro et al. (2010), we also expect differences in body mass, clinical measures and blood cell counts between seasons.

### **Material and Methods**

#### 1. Animals and study area

We studied 12 free-living golden-headed lion tamarins (L. chrysomelas) (10 adults and 2 subadults), belonging to two groups - named RIB (N = 6) and MRO (N = 6) - inhabiting fragments of Atlantic Forest (details in Table 1). The number of individuals in each group varied throughout the study period due to events such as births, predation, disappearance and migration to other groups. For instance, the dominant male of the RIB group (82M, Table 1) was preyed upon on December 13th, 2016. Our suspicion that this male underwent predation is based on hearing an alarm vocalization in the forest, after which we did not see the animal again. Sometime later, field assistants found its radio collar on the ground. The day after the predation, another adult male (126M, Table 1) joined the group. In turn, in the MRO group, the number of individuals varied from six to eight in November 2016 with the birth of twins. The data collected on the health and behavior of these infants, however, did not enter into the analyses presented here. At the beginning of the study, we classified as adults those individuals older than 18 months and/or weighing above 550g, following Dietz & Barker (1993); while sub-adults were those between 12 and 18 months, following Miller et al. (2003).

Table 1. Characterization of individual golden-headed lion tamarins in each group.

Animal	Group	Sex	Weight (kg)	Length (mm)	Observations
82M	RIB	М	0.65	610	Breeder
92F	RIB	F	0.69	590	Breeder
93F	RIB	F	0.65	605	Breeder
118M	RIB	Μ	0.61	607	
119F	RIB	F	t	†	
126M	RIB	Μ	0.58	615	
102M	MRO	Μ	0.58	690	Breeder
115M	MRO	Μ	0.63	636	
120F	MRO	F	0.48	565	Subadult
121F	MRO	F	0.43	586	Subadult
125F	MRO	F	0.61	630	
1F	MRO	F	†	t	Breeder

Symbol codes: RIB: Ribeiro; MRO: Manoel Rosa; Sex: M: male; F: female. <sup>†</sup> No data available.

The groups live in a degraded area, named Degraded Forest fragments embedded within an Agricultural Matrix of pastures (DFAM) (Costa et al. 2020) (Figure 1). Besides the cultivation of cocoa (Theobroma cacao), through the traditional system of growing cocoa under the native canopy, which is locally known as 'cabruca', this area is characterized by forest fragments (classified as advanced secondary, medium secondary and initial secondary forest fragments, Figure 1) interspersed with different types of agricultural activities such as horticultural crops (vegetables, medicinal, aromatic, and ornamental plants), pasture, rubber plantation (Hevea brasiliensis) and cupuaçu (Theobroma grandiflorum) (Figure 1). This area belongs to two neighboring private properties (Santo Antônio and Manoel Rosa farms) located in the municipality of Una, Bahia state, Brazil (15°15'52" S, 39°8'46" W). During the study period (Aug/2016 to Aug/2017), the RIB group that lived at Santo Antônio farm occupied 17.7 ha of home range, while the MRO group that lived at Manoel Rosa farm occupied 48.1 ha of home range. Both groups share a common home range area - home



Figure 1. Characterization of the study area, with all the forest types (classified as advanced secondary, medium secondary and initial secondary forest fragments); sites with anthropogenic activities ('cabruca': cocoa (*Theobroma cacao*) under the native canopy, horticultural crops, pasture, rubber plantation (*Hevea brasiliensis*) and cupuaçu (*Theobroma grandiflorum*)); and the home range of the two groups of golden-headed lion tamarins (*L. chrysomelas*) (group Ribeiro: RIB and group Manoel Rosa: MRO) living in Una, Bahia, Brazil.

range overlap – of 3.0 ha (Coutinho 2018). Throughout the observations, we recorded some occasional contacts between the groups. At the time of contact, there were many agonistic vocalizations by all individuals in the groups and chases between males from different groups that, in some cases, ended in fights and bites. On other occasions, in contrast, we also saw copulation between males and females from different groups.

Individuals were captured prior to the start of the study in March 2016 (late summer) and recaptured in September 2016 (late winter) using tomahawk traps (0.48 m length  $\times$  0.15 m width  $\times$ 0.15 m height), baited with bananas, following Dietz et al.'s (1996) procedures. Following capture, we took the animals to a field laboratory where they were anesthetized (10 mg/kg Ketamine and 0.3 mg/kg Midazolam, IM) (see Catenacci et al.2016a) to receive a unique tattoo number, made on the interior part of their right thigh for permanent identification, and a dye mark (Nyanzol Dye®) for field observations. Thereafter, we determined the tamarins' sex, estimated their age and, besides taking blood samples, performed a clinical evaluation. We collected biometric data [body mass (kg), total and tail length (cm)]; and collected other clinical measures during sedation [heart rate (bpm); respiratory frequency (mpm); and body temperature (°C)]. One must take into account that physical restraint and sedation may have affected such measures. Later, we calculated the body mass index, which was determined by the relationship between the tamarin's body mass and size (the body weight in grams divided by the square of the head and body length in cm (excluding the tail) following Soto-Calderón et al. (2016).

We collected blood samples by puncture of the femoral vein, at the arteriovenous plexus in the inguinal region, in a maximum collection volume of 3.0 mL. These samples were stored in sterile 4.0 mL tubes containing EDTA  $K_3$  and cooled for hematological analyses, which took place the day after collection. The hematocrit, leukocytes and the hemoglobin concentration were performed using an automated cell counter (ABX Vetcounter, Horiba<sup>TM</sup>, Montpellier, France). The leukocyte differential count, aiming to determine the percentage of basophils, eosinophils, neutrophil rods, segmented neutrophils, lymphocytes and monocytes, was obtained from the examination of blood smears stained with Panoptic. The reference values used for the evaluation of hematological parameters were based on the intervals established for *Leontopithecus* sp. (Verona & Pissinati 2014).

One adult male of the MRO and two adult males of the RIB group were equipped with a radio collar (model RI-2D, Holohil Ltd., Ontario, Canada) for subsequent monitoring and field observation using radiotelemetry. As a rule, we established that the tamarin needed to weigh over 550 g to receive the radio-collar. Therefore, the radio-collars were placed on the dominant individuals, who were usually the heaviest. Besides being heavier, the chances that the dominant ones would leave the group and thus take the radio-collar were smaller. Tamarins were kept in the field laboratory overnight to ensure complete recovery from anesthesia and were released in the early morning in the same site where they were captured. All procedures were carried out with the assistance of a primate-specialist veterinarian.

#### 2. The abiotic data collection and evaluation of temporal availability of ripe fruits

Daily temperature, total rainfall and daylength data were obtained from the INMET website (www.inmet.gov.br, accessed 18 June 2018)

http://www.scielo.br/bn

for Una-BA Automatic Station (A437). Minimum and maximum temperatures of each day were determined and mean monthly temperature was calculated. To determine the total monthly rainfall, all daily precipitation data were summed. Finally, the mean monthly daylength was calculated based on the time the sun rose and set each day.

We used linear transects to evaluate temporal change in availability of ripe fruits from August 2016 through August 2017. Six transects were made within the home range of the studied groups. Transect size varied between 45 and 225 meters (mean = 155 meters), depending on home range size and format. We marked trees that are part of golden-headed lion tamarins' diet, following Catenacci et al. (2016a) procedures. Six to 10 trees of each species (native or not) were tagged on or near the transects, considering only trees in sites up to five meters on each side of transect, totalizing 129 marked trees, belonging to 14 species. For phenological evaluation, only trees with diameter at breast height (DBH)  $\geq$  5 cm were considered. In order to quantify fruiting phenophase, we considered a scale from zero to four (0 = no fruiting, 1 = between 1%and 25% of tree crown with mature fruits, 2 = between 26% and 50% of tree crown with mature fruits, 3 = between 51% and 75% of tree crown with mature fruits, 4 = between 76% and 100% of tree crown with mature fruits) (Fournier 1974). To correct the differences of crown volume between trees of the same and different species, the intensity index of mature fruits of each tree was multiplied by its diameter at breast height (DBH), producing values without unity for monthly availability of fruits of each tree (Catenacci et al. 2016a). Based on these individual scores, overall fruit availability per month was calculated for all trees monitored along transects.

# 3. Behavioral data collection and parasitological analysis of fecal sample collection

We followed the groups for 12 months in two periods (from August 2016 to January 2017 and March to August 2017) for behavioral observation. Each group was followed for two consecutive days per month, approximately 11 hours per day, resulting in 528 hours of data collection. Data collection started in the morning (approximately 0530 am), using radio-telemetry to localize the tamarins before they woke up in their sleeping site (tree hollows). Thus, groups were followed from the moment animals left the sleeping site until they returned to the same sleeping site or a different one in the late afternoon (approximately 0500 pm). The paint marks of animals disappeared in February 2017 and observations were suspended and resumed in March 2017, following the capture and remarking of the animals.

We collected behavioral data using the focal sampling method (Altmann 1974); each focal lasted 10 min/animal. Collecting 10 minutes of focal animal from the tamarins in the field was very difficult, because sometimes the animal would hide and we could not find it again. Sometimes they walked a lot, making it difficult to follow the focal animal, which led to a pause (time-off) in observation. Some days, we managed to collect two or three rounds for each animal, but on other days it was impossible to collect more than one round per individual. Thus, for the analyses, we standardized one round with all individuals of the group for the analyses (10 min/animal per day), which we had in common for all animals (from both groups) on all collection days. As we observed each group for two days each month, this totaled 20 minutes/animal/month. At the beginning of each observation day, we randomized the order in which animals were observed. If the animal

disappeared from sight, the observation was interrupted and resumed when the animal was visible again. The behaviors of animals were voice-recorded (RR-US450 Panasonic, Ontario, Canada). Later, we calculated the proportion of observation time that each animal spent on specific behavioral patterns (exploration, eating insects and eating fruits) (Table 2).

During behavioral data collection, we also collected feces samples immediately after defecation and stored these on ice-styrofoam for further qualitative and quantitative endoparasite evaluation. Sometimes the feces fell on leaves in the trees, sometimes on the forest floor. When they fell on the forest floor, we collected only the inner portion of the sample to decrease the chances of contamination. At the end of each observation day we weighed the collected feces samples and stored them in 4% formaldehyde for further parasitological analysis (see Monteiro et al. 2007) one week later. The amount of each feces sample ranged from 0.5 to 1.5 g. If more than one feces sample from the same individual was collected at different times of the day, a pool was made with these samples, which were stored in formaldehyde in the same container. The identification of parasite and parasite load (EPG: number of eggs/g of feces) was performed following the modified Ritchie technique, adopted by Monteiro et al. (2003) and Monteiro et al. (2007) for golden lion tamarin (Leontopithecus rosalia).

 Table 2. Behavioral patterns recorded by direct observation of individual golden-headed lion tamarins.

<b>Behavioral patterns</b>	Description
Exploration <sup>†</sup>	Individual manipulates substrates such
	as tree trunks, bromeliads, foliage and
	vines, with hands, in search of food. The
	exploration can be initially visual (visual
	scanning), following manipulation of
	substrates.
Eating insects <sup>†</sup>	Individual grabs, chews, and intakes insects.
Eating fruits <sup>†</sup>	Individual grabs, chews, and intakes fruits.

<sup>†</sup>Adapted from (Raboy & Dietz 2004).

#### 4. Statistical analysis

As the data vary in different scales we log-transformed them and, after applying Ryan-Jones tests, we verified that all data showed normal distribution. Following that, to test our predictions of associations between abiotic factors and fruit availability and between fruit availability and endoparasite infection, we applied a Pearson correlation matrix including the abiotic data (ambient temperature, rainfall and daylength), availability of ripe fruits and parasite loads. We included in this correlation matrix the mean monthly proportion of observation time that the tamarins spent on specific behavioral patterns (exploration, eating insects and eating fruits) as well. Subsequently, we performed linear regression tests to verify the relationships between ambient temperature, daylength and endoparasite loads. We used the student's t-test to compare endoparasite load in the RIB and MRO groups. We also used the student's t-test to compare the tamarins' body mass; body mass index; heart rate (bpm); respiratory frequency (mpm); and body temperature (°C) data of the five tamarins (three females and two males), which we captured in both seasons (late summer vs late winter). Blood counts [hematocrit (%); erythrocytes (×10<sup>6</sup>/µL); hemoglobin (g/dL); leucocytes (%); segmented neutrophils (%); and lymphocytes (%)] between seasons (late summer vs late winter) of three tamarins (two males and one female) captured in both seasons were also compared through t-tests. We used Minitab v. 19.1 software (Minitab Inc., State College, PA) for all analyses, considering  $\alpha < 0.05$ .

#### Results

Total rainfall during the study period was 1338 mm, with rainfall peak in June and July 2017, while October and December 2016 were the driest period of study (Figure 2). The mean ambient temperature did not vary much during the study period (Figure 1), with an annual average of 24.4°C (standard error – SE = 0.5). The mean minimum and maximum monthly temperatures were 21.9°C (SE = 0.1) and 26.5°C (SE = 0.5), respectively. Daylength was higher from October to March (late spring and summer) and lower from May to July (late autumn and winter) (Figure 2).



Figure 2. Mean (+SE) eggs per gram (EPG, left y-axis) in the RIB and MRO groups of golden-headed lion tamarins (*L. chrysomelas*) living in Una, Bahia, Brazil, mean monthly ambient temperature (°C), total monthly rainfall (mm, right y-axis), mean monthly ripe fruit availability (right y-axis) and mean monthly daylength (right y-axis) over the data collection period. All data were log-transformed.

E	<b>S</b>		2	016				2017								
	Species	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug		
Anacardiaceae	Anacardium occidentale									X (42.9)						
Melastomataceae	Henriettea succosa	X (12.2)	X (13)	X (13)	X (37.8)					X (37.8)	X (37)	X (67)	X (106)	X (112)		
	Miconia hypoleuca	X (98.9)	X (89.5)	X (53.1)	X (20.9)			X (15.8)				X (19.5)	X (6.1)	X (21.2)		
	Miconia mirabilis	X (48.7)	X (36.3)		X (9.6)	X (19.2)	X (21.9)			X (15.8)	X (81.3)	X (164)	X (169)	X (130.1)		
Mimosaceae	Inga thibaudiana									X (62.9)	X (9.1)	X (148)	X (116.1)	)		
	Inga edulis											X (21.3)				
Moraceae	Pouroma velutina						X (58.7)	X (33.9)	X (34.6)	X (22.7)	X (64.5)					
	Helicostylis tomentosa	X (17)			X (17)							X (21.4)				
Myrtaceae	t								X (12.8)							
Sapotaceae	Chrysophyllum splendens					X (50.5)					X (71.6)	X (113.8)				
	Pouteria grandiflora								X (53.8)	X (53.8)						

Table 3. Plant species observed with mature fruits (X) and scores of ripe fruit availability (between brackets)\* during phenological survey from August 2016 to August 2017.

\*The fruit availability scores of each tree species were determined by multiplying the intensity index of mature fruits of each tree by its diameter at breast height (DBH). Symbol code: † No data available.

Table 4.	Endoparasites detected in go	lden-headed lion	tamarin grou	ps in Ribeiro
(RIB) aı	nd Manoel Rosa (MRO) grou	ps from August	2016 to Aug	ust 2017.

Occurrence newied	Group									
Occurrence period -	RIB	MRO								
Aug/16	Prostenorchis sp.	Prostenorchis sp.								
Sep/16	Prostenorchis sp.	Prostenorchis sp.								
Oct/16	Prostenorchis sp.	Prostenorchis sp.								
Nov/16	Prostenorchis sp.,	Prostenorchis sp.								
	Trypanoxyuris sp.									
Dec/16	Prostenorchis sp.	Prostenorchis sp.								
Jan/17	Prostenorchis sp.,	Prostenorchis sp.								
	Primasubulura sp.,									
	Spiruridae									
Feb/17	t	t								
Mar/17	t	Prostenorchis sp.								
Apr/17	Prostenorchis sp.,	Negative								
•	Spiruridae									
May/17	Prostenorchis sp.,	Prostenorchis sp.								
	Spiruridae									
Jun/17	Prostenorchis sp.	Negative								
Jul/17	Prostenorchis sp.	Prostenorchis sp.								
Aug/17	Prostenorchis sp.	Prostenorchis sp.								

<sup>†</sup>No data available.

Ripe fruit availability varied over the study period (Figure 2, Table 3). The highest scores of ripe fruit availability happened from April to August 2017, while the lowest scores occurred from October 2016 to January 2017 (Figure 2). There were no significant differences in endoparasite loads between the RIB and MRO groups over the year (t-test = 1.48, p = 0.85, Figure 2). We found the acanthocephalus *Prostenorchis* sp. in both groups in all months, except in April and June 2017 in the MRO group (Table 4). The RIB group showed greater endoparasite diversity in comparison to the MRO group (Table 4). In this group, we found nematodes *Trypanoxyuris* sp., *Primasubulura* sp. and Spiruridae together with *Prostenorchis* sp. (Table 4).

Contrary to what we expected, there was no correlation between ripe fruit availability and insect-eating behavioral pattern ( $r_{Pearson} = 0.08$ , p = 0.809, Table 5). Furthermore, there was no correlation between endoparasite loads and the behavioral pattern of eating insects ( $r_{Pearson} = 0.28$ , p = 0.382, Table 5). However, there was a negative correlation between mean monthly ambient temperature and endoparasite loads ( $r_{Pearson} = -0.73$ , p = 0.007, Table 5). Endoparasite loads increased as ambient temperature decreased, according to the equation 1:

Log y=

 $-6.52 \text{Log x} + 10.39 (\text{F1}, 10 = 11.49, \text{R}^2 = 0.54, \text{p} = 0.007) (\text{Figure 3a})$ 

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#### Food shortages and tamarins' health

Table 5. Pearson correlation matrix (coefficients and p-values) between mean monthly endoparasite loads (EPG: number of eggs/g of feces of tamarins groups), mean monthly environmental temperature (Temp), monthly scores of ripe fruit availability (Availab), mean monthly daylength (Daylength), total monthly rainfall (Rainfall), and mean monthly proportion of observation time that the tamarins spent on specific behavioral patterns (Explor: exploratory behavior; Insects: eating insects; Fruits: eating fruits) of golden-headed lion tamarins living in degraded fragments of Atlantic forest in Southern Bahia.

Variables	EPG	Temp	Availab	Rainfall	Daylength	Explor	Insects
Temp	-0.73 (0.007)						
Availab	0.54 (0.069)	-0.40 (0.193)					
Rainfall	0.22 (0.491)	-0.20 (0.533)	0.58 (0.048)				
Daylength	-0.61 (0.036)	0.48 (0.112)	-0.54 (0.069)	-0.74 (0.006)			
Explor	0.23 (0.464)	-0.05 (0.884)	-0.36 (0.247)	-0.33 (0.298)	0.07 (0.841)		
Insects	0.28 (0.382)	-0.23 (0.466)	0.08 (0.809)	-0.52 (0.085)	0.04 (0.898)	0.47 (0.121)	
Fruits	0.21 (0.521)	-0.10 (0.779)	0.39 (0.210)	0.19 (0.558)	-0.22 (0.485)	-0.12 (0.722)	0.21 (0.509)

\*Items in bold are those significant (p < 0.05).



Figure 3. Relationship between mean monthly ambient temperature (°C) (a), mean monthly daylength (b), and endoparasite load (EPG: eggs per g) in golden-headed lion tamarins (*L. chrysomelas*). All data were log-transformed.

	Data co	llection		
Parameters	Late summer	Late winter	t-value	p-value
Clinical measures $(n = 5)$				
Body mass	581 (25)	538 (48)	0.80	0.459
Body mass index	0.01 (0.00)	0.01 (0.00)	-0.28	0.786
Heart rate (bpm)	251.2 (16.0)	244.8 (26.0)	0.21	0.840
Respiratory frequency (mpm)	45.6 (7.4)	50.4 (3.2)	-0.59	0.580
Body temperature (°C)	37.7 (0.2)	37.0 (0.2)	2.21	0.062
Blood counts $(n = 3)$				
Hematocrit (%)	37.2 (1.8)	40.0 (1.9)	-1.05	0.373
Erythrocytes (x10 <sup>6</sup> /µL)	5.6 (0.2)	5.8 (0.3)	-0.64	0.565
Hemoglobin (g/dL)	12.7 (0.7)	12.8 (0.6)	-0.14	0.894
Leukocytes (%)	7.1 (1.5)	7.5 (1.0)	-0.23	0.834
Segmented neutrophil (%)	80.3 (5.5)	77.7 (4.1)	0.39	0.724
Lymphocyte (%)	17.3 (5.0)	19.7 (4.4)	-0.35	0.751

Table 6. Means (standard error) of clinical measures and blood counts of golden-headed lion tamarins living in degraded fragments of Atlantic forest in Southern Bahia according to the season.

There was also a negative correlation between daylength and endoparasite loads ( $r_{Pearson} = -0.61$ , p = 0.036, Table 5). Endoparasite loads increased as daylength decreased, according to the equation 2:

Log y =

-8.55Log x + 25.80(F1,10 = 0.84, R<sup>2</sup> = 0.37, p = 0.036)(Figure 3b)

There was a trend of positive correlation between endoparasite loads and ripe fruit availability ( $r_{pearson} = 0.54$ , p = 0.069, Table 5), with a tendency of higher endoparasite parasite loads in winter months with higher ripe fruit availability. Despite that, endoparasite loads were not correlated with the behavioral pattern of eating fruits ( $r_{pearson} = 0.21$ , p = 0.521, Table 5). Moreover, endoparasite loads were neither correlated with rainfall ( $r_{pearson} = 0.22$ , p = 0.491) nor with the behavioral pattern of exploration ( $r_{pearson} = 0.23$ , p = 0.464, Table 5).

All animals appeared in general good health during the clinical examination performed after the captures in late summer and late winter. Both the body mass and body mass index did not differ between seasons (Table 6). There was also no difference between the seasons for the heart rate, respiratory frequency, and body temperature (Table 6); nor were there differences in blood counts between seasons (Table 6).

#### Discussion

Although we did not record a great variation in the ambient temperature in southern Bahia, which remained around 24°C throughout the year, we found a negative correlation between temperature and parasite load. The golden-headed lion tamarin showed higher parasite load during the winter and relatively colder months. Additionally, daylength influenced endoparasite infections as well. The precise reasons for these associations, and their causal direction, cannot be determined from the current data. Further research may indicate whether the increase in endoparasite loads during the months of lower temperatures and with shorter days occurs due to a drop in animals' immune system, as reported for other mammals, including humans (Dowell 2001). Furthermore, physiological changes due to alteration in photoperiod may explain the host's increased susceptibility to pathogens during colder periods (Dowell 2001).

Our study shows that periods of higher ripe fruit availability occurred during the months with higher rainfall. This result follows the general pattern described for tropical forests. In tropical forests, there is usually higher ripe fruit availability during the rainy season (Van Schaick et al. 1993, Mendoza et al. 2017). In agreement with our prediction, ripe fruit availability was higher from the end of fall and during the rainy winter months (from April to August), as previously recorded for this area (Pessoa 2008, Catenacci et al. 2016a). From March, when the days are getting shorter, the availability of ripe fruits begins to increase, and this peaks in June. In this period, the fruits with most availability were from the families Melastomataceae and Mimosaceae. These results may explain the trend of increased ripe fruit availability along with the decrease in daylength.

Differently from our prediction, there was no correlation between ripe fruit availability and endoparasite loads. Additionally, we found no correlation between the intake of insects along with the decrease in the availability of ripe fruits. This last result contradicts the reports of Guidorizzi (2008) on increased searching for insects by the golden-headed lion tamarin due to decreased availability of ripe fruits in semideciduous forest. The relationship between lower ripe fruit availability and intake of other food items, such as the intake of insects, could lead to greater infection by parasites with an indirect life cycle (Gillespie et al. 2005, Kalousová et al. 2014). However, the consumption of these invertebrates occurs throughout the year in ombrophilic forest, as observed by Catenacci et al. (2016a). Therefore, throughout the year animals can become infected with endoparasites, as the consumption of only one infected insect is enough to promote an increase in the parasitic load. Moreover, differences in floristic, climatic and anthropogenic pressures in these two habitats can influence the pattern of consumption of fruits and invertebrates by the golden-headed lion tamarin inhabiting these different forest types (Guidorizzi 2008).

Greater endoparasite diversity was found in the RIB group when compared to the MRO. Some of these endoparasites (Spiruridae, *Primasubulura* sp. and *Prosthenorchis* sp.) are usually transmitted by the ingestion of infected invertebrates (Stunkard 1953, Melo 2004). Additionally, *Trypanoxyuris* sp., which was also found in tamarins from the RIB group, is transmitted to the host by ingestion of fecal material contaminated with parasite eggs (Stuart et al. 1998). One possible explanation for the greater parasite diversity in the RIB group, and not tested herein, is the smaller home range (17.7 ha) occupied by this group in comparison with the MRO group (48.1 ha) (Coutinho 2018). Previous studies have showed that the smaller the area available, the greater the contact with parasites the animal will have, because they are forced to travel constantly along the same routes in the forest, increasing infection risk and re-infection rates (Gillespie et al. 2005, Gillespie & Chapman 2008, Nunn et al. 2011).

*Prosthenorchis* sp., the most common endoparasite detected in goldenheaded lion tamarins, is usually present in primate species (Chandler 1953, Machado-Filho 1950; Stoner et al. 2005) and other mammals, such as carnivores (Pérez et al. 2013). This acanthocephalus parasite is associated with severe intestinal disorders, and may lead to the death of the host (Melo 2004, Pissinatti et al. 2007, Catenacci et al. 2016b). This parasite is mainly found in areas with greater anthropogenic disturbance when compared to more conserved environments (Catenacci et al. 2018), and it could be used as an indicator of environmental health quality. Thus, as previously highlighted by Catenacci et al. (2018), endoparasite evaluation in freeliving primates may allow a better understanding of how animals' health is associated with environmental health. Therefore, further study must be done to compare areas with different levels of anthropogenic disturbance to guarantee the causes of this parasite's presence.

Differently from our prediction as well, despite the high variation in availability of ripe fruits throughout the year, there were no differences in body mass, body mass index (which provides a more accurate measure to assess the body condition of primates in the field), clinical measures, and blood counts of tamarins between seasons. The lack of changes in general health status between relatively dry summers and rainy winters can be explained by the behavioral flexibility of tamarins facing anthropogenic changes in their habitat, as previously highlighted by Catenacci et al. (2016a) and Coutinho (2018). In the present and previous studies (Oliveira et al., 2010, Catenacci et al., 2009, Catenacci et al., 2016a, Coutinho 2018), it was possible to observe that golden-headed lion tamarins are usually observed foraging among the hundreds of plant species they use as a food source, which include both native and exotic species. Thus, in times of native fruit scarcity, the tamarins eat cultivated species, such as the banana (Musa spp.), jackfruit (Artocarpus heterophyllus), and cocoa (Theobroma cacao) (Catenacci et al. 2016a, Coutinho 2018). However, we should consider our results as preliminary, because we were able to collect health status data only from a small number of animals. The small sample size is justified because we used a passive trap (tomahawk traps), which allowed us to collect data from those animals that voluntarily entered the traps in both seasons. Additionally, we were not always able to collect blood samples from all captured individuals. Therefore, further study may confirm our comparisons between seasons with greater and lesser availability of ripe native fruits by monitoring a larger number of individuals throughout the year.

Our results showed that abiotic factors, such as rainfall, temperature and daylength, are related to food availability and/or endoparasite infections in golden-headed lion tamarins. Therefore, these results have important implications for *L. chrysomelas* conservation and health and for further epidemiology studies.

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#### **Author Contributions**

Thaise da Silva Oliveira Costa: Contribute to the study's conception and design, was responsible for material preparation, data collection and analysis, contributed substantially to the interpretation of the data and wrote the initial draft of the manuscript.

Sérgio Luiz Gama Nogueira-Filho: Contribute to the study's conception and design, was responsible for data analysis and contributed substantially to the interpretation of the data as well as to the preparation of the manuscript and critical review of the text.

Kristel Myriam De Vleeschouwer: Contribute to the study's conception and design, and commented on previous versions of the manuscript and revised the text critically.

Luciana Aschoff Coutinho: Contribute to the study's conception and design, and commented on previous versions of the manuscript and revised the text critically.

Selene Siqueira da Cunha Nogueira: Principal Investigator, contribute to the study's conception and design, contributed substantially to the data analysis and interpretation of the data as well as to the preparation of the manuscript and critical review of the text.

#### **Conflicts of Interest**

The authors declare no conflicts of interest.

#### Ethics

All methods used were approved by the Animal Welfare and Ethical Review Body at the University of Bristol (UB/18/032) in accordance with the U.K. Animals (Scientific Procedures) Act, 1986 and associated guidelines, EU Directive 2010/63/EU for animal experiments. Additionally, all methods used were approved by the Committee of Ethics for Animal Use (CEUA) at the Universidade Estadual de Santa Cruz (proc. # 018/2015) and the Brazilian Environmental Agency (ICMBio/SISBIO) (# 23457-6 and # 471783).

# Data Availability

The datasets generated and/or analyzed during the current study are available at:

https://10.6084/m9.figshare.17111867

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# Early larval development of the rock shrimps *Sicyonia dorsalis* Kingsley, 1878 and *S. typica* (Boeck, 1864) (Dendrobranchiata) with remarks of larval morphology of Sicyoniidae Ortmann, 1898

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*Abstract:* The aim of this study was to describe and illustrate the early larval stages, *i.e.*, the complete naupliar development and the first protozoea (PZI) of *Sicyonia dorsalis* and *S. typica* obtained under laboratory conditions. We also provide remarks from a comparative analysis of the morphology of these stages among representatives of the genus and furnish morphological characteristics to distinguish them from another penaeoidean in the plankton. Our results indicate that the naupliar development of *Sicyonia* is composed of five stages (NI to NV). No differences were found in the morphology of the naupliar and PZI stages of the two studied species, even though they are considered phylogenetically distant into the genus. We suspect that morphological differences arise later during ontogenetic development. The comparisons with larval descriptions of congeners revealed that naupliar stages and PZI were very similar, nevertheless, some morphological differences were observed. As illustrated here, there is a clear need of new descriptions of the studied group and generalizations and conclusions of larval morphology patterns at this point need to be made with caution, because data of a still insufficient number of species is available. *Keywords: Decapoda; larval morphology; metanauplius; nauplius; Penaeoidea; protozoea.* 

# Desenvolvimento larval inicial dos camarões-pedra *Sicyonia dorsalis* Kingsley, 1878 e *S. typica* (Boeck, 1864) (Dendrobranchiata) com observações sobre a morfologia larval de Sicyoniidae Ortmann, 1898

**Resumo:** O objetivo deste estudo foi descrever e ilustrar os estágios larvais iniciais, ou seja, o desenvolvimento naupliar completo e a primeira protozoea (PZI) de *Sicyonia dorsalis* e *S. typica* obtidos em laboratório. Também fornecemos observações a partir de uma análise comparativa da morfologia desses estágios entre representantes do gênero e as características morfológicas para distingui-los de outros Penaeoidea no plâncton. Nossos resultados indicam que o desenvolvimento naupliar de *Sicyonia* é composto por cinco estágios (NI a NV). Não foram encontradas diferenças na morfologia dos estágios naupliares e PZI das duas espécies estudadas, apesar de serem consideradas filogeneticamente distantes dentro do gênero. Nossa hipótese é que as diferenças morfológicas surgem mais tarde durante o desenvolvimento ontogenético. As comparações com as descrições larvais de congêneres revelaram que os estágios naupliares e PZI são muito semelhantes, no entanto, algumas diferenças morfológicas foram observadas. Conforme ilustrado aqui, há uma clara necessidade de novas descrições do grupo estudado e generalizações e conclusões de padrões na morfologia larval neste momento precisam ser feitas com cautela, pois dados de um número ainda insuficiente de espécies estão disponíveis.

Palavras-chave: Decapoda; morfologia larval; metanáuplio; náuplio; Penaeoidea; protozoea.

#### Introduction

The monotypic family Sicyoniidae Ortmann, 1898 is one of five families included among the Penaeoidea Rafinesque, 1815, with 52 described species distributed worldwide in tropical and subtropical areas of the Atlantic, Pacific, and Indian oceans (Pérez Farfante & Kensley 1997, De Grave & Fransen 2011). From the nine species already registered in the Atlantic coast of Americas, six occur in Brazilian waters: *Sicyonia dorsa*lis Kingsley, 1878, *Sicyonia typica* (Boeck, 1864), *Sicyonia laevigata* Stimpson, 1871, *Sicyonia parri* (Burkenroad, 1934), *Sicyonia burkenroadi* Cobb, 1971, and *Sicyonia olgae* Pérez Farfante, 1980 (D'Incao 1995, Pérez Farfante & Kensley 1997, De Grave & Fransen 2011). Among these, *S. dorsalis, S. laevigata, S. parri*, and *S. typica* occur in the southeastern subtropical region of Brazil (Costa et al. 2000, Mantelatto et al. 2022).

Sicyonia dorsalis and S. typica have being found in shallow coastal regions, from North Carolina (USA) to Rio Grande do Sul (Brazil) (D'Incao 1995, Mantelatto et al. 2022). Even though rock shrimp species are currently not commercially exploited in Brazil, they are part of the by-catch of penaeid shrimp fisheries of high economic interest (Keunecke et al. 2007, Costa et al. 2016). Sicyonia dorsalis and S. typica are the most abundant sicyoniid species in the bycatch of the trawling of commercial species such as the seabob shrimp Xiphopenaeus spp. Smith, 1869 and the pink shrimp Farfantepenaeus spp. Burukovsky, 1997, respectively (Costa et al. 2005, Costa & Simões 2016). As explained by Carreton et al. (2020), a key aspect of fisheries science is the study of species connectivity, and planktonic larvae directly influence this mechanism by its dispersal capability. In this context, correct identification of dendrobranchiate larvae by means of larval keys (e.g., Calazans 1993, Carreton et al. 2020) is particularly useful for fisheries science because it can furnish information on the spawning areas as initial stages occur from a few hours to a few days after hatching (Martin et al. 2014).

*Sicyonia dorsalis* has already been studied in relation to copulation and insemination system (Bauer 1992, 1996a, b), and population dynamics (Castilho et al. 2008a, b). Published information on the biology of *S. typica* is not available, except for mentions in ecological studies on the benthic community (Fransozo et al. 2002, Costa et al. 2000, 2003, Castilho et al. 2008c, Pantaleão et al. 2016, among others). In a study of integrative analysis of sperm ultrastructure and molecular phylogeny, Camargo et al. (2015) showed that these two species are not closely related within the genus.

After a review of the larval descriptions of *Sicyonia* we noted that less than 10% of the species had at least some larval stage described. Information on larval morphology of *Sicyonia* is currently limited to five species: *S. sculpta* H. Milne Edwards, 1830 by Monticelli & Lo Bianco (1900); *S. carinata* (Brünnich, 1768) by Heldt (1938); *S. stimpsoni* Bouvier, 1905 as *Eusicyonia stimpsoni* (Bouvier) by Pearson (1939); *S. wheeleri* Gurney, 1943 by Gurney (1942) and Gurney (1943); and *S. brevirostris* Stimpson, 1871 by Cook & Murphy (1965). In addition to these five species, a protozoea III and the decapodid of *Sicyonia* sp. were described by Paulinose (1982). The larval descriptions of *S. stimpsoni* by Pearson (1939) and *Sicyonia* sp. by Paulinose (1982) were carried out from plankton samples.

The knowledge of larval morphology is important to solve phylogenetic issues, besides allowing the elaboration of identification keys for the study of larval ecology (Iorio et al. 1990, GonzálezGordillo & Rodriguez 2000, Vela & González-Gordillo 2016). One of the best ways to safely describe penaeid larvae is to obtain them in the laboratory, starting with the eggs of adults identified with security (Jackson et al. 1989). Thus, the aim of this study was to describe and illustrate for the first time the early larval stages of *S. dorsalis* and *S. typica* obtained under laboratory conditions. We also provide remarks from a comparative analysis of the morphology of these stages among representatives of the genus.

### **Material and Methods**

One female of *Sicyonia dorsalis* and two of *S. typica* with developed ovaries were captured at Ubatuba, state of São Paulo, Brazil (23°26'13″S;45°04'4″W) in October 2012 and July 2013, respectively. Collections were made at 10 m depth, using a shrimp-fishing boat equipped with two otter-trawl nets with 5 m door openings, mesh size 20 mm and 18 mm in the cod end.

The females were transported alive to Laboratory of Biology of Marine and Freshwater Shrimps (LABCAM) and maintained in individuals 2-liter containers with seawater from the sampling site until spawning, when females were removed from the containers. No food was offered to the females during this period. After spawning, the carapace length (posterior margin of the ocular orbit to the posterior margin of the carapace = CL mm) of females was measured with a digital caliper of 0.01 mm accuracy and they were conserved with ethyl alcohol 98%. The hatched larvae were mass-reared with no food offer, under continuously moderate aeration and constant 25°C and salinity 33 in small beakers of 500 ml. Twenty individuals with active natatory behavior were removed every 3 h and conserved in a mixture (1:1) of ethyl alcohol (80%) and glycerin. The initial number of larvae per batch was not quantified. Experiments were stopped after the first protozoeal stage because all larvae died during this stage.

Dissections, drawings, and measurements were made under a Zeiss Stemi 2000C trinocular stereomicroscope, and a Leica DM750 microscope equipped with a camera lucida. Morphological description and measurement of each larval stage were based on the observation of at least 10 individuals. Larvae were measured as follows: total length (TL) of nauplius, from the apical to caudal margins, excluding furcal spines; total length (TL) of protozoea, from the apical margin of carapace to the apex of telson, excluding furcal spines; carapace length (CL) of protozoea, the distance between the postorbital margin and the median posterior border of the carapace (Ronquillo & Saisho 1997, Ronquillo et al. 2006). All measurements were made with an ocular micrometer. GraphPad Prism 8.0.2 (GraphPad Software, Inc., San Diego, CA, USA) was used for size data (TL) analysis. Data were evaluated by Shapiro-Wilk normality test. Considering a 2-way layout, interaction means were compared using analysis of variance (ANOVA) followed by Sidak's post hoc test. Data were shown as the mean  $\pm$  SD and results were considered statistically significant when p < 0.05.

Nomenclature of larval stages and body parts followed Dall et al. (1990), Leong et al. (1992) and Ronquillo et al. (2006). Because there is no standardization for larval descriptions of Penaeoidea until now, sequence of larval descriptions followed the standards proposed for brachyuran larval descriptions (Clark et al. 1998, Clark & Cuesta 2015) complemented by standards of larval descriptions of penaeoideans (Ronquillo & Saisho 1997, Carreton et al. 2020) and caridean shrimps

(Pantaleão et al. 2020). Setal terminology is based on that used by Garm (2004).

Parental females and respective larvae (from each obtained stage) were deposited as voucher specimens at the Crustacean Collection of the Biology Department of Faculty of Philosophy, Sciences and Letters at Ribeirão Preto (FFCLRP), University of São Paulo (USP), Brazil (CCDB/FFCLRP/USP) under access numbers: CCDB 6676 and CCDB 6677, for *S. dorsalis* and *S. typica*, respectively. Tissue samples were taken from the parental females for molecular analysis of partial fragments of the ribosomal rRNA, 16S rRNA gene to confirm identification (GenBank Accession number OM971000 and OM970999 for *S. dorsalis* and *S. typica*, respectively).

A comparative analysis of selected characters of the naupliar stages and first protozoeal stage of *Sicyonia* species was performed using original descriptions and illustrations of each species. Larval stages from some studies were not included (naupliar, protozoeal or both) in the comparisons for different reasons, such as being very brief, *i.e.*, without sufficient morphological details to allow comparisons (Monticelli & Lo Bianco 1901, Gurney 1943) and/or obtained from plankton samples without assurance of the identification (Pearson 1939, Paulinose 1982).

#### Results

The parental females of *S. dorsalis* had a CL of 11.71 mm, and *S. typica* of 13.20 mm and 21.32 mm. Spawnings were observed between 10:00 and 12:00 p.m., and about 90% of larvae emerged 12 h after spawning time. The larvae passed through 5 naupliar stages (NI to NV) before reaching first protozoeal stage (PZI) in a minimum of about two days (48h) from hatching (Table 1). The naupliar and PZI stages of *S. dorsalis* and *S. typica* were completely described in detail. Size (TL) of larvae differed among each larval stage but did not differ between species in each larval stage (two-way ANOVA, p < 0.05) (Figure 1). As the external morphology did not differ between species, illustrations were made for both species together.

# Larval description

Order DECAPODA Latreille, 1802 Suborder DENDROBRANCHIATA Spence Bate, 1888 Family SICYONIIDAE Ortmann, 1898 Genus *SICYONIA* H. Milne Edwards, 1830 *Sicyonia dorsalis* Kingsley, 1878 and *Sicyonia typica* (Boeck, 1864) [Figures 2–3(A–H)]

**Table 1.** Chronology of larval development of *Sicyonia dorsalis* Kingsley, 1878 and *S. typica* (Boeck, 1864) from Ubatuba, state of São Paulo, Brazil, at 25 °C and 33 of salinity.

Cumulative time (hours)	Stage
00	First nauplius (NI)
06	Second nauplius (NII)
13	Third nauplius (NIII)
21	Fourth nauplius (NIV)
37	Fifth nauplius (NV)
47	First protozoea (PZI)



**Figure 1.** Total length (TL) of *Sicyonia dorsalis* Kingsley, 1878 and *S. typica* (Boeck, 1864) naupliar and first protozoeal (PZI) stages. The TL was measured in ten larvae of each developmental stage of both species and compared using two-way ANOVA followed by Sidak post hoc test. Different letters represent significant differences (p < 0.05) among stages. NI. Fist nauplius; NII. Second nauplius; NIII. Third nauplius; NIV. Fourth nauplius; NV. Fifth nauplius; PZI. First protozoea.

#### FIRST NAUPLIUS (NI) (Figure 2)

Dimensions: Sicyonia dorsalis TL:  $0.275 \pm 0.002$  mm; S. typica TL:  $0.276 \pm 0.002$  mm (10 larvae from each species).

- *Body:* ovoid and unsegmented, with pairs of antennules, antennae and mandibles; labrum projects ventrally from enlarged cephalic region; median ocellus located near anterior end; furcal spine formula 1 + 1 + 1.
- *Antennule:* uniramous; with 2 short ventrolateral, 1 dorsolateral, and 2 terminal simple setae plus a small terminal spine.
- Antenna: endopod with 2 small ventrolateral and 2 terminal simple setae plus a small terminal spine; exopod with 5 ventrolateral simple setae plus a small terminal spine.
- *Mandible:* endopod and exopod with 1 subterminal and 2 terminal simple setae.

#### SECOND NAUPLIUS (NII) (Figure 2)

Dimensions: Sicyonia dorsalis TL:  $0.298 \pm 0.003$  mm; S. typica TL:  $0.297 \pm 0.003$  mm (10 larvae from each species).

- *Body*: similar to previous stage, except for the absence of the median protuberance on the posterior rounded region; furcal spine formula 1 + 1.
- *Antennule*: uniramous; with 3 small ventrolateral simple, 1 dorsolateral simple and 3 (2 simple and 1 plumose) terminal setae; minute distal spinules on outer margin, as illustrated.
- *Antenna*: endopod with 2 small ventrolateral simple and 2 terminal plumose setae plus a small terminal spine; exopod with 5 ventrolateral plumose setae plus a small terminal spine.
- Mandible: as in previous stage, but all setae are plumose.

# THIRD NAUPLIUS (NIII) (Figure 2)

Dimensions: Sicyonia dorsalis TL:  $0.325 \pm 0.003$  mm; S. typica TL:  $0.325 \pm 0.004$  mm (10 larvae from each species).

*Body*: similar to previous stage; a depression separates two developing furcal processes; furcal spine formula 3 + 3.



Figure 2. *Sicyonia dorsalis* Kingsley, 1878 and *S. typica* (Boeck, 1864), naupliar stages, ventral view. NI. Fist nauplius; NII. Second nauplius; NIII. Third nauplius; NIV. Fourth nauplius; NV. Fifth nauplius. (Scale bar = 0.2 mm).

- *Antennule*: uniramous with annular indentions; 3 small ventrolateral simple and 3 (1 simple and 2 plumose) terminal setae; minute distal spinules on outer margin, as illustrated.
- *Antenna*: endopod with 2 small ventrolateral simple and 3 terminal plumose setae; exopod with 4 ringlets with transversal incomplete separations, 6 plumose setae on the inner side (1, 1, 1, 3), plus a small terminal spine.

Mandible: unchanged.

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# FOURTH NAUPLIUS (NIV) (Figure 2)

Dimensions: Sicyonia dorsalis TL:  $0.353 \pm 0.003$  mm (10 larvae); S. typica TL:  $0.354 \pm 0.002$  mm (10 larvae from each species).

*Body*: similar to previous stage except for the elongation of the abdominal region, with outline of developing limbs (maxillule, maxilla and first and second maxillipeds) evident following mandible; furcal spine formula 5 + 5.

*Antennule*: unchanged, except by the number of annular indentions. *Antenna*: endopod unchanged; exopod with 5 ringlets with 6 plumose

setae on the inner side (1, 1, 1, 1, 2), plus a simple seta on the inner side and a small terminal spine on the fifth ringlet.

Mandible: unchanged.

# FIFTH NAUPLIUS (NV) (Figure 2)

*Dimensions: Sicyonia dorsalis* TL:  $0.397 \pm 0.012$  mm (10 larvae); *S. typica* TL:  $0.396 \pm 0.011$  mm (10 larvae from each species).



**Figure 3.** *Sicyonia dorsalis* Kingsley, 1878 and *S. typica* (Boeck, 1864), first protozoea (PZI). I. A. Dorsal view; B. Antennule; C. Antenna; D. Mandibules; E. Maxillule; F. Maxilla; G. First maxilliped; H. Second Maxilliped. (Scale bar: A = 0.5 mm; D, E, F = 0.05 mm; B, C, G, H = 0.1 mm).

*Body*: abdominal region has become slender; furcal spine formula 6-7+6-7.

*Antennule*: inner and outer margins with rows of minute spinules on the annular indentions as illustrated; 3 (1 small simple and 2 plumose) ventrolateral, 1 dorsolateral simple and 5 (2 simple and 3 plumose) terminal setae.

- Antenna: coxa and basis without setae; endopod 2-segmented with 4 simple setae arranged 2 + 2 and 4 terminal plumose setae, respectively; exopod with 6 ringlets with 8 plumose setae on the inner side (1, 1, 1, 1, 1, 3), plus a marginal simple seta on the inner side of first ringlet and a small terminal spine on the outer side of fifth ringlet; rows of minute spinules on inner and outer margin of endopod and exopod, as illustrated.
- *Mandible*: basal nodule (gnathobase) with initial serration; endopod with 1 ventrolateral simple and 3 terminal plumose setae; exopod with 3 terminal plumose setae; rows of minute spinules on inner and outer margin of endopod and exopod, as illustrated.
- *Maxillule, Maxilla, First maxilliped* and *Second maxilliped*: present as biramous non-articulated buds; primordial setae present at tips of endopods and exopods.

# FIRST PROTOZOEA (Figures 3A-H)

Dimensions: Sicyonia dorsalis CL  $0.340 \pm 0.009$  mm, TL  $0.737 \pm 0.015$  mm; S. typica CL  $0.341 \pm 0.009$  mm, TL  $0.740 \pm 0.008$  mm (10 larvae from each species).

- *Carapace* (Figure 3A): almost rounded, longer than wider, reaching the level of the second maxilliped, without rostrum; frontal organs visible at the anterior part; naupliar eye present flanked by compound eyes visible through the carapace; 7 thoracic somites visible.
- *Antennule* (Figures 3A, B): consisting of 3 articles; proximal article subdivided in 5 ringlets with 0, 0, 0, 0, 1 sparsely plumose seta; second article with 4 (1 marginal and 1 terminal sparsely plumose and 2 terminal simple) setae; distal article with 3 (1 marginal and 2 terminal) aesthetascs and 3 terminal plumose setae; minute spinules on outer margin of second and third articles, as illustrated.
- *Antenna* (Figures 3A, C): shorter than antennule; peduncle 2-segmented, proximal segment without setae, distal segment with 1 terminal sparsely plumose seta; endopod 2-segmented with 5 (2 proximal and 3 terminal) sparsely plumose and 6 (1 proximal simple and 5 terminal sparsely plumose) setae, respectively; exopod with 12 ringlets with 12 sparsely plumose setae, 10 on the inner side (0, 0, 0, 0, 1, 1, 1, 1, 1, 1, 3) and 2 on the outer side (0, 0, 0, 0, 1, 0, 1, 0, 0, 0).
- *Mandible* (Figure 3D): incisor and molar processes well developed; palp absent.
- *Maxillule* (Figure 3E): coxal endite with 7 (1 simple, 1 denticulate and 5 plumose) setae; basial endite with 2 cuspidate processes and 2 plumose setae; endopod 3-segmented, with 3 (1 cuspidate and 2 sparsely plumose), 2 sparsely plumose and 5 sparsely plumose setae, respectively; exopod margin with 4 long plumose setae.
- Maxilla (Figure 3F): coxal endite bilobed, with 8 plumose and 3 (2 plumose and 1 sparsely plumodenticulate) setae on proximal and distal lobes, respectively; basial endite bilobed, with 4 (1 sparsely plumose, 1 sparsely plumodenticulate and 2 plumose) and 3 (1 simple, 1 sparsely plumodenticulate and 1 plumose) setae on proximal and distal lobes,

respectively; endopod 4-segmented, with 3 (1 simple and 2 sparsely plumose), 2 sparsely plumose, 3 sparsely plumose and 3 sparsely plumose setae, respectively; exopod (scaphognathite) margin with 5 long plumose setae; microtrichia on margins of coxal endite, basial endite and endopod, as illustrated.

- *First maxilliped* (Figures 3A, G): coxa with 4 sparsely plumose setae arranged 1 + 1 + 1 + 1; basis with 12 sparsely plumose setae arranged 3 + 3 + 3 + 3; endopod 4-segmented with 3, 1, 2, 5 sparsely plumose setae, respectively; exopod with 6 (4 marginal and 2 distal) sparsely plumose setae and 1 subterminal plumose seta; microtrichia on inner margin of exopod.
- Second maxilliped (Figure 3A, H): coxa without setae, with a terminal process on outer margin; basis with 2 sparsely plumose setae arranged 1 + 1; endopod 4-segmented, with 1, 1, 1 sparsely plumose, and 5 (1 subterminal simple and 4 sparsely plumose) setae, respectively; exopod with 5 (3 marginal and 2 distal) sparsely plumose setae.
- Third maxilliped: absent.

Pereiopods: absent.

- *Pleon* (Figure 3A): pleomeres not completely differentiated, fused with the telson and unarmed.
- Pleopods: absent.

Uropods: absent.

*Telson* (Figure 3A): broadly bifurcate, each branch with 7 plumose setae with distinct number of setules as illustrated.

#### Discussion

In the present study, no differences were found in the morphology and size of the naupliar and first protozoeal stages of two species of *Sicyonia* that occur on the southeast coast of Brazil, even though these species are considered phylogenetically distant into the genus (see Camargo et al. 2015). Thus, it is possible that morphological differences arise later during ontogenetic development, and that some differences in relation to other congeners (Tables 2 and 3) are result of misidentification in previous studies, as discussed below.

In the published larval descriptions of *Sicyonia* there are reports of different numbers of naupliar stages. In descriptions based on plankton samples, Pearson (1939) observed five. Studying naupliar development in the laboratory, Heldt (1938) described eight stages for *S. carinata* while Cook & Murphy (1965) observed five stages, similar to our results and probably the common number of stages of naupliar development of *Sicyonia*. Another divergent result was observed by Gurney (1943) who distinguished only three stages for *S. wheeleri* in the laboratory.

Interestingly, Gurney (1943) mentioned that he was convinced that the naupliar stages are not so numerous in *S. wheeleri* as eight in *S. carinata* (Heldt 1938); but he believed that there may be more than he had seen (three stages). Gurney (1943) also mentioned that it was probable that the first stage (NI) may have been missed, and that he was able to state with certainty that there was no moult, or at least no observable change, between 9 a.m. and 6 p.m. on the day of hatching. Thus, Gurney (1943) probably missed some stages, and for this reason, together with the lack of many morphological details, we have not included descriptions of *S. wheeleri* in our comparative table of naupliar development (Table 2). The loss of some naupliar

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Table 2. Comparison of selected morphological characters of naupliar stages of the genus *Sicyonia*. Abbreviations: ps = plumose seta; seg. = segmented; sp = spine; ss = simple seta.

Source			Heldt (1938)	Cook & Murphy (1965)	Present study	Present study		
Species			Sicyonia carinata	Sicyonia brevirostris	Sicyonia dorsalis	Sicyonia typica		
Locality			Tunisia	Gulf of Mexico	Brazil	Brazil		
	TL (mm)		0.26	0.3 (0.28 - 0.32)	$0.275\pm0.002$	$0.276\pm0.002$		
	Antenulle		5ss + 1sp	5ss + 1sp	5ss + 1sp	5ss + 1sp		
		Endopod	4ss + 1sp	4ss	4ss + 1sp	4ss + 1sp		
First	Antenna	Exopod	5ss + 1sp	5ss	5ss + 1sp	5ss + 1sp		
nauplius (NI)	M 111	Endopod	3ss	3ss	3ss	3ss		
	Mandible	Exopod	3ss	3ss	3ss	3ss		
	Buds of other limbs		absent	absent	absent	absent		
	Furcal formula		1 + 1	1 + 1	1 + 1	1+1		
	TL (mm)		-	0.31 (0.29 - 0.34)	$0.298\pm0.003$	$0.297\pm0.003$		
	Antenulle		6 setae	6 setae	6ss + 1ps	6ss + 1ps		
	A	Endopod	4 setae + 1sp	4 setae	2ss + 2ps + 1sp	2ss + 2ps + 1sp		
Second	Antenna	Exopod	5 setae + 1sp	6 setae	5ps + 1sp	5ps + 1sp		
nauplius (NII)	M 111	Endopod	3 setae	3 setae	3ps	3ps		
	Mandible	Exopod	3 setae	3 setae	3ps	3ps		
	Buds of other limbs		absent	absent	absent	absent		
	Furcal formula		1 + 1	1 + 1	1 + 1	1 + 1		
	TL (mm)		0.32	0.35 (0.32 - 0.37)	$0.325\pm0.003$	$0.325\pm0.004$		
	Antenulle		6 setae	6 setae	4ss + 2ps	4ss + 2ps		
	A	Endopod	5 setae	5 setae	2ss + 3ps	2ss + 3ps		
Third	Antenna	Exopod	6 setae + 1sp	7 setae	6ps + 1sp	6ps + 1sp		
nauplius (NIII)	Man Jihia	Endopod	3ps	3 setae	3ps	3ps		
	Mandible	Exopod	3ps	3 setae	3ps	3ps		
	Buds of other limbs		outline	outline	absent	absent		
	Furcal formula		2 + 2	3 + 3	3 + 3	3 + 3		
	TL (mm)		0.33 - 0.34	0.37 (0.33 - 0.40)	$0.353\pm0.003$	$0.354\pm0.002$		
	Antenulle		6 setae	7 setae	4ss + 2ps	4ss + 2ps		
		Endopod	5 setae	5 setae	2ss + 3ps	2ss + 3ps		
Fourth	Antenna	Exopod	6 setae + 2sp	8 setae	4-seg., 6ps + 1ss + 1sp	4-seg., 6ps + 1ss + 1sp		
naupnus (NIV)	Mandihla	Endopod	3ps	3 setae	3ps	3ps		
	Mandible	Exopod	3ps	3 setae	3ps	3ps		
	Buds of other limbs		outline	outline	outline	outline		
	Furcal formula		4 + 4	5 + 5	5 + 5	5 + 5		
	TL (mm)		0.38 - 0.40	0.44 (0.38 - 0.46)	$0.397\pm0.012$	$0.396\pm0.011$		
	Antenulle		9 setae	10 setae	4ss + 5ps	4ss + 5ps		
		Endopod	8 setae	8 setae	4ss + 4ps	4ss + 4ps		
Fifth	Antenna	Exopod	9 setae	9 setae	5-seg., 1ss + 8ps + 1sp	5-seg., 1ss + 8ps + 1sp		
	Mandible	Endopod	3ps	3 setae	1ss + 3ps	<b>1ss</b> + 3ps		
	1vianui010	Exopod	3ps	3 setae	3ps	3ps		
	Buds of other limbs		present	present	present	present		
	Furcal formula		7 + 7	7 + 7	6 - 7 + 6 - 7	6 - 7 + 6 - 7		

stages during cultivation of larvae in the laboratory is probably common during the study of larval development of penaeoids as the morphological changes between naupliar stages are very subtle making it difficult to differentiate them with observations of live animals under a stereomicroscope. In this way, constant and rigorous monitoring during cultivation is essential.

Regarding naupliar development, it was possible to compare the morphology of the studied species with available descriptions of S. brevirostris (Cook & Murphy 1965) and S. carinata (Heldt 1938) (Table 2). The morphology of naupliar stages was very similar. Even so, it was detected some differences in all stages. In the NI, S. brevirostris is the single species that lacks a spine at the apex of both endopod and exopod of the antenna; this spine was also not described for S. brevirostris on the endopod of NII. For the NII, the species studied here presented an extra seta (total of seven) on the antennule, when compared with S. brevirostris and S. carinata. The NIII of S. carinata was the single species with furcal formula 2 + 2, while the others had 3+3; furcal formula of NIV was also different between S. carinata (4+4) and the others (5+5). The NIV of S. brevirostris was the single species with seven setae on the antennule, while others had six. The NV of S. brevirostris also had one more seta (ten) in the antennule than other species (nine); additionally, a spine on the exopod of antenna and a simple seta on the endopod of mandible were found only in S. dorsalis and S. typica. In relation to size, we observed a gradual increase in the TL of larvae during naupliar development, and a faster growth (almost doubling the size) in the passage to PZI. These results were very similar to the observed for S. brevirostris and S. carinata (see Tables 1 and 2, and references therein) and seems to be a pattern for the early larval development of sycioniids.

As aforementioned, Heldt (1938) obtained eight naupliar stages of S. carinata under laboratory conditions at approximately 20°C. To perform morphological comparisons, we matched the stages obtained in the present study with those of S. carinata. In general, the NI, NII and NIII described by Heldt (1938) are very similar with the same stages obtained here. After that, Heldt's NIV and NV showed no differences and probably correspond to the NIV of the other species, while the NVI, NVII and NVIII seem to have gradually acquired the characteristics corresponding to the NV (or metanauplius) of congeners. Among other species and stages, Heldt (1938) described the naupliar development and PZI of Penaeus kerathurus (Forskål, 1775) as Penaeus trisulcatus (Leach, 1814 [in Leach, 1813-1815]) and explained that the larvae of S. carinata were practically identical. However, in the study of Heldt (1938) there is an illustration of S. carinata (Figure 56, 2) with a naupliar stage in which furcal formula is 3 + 3, and this formula was not mentioned for any of the eight described stages. Therefore, it is possible that some observed differences from Table 2 (such as the 2 + 2 furcal formula of NIII of S. carinata) are a result of undescribed details rather than actual morphological differences.

The morphology of the first protozoa was also similar, but it is possible to point out characteristics that distinguish the species described so far (Table 3). Both species studied here and *S. carinata* have eight setae in the antennule, while for *S. wheeleri* and *S. brevirostris* the exact number was not mentioned, and the three aesthetascs were described only in the present study; *S. breviostris* and *S. carinata* had one and two less setae on the endopod of antenna, respectively, when compared with the species studied here; endopod of maxillule of S. brevirotris and S. carinata had one less seta on the proximal lobe (formula of 2,2,5, while 3,2,5 for S. dorsalis and S. typica); coxal endite of maxilla with 7 + 4 and 9 + 3 setae in S. brevirostris and S. carinata, respectively, instead of 4 + 3, for S. dorsalis and S. typica; basial endite of maxilla with 3 + 3 setae in S. brevirostris and S. carinata, instead of 4 + 3, for S. dorsalis and S. typica; proximal segment of endopod of maxilla with one less seta in the proximal segment of S. brevirostris (formula of 2,2,3,3, while 3,2,3,3 for S. carinata, S. dorsalis and S. typica); basis of first maxilliped with 9-11 setae, while S. carinata, S. dorsalis and S. typica had 12 setae, and endopod with one less seta in the proximal segment of S. brevirostris (formula of 2,1,2,5 instead of 3, 1,2,5 for S. carinata, S. dorsalis and S. typica); exopod of the second maxilliped with five setae in S. dorsalis and S. typica, and with six setae in S. breviostris and S. wheeleri; and finally, the third maxilliped is absent in both species described here, but it appears as biramous buds in all other species.

Regarding all described stages here (NI to NV and PZI), other morphological differences were found during our descriptions in relation to congeners. We found small terminal spinules at the antennule of NII, NIII and NIV, and along practically the entire length of the limbs (antennule, antenna, and mandible) of the NV, which were not described for other *Sicyonia* species (Gurney 1943, Heldt 1938, Cook & Murphy 1965). It would be premature to conclude if these differences are exclusive of the studied species, as well as to affirm if they are real differences or effect of misidentification, considering the low number of available descriptions that fit modern standards. The descriptions of *S. brevirostris* and *S. wheeleri* are somewhat brief and did not include several details, as the types of setae that were practically not mentioned by Cook and Murphy (1965) and very few limbs or regions of the body were described for *S. wheeleri* (Gurney 1943).

A conspicuous terminal spine in the antennule of first nauplius (NI) is probably present in all studied sicyoniids to date (see Table 2 and references therein). We hypothesize that this morphological character, together with the aforementioned spinules (antennule of NII, NIII, NIV and all limbs of NV) could represent informative characteristics to differentiate the genus in the plankton. Considering previous descriptions of penaeoideans that occur in Brazilian coast, these characteristics were not observed in any of them. These larval descriptions include: Litopenaeus schmitti (Burkenroad, 1936) (Garcia-Pinto & Ewald 1974), Pleoticus muelleri (Spence Bate, 1888) (Iorio et al. 1990), Artemesia longinaris Spence Bate, 1888 (Boschi & Scelzo 1977), Rimapenaeus constrictus (Stimpson, 1871) (Pearson 1939, from plankton), and Xiphopenaeus sp. (Heller, 1862) (Renfro & Cook 1962). Further advancements in descriptions and redescriptions will be required to confirm if the pointed characteristics are generalities of Sicyonia and could be used in identification keys for sympatric penaeoidean species, as well as for the phylogenetic contextualization, also because we used larvae from one and two females for S. dorsalis and S. typica, respectively, and possible intraspecific natural variations could not be detected.

After morphological descriptions of PZI of *S. dorsalis* and *S. carinata* we tested the efficacy of the key to the larvae of the dendrobranchiate genera from Southern Brazilian coast proposed

#### Early larval development of Sicyonia spp.

**Table 3.** Comparison of selected morphological characters of first protozoea (PZI) of the genus *Sicyonia*. Abbreviations: ae = aesthetascs; cp = cuspidate process; ds = denticulate seta; ps = plumose seta; seg. = segmented; sp = spine; ss = simple seta; sps = sparsely plumose seta; rl = ringlet; NA = not available in descriptions.

Source		Heldt (1938)	Gurney (1943)	Cook & Murphy (1965)	Present study	Present study	
Species		Sicyonia carinata	Sicyonia wheeleri	Sicyonia brevirostris	Sicyonia dorsalis	Sicyonia typica	
Locality		Tunisia	Bermuda	Gulf of Mexico	Brazil	Brazil	
CL (mm)		0.30	NA	0.33 (0.30 - 0.36)	$0.34\pm0.009$	$0.34 \pm 0.008$	
TL (mm)		0.76 - 0.86	0.7 - 0.75	0.81(0.70 - 0.89)	$0.74\pm0.015$	$0.74 \pm 0.008$	
	Proximal article	5-seg., 1seta	5-seg., 1 seta	1 seta	5-seg., 1sps	5-seg., 1sps	
Antenulle	Second article	7	NA	3 setae	2ss + 2sps	2ss + 2sps	
	Distal article	/ setae	NA	6 setae	3ae + 3ps	3ae + 3ps	
	Peduncle distal article	NA	NA	1 seta	1sps	1sps	
Antenna	Endopod	2-seg., 9 setae	NA	2-seg., 10 setae	2seg., 1ss + 10ps	2seg., 1ss + 10ps	
	Exopod	9rl, 12 setae	12 setae	7–9rl, 12 setae	12rl, 12sps	12rl, 12sps	
	Coxal endite	7 setae	NA	7 setae	1ss + 1ds + 5ps	1ss + 1ds + 5ps	
	Basial endite	4 setae	NA	2cp + 2 setae	2cp + 2ps	2cp + 2ps	
Maxillule	Endopod (setation)	3-seg., 2,2,5	NA	3-seg., 2,2,5	3-seg., 3,2,5	3-seg., 3,2,5	
	Exopod	4ps	NA	4 setae	4ps	4ps	
	Coxal endite (setation)	bilobed, 9 + 3	NA	bilobed, 7 + 4	bilobed, 8 + 3	bilobed, 8 + 3	
Maxilla	Basial endite (setation)	bilobed, 3 + 3	NA	bilobed, 3 + 3	bilobed, 4 + 3	bilobed, 4 + 3	
	Endopod (setation)	4-seg., 3,2,3,3	NA	4-seg., 2,2,3,3	4-seg., 3,2,3,3	4-seg., 3,2,3,3	
	Exopod	5ps	NA	5 setae	5ps	5ps	
	Coxa	4ps	NA	4 setae	4 sps (1 + 1 + 1 + 1 + 1)	4 sps (1 + 1 + 1 + 1 + 1)	
Fist maxilliped	Basis	12 setae	NA	9–11 setae	12sps (3 + 3+ 3 + 3)	12sps (3 + 3 + 3 + 3)	
-	Endopod (setation)	4-seg., 3,1,2,5	4-seg.	4-seg., 2,1,2,5	4-seg., 3,1,2,5	4-seg., 3,1,2,5	
	Exopod	7 setae	7 setae	7 setae	6sps + 1ps	6sps + 1ps	
	Coxa	NA	NA	without setae	without setae	without setae	
C 1	Basis	NA	NA	2 setae (1 + 1)	2sps (1 + 1)	2sps (1 + 1)	
Second maxilliped	Endopod (setation)	4-seg.	4-seg.	4-seg., 1,1,1,5	4-seg., 1,1,1,5	4-seg., 1,1,1,5	
	Exopod	NA	6 setae	6 setae	5sps	5sps	
Third maxilliped		biramous bud	biramous bud	biramous bud	absent	absent	
Furcal formula		7 + 7	7 + 7	7 + 7	7 + 7	7 + 7	

by Calazans (1993). The characteristics that lead to PZI stage are: eyes not mobile, covered by carapace; unsegmented abdomen; and pereiopods absent. Regarding the PZI of *Sicyonia*, the following characteristics were used: spine absent on anterior portion of carapace; frontal organs present; antennule and antenna of different lengths; antennule about twice as long as antenna; and formula of antennal protopod (distal article) and endopod (proximal and marginal setae) is 1 + 2 + 3 [see Figure 2C of Calazans (1993) for details]. Therefore, we can conclude that the characteristics used in the previous key for the PZI of the genus proved to be efficient, and adjustments are not necessary.

As evidenced in the present study, there is a clear need of new larval descriptions of sicyoniids. As pointed out by Martin et al. (2014) and illustrated by the descriptions of two species conducted here, the penaeoidean protozoeal stages are very difficult to be distinguished at species level. In this sense, sampling of plankton and the use of refined techniques such as DNA-barcode will be useful to enable morphological descriptions of the entire larval development, when capturing reproductive females becomes difficult or even obtaining the complete cycle in the laboratory. With an increase in penaeoidean larval descriptions from Brazilian coast we will be able to contribute to the identification of plankton samples, helping to recognize spawning sites, which will allow us to improve the decisions for the conservation of such species, especially regarding fishing.

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#### **Associate Editor**

Tito Lotufo

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João Alberto Farinelli Pantaleão: Substantial contribution in the concept and design of the study, contribution to data collection, analysis, and interpretation; contribution to manuscript preparation.

Régis Augusto Pescinelli: Contribution to data collection; contribution to data analysis and interpretation; contribution to manuscript preparation.

Fernando Luis Mantelatto: Substantial contribution in the concept and design of the study; contribution to data collection; contribution to critical revision, adding intellectual content; mentored work, funding acquisition.

Rogério Caetano Costa: Substantial contribution in the concept and design of the study; contribution to data collection; contribution to critical revision, adding intellectual content; mentored work, funding acquisition.

# **Conflicts of Interest**

The authors declare that they have no conflict of interest related to the publication of this manuscript.

### Data Availability

Supporting data are available at <https://doi.org/10.48331/ scielodata.EXB8J5>.

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# *Xylobotryum portentosum* (Mont.) Pat. (Xylobotryomycetes, Ascomycota): a rare fungal species newly found in Southeastern Brazil

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*Abstract: Xylobotrum portentosum* (Mont.) Pat. is a striking Neotropical fungal species but it has been reported only a few times from Southern Brazil (States of Paraná and Santa Catarina), found in remnants of Atlantic Forest. Herein we report the species for the first time from the Southeastern Region of Brazil (State of São Paulo). A brief description and color photographs of the fresh specimen are presented. *Keywords: didymospore; Neotropical funga; pyrenomycetes; xylarioid fungi.* 

# *Xylobotryum portentosum* (Mont.) Pat. (Xylobotryomycetes, Ascomycota): uma espécie rara de fungo encontrada na Região Sudeste do Brasil

**Resumo:** Xylobotrum portentosum (Mont.) Pat. é uma espécie notável de fungo neotropical que foi registrada apenas poucas vezes para a Região Sul do Brasil (Paraná e Santa Catarina), encontrada em remanescentes de Mata Atlântica. Neste trabalho a espécie é reportada pela primeira vez para a Região Sudeste do Brasil (Estado de São Paulo). São apresentadas uma breve descrição e fotografias coloridas do espécime fresco. **Palavras-chave:** didimosporo; funga neotropical; fungos xylarioides; pirenomicetos.

# Introduction

*Xylobotryum* Pat. is a widely distributed genus found in warm areas (tropical and subtropical) worldwide (Müller & von Arx 1962, Rossman 1976, Ju & Rogers 1994). It is a curious taxa since species produce dark carbonaceous stromata which are similar to *Xylaria* species, but perithecia are naked and ascospores are two-celled (Trierveiler-Pereira et al. 2008). The genus position within Ascomycota was uncertain until recently, but molecular data support that it belongs to a distinct family, order and class – Xylobotryaceae Voglmayr & Jaklitsch, Xylobotryales Voglmayr & Jaklitsch and Xylobotryomycetes Voglmayr & Jaklitsch, respectively (Voglmayr et al. 2019).

Six species have been described for the genus (Robert et al. 2005), but only two are currently accepted: *X. portentosum* (Mont.) Pat. and *X. andinum* Pat. (Voglmayr et al. 2019). *Xylobotrum portentosum* have been reported from Central and South America (Guzmán & Piepenbring 2010), but in Brazil there are only a few records from the Southern Region: State of Santa Catarina (Möller 1901, Trierveiler-Pereira et al. 2008) and Paraná (Meijer 2006), all of them from the Atlantic Forest biome. The species is lignicolous and all Brazilian specimens were gathered in fern trees (*Cyathea* sp.).

In this manuscript we present information about a specimen of *X*. *portentosum* collected in the State of São Paulo, Brazil.

# **Material and Methods**

The specimen was collected at Carlos Botelho State Park (Parque Estadual Carlos Botelho – PECB), located in the southern region from the State of São Paulo, Brazil (Figure 1). This conservation unit was created in 1982 and shelters more than 37,000 hectares of mountainous area of Atlantic Forest, with altitudes ranging from 50 to 975 meters above sea level. The vegetation is mainly montane and submontane rainfores (Lima et al. 2011).

Stromata were found growing on a dead fern tree lying on the ground (*Cyathea* sp.) and were photographed using digital camera. Samples were taken to the Mycological Studies Laboratory (LEMic) at Federal University of São Carlos, where macro and microscopic analysis were performed. Macroscopic analysis consisted of the observation of stromata and perithecia color, size and shape. For microscopic characterization, the perithecial content of dried specimen was removed with the aid of a histological needle after perithecia rehydratation with 3% KOH, and mounted on glass slides with 1% floxin + 3% KOH, and Melzer reagent. Identification and morphological classification were done by consulting the specialized literature (Müller & von Arx 1962, Trierveiler-Pereira et al. 2008). Voucher is deposited at the Mycological Collection from the Herbarium SPSC (Federal University of São Carlos, Buri, São Paulo, Brazil), with duplicate at Herbarium SP-Fungi (Instituto de Pesquisas Ambientias, São Paulo, Brazil).



Figure 1. Geographic distribution of *Xylobotryum portentosum* in Brazil. Dots represent known records: Santa Catarina (SC), Paraná (PR), and São Paulo (SP – this study). Map elaborated by Amanda Prado-Elias.

# Results

*Xylobotryum portentosum* (Mont.) Pat., Bull. Soc. Myc. France 16: 185. 1900.

**Examined specimen:** BRAZIL, SÃO PAULO: Sete Barras, Parque Estadual Carlos Botelho, Trilha da Figueira, **24° 11' 40.9" S** and **47° 55' 16.9" W**; 18.IV.2022; leg. *L. Trierveiler-Pereira & J.M. Baltazar* (SPSC; SP-Fungi 513077), on dead trunk of *Cyathea* sp.

**Description:** see Trierveiler-Pereira et al. (2008) and Voglmayr et al. (2019).

**Diagnostic characters:** The examined specimen presents unbranched, more rarely apically branched, erect, stipitate, black, stromata (Figure. 2A–C), 1.5–5.5 cm tall, 0.2–0.6 cm in diam., becoming hollow; bearing crowded, conspicuous, naked, sessile, black perithecia over the stromatal surface, ca. 0.5 mm in diam, subglobose, apically papillate. Asci are bitunicate, cylindrical, long-stipitate, with apex not bluing in Melzer's iodine reagent, containing 8 uniseriate to irregularly biseriate ascospores; ascospores 1-septate, oblong-ellipsoid to fusoid, light brown to dark brown, smooth (Figure 2D),  $9-13 \times 3-4.5 \mu$ m, with longitudinal germ slits extending over the whole length of the ascospore, usually difficult to observe in light microscopy.

**Taxonomic and morphological comments:** Macro and microscopic features of the studied material match the description of Brazilian specimens presented by Trierveiler-Pereira et al. (2008), except that some stromata have branched, fertile apices (Figure 2B). *Xylobotryum andinum* is microscopically very similar to *X. portentosum* regarding ascospore characters, but it differs macroscopically due to its corymbose stromata (a cluster of naked perithecia whose lower stipes are proportionally longer so that the perithecia form a flat or slightly convex head). Moreover, *X. andinum* has a broader geographic distribution, including paleo and neotropical areas. Color photographs of *X. andinum* are presented by Voglmayr et al. (2019).

**Known distribution:** Neotropical, with records from Brazil, Chile, Colombia, Costa Rica, Dominica, Ecuador, French Guiana, Guadeloupe, Guyana, Jamaica, Martinique, Nicaragua, Panama, Peru, and Puerto Rico (Voglmayr et al. 2019).



**Figure 2.** *Xylobotryum portentosum*. A. Stromata *in situ*. B. Stroma with branched fertile apex. C. Stromata *ex situ*. D, E. Ascospores within ascus. Scale bars: A, C = 3 cm; B = 1 cm; D, E = 10  $\mu$ m. Photographs by Larissa Trierveiler-Pereira.

# Discussion

When firstly reported from Brazil, the species was identified as *Trachyxylaria phaeodidyma* Möller (Möller 1901), but the synonym with *X. portentosum* was later proposed by Müller & von Arx (1962). *Xylobotryum rickii* (Theiss.) Lloyd, a name proposed for a Brazilian specimen collected in the State of Rio Grande do Sul, corresponds to a *Xylaria* species (Rossman 1976). In Brazil, *X. portentosum* is known from the Southern Region (Santa Catarina and Paraná) and herein we present the first record of the species from Southeastern Brazil, from the State of São Paulo (Figure 1). Here, it is important to emphasize that São Paulo is the Brazilian State with the better known mycodiversity, with record of 1,900 fungal species (BFG 2022).

In Brazil, the species has only a few reports from preserved areas of Atlantic Forest (dense ombrophilous forests). The authors have been collecting macrofungi for almost 20 years now in several areas of Atlantic Forest in Brazil (Southern, Southeastern and Northeastern regions) and have spotted the species only twice: once in April 25th, 2005 in Corupá, State of Santa Catarina (26°23'53.7"S, 49°20'55.3"W – voucher not preserved), and in São Paulo (present study), indicating that its occurrence is rare.

Considering that the Atlantic Forest is a biome much reduced compared to its original area (Rezende et al. 2018), and that in Brazil fungal species are not currently being considered in conservation policies, it would be interesting to evaluate the species conservation status and discuss conservation actions.

#### Acknowledgments

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### **Associate Editor**

Carlos Joly

#### **Author Contributions**

Larissa Trierveiler-Pereira: contributed to conceptualization; collection of the specimen; identification at field and laboratory and writing the original draft; review and editing the manuscript.

Juliano M. Baltazar: contributed to conceptualization; collection of the specimen; writing the original draft; review and editing the manuscript.

# **Conflicts of Interest**

The author declare that they have no conflict of interest related to the publication of this manuscript.

# Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

#### **Data Availability**

https://specieslink.net/col/SP-Fungi/ (Voucher: SP-Fungi 513077).

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# The Kunming-Montréal Global Biodiversity Framework

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The Kunming-Montréal Global Biodiversity Framework (GBF), approved by the Fifteenth Conference of the Parties (COP15) of the Convention on Biological Diversity (CBD) is a major win for our planet and for all of humanity, charting a new course away from the relentless destruction of habitats and species. The meeting was attended by 188 governments (95% of all 196 Parties to the UN CBD).

In addition to the GBF, the meeting approved a series of related agreements on its implementation, including planning, monitoring, reporting and review; resource mobilization; helping nations to build their capacity to meet the obligations; and digital sequence information on genetic resources.

For example, The Global Environment Facility was requested to establish, as soon as possible, a Special Trust Fund to support the implementation of the Global Biodiversity Framework ("GBF Fund"). The fund would complement existing support and scale up financing to ensure the timely implementation of the GBF with adequate, predictable and timely flow of funds.

Among the global targets for 2030 approved are:

- Effective conservation and management of at least 30% of the world's lands, inland waters, coastal areas and oceans, with emphasis on areas of particular importance for biodiversity and ecosystem functioning and services. The GBF prioritizes ecologically-representative, well-connected and equitably-governed systems of protected areas and other effective areabased conservation, recognizing indigenous and traditional territories and practices. Currently 17% and 10% of the world's terrestrial and marine areas respectively are under protection.
- Have restoration completed or underway on at least 30% of degraded terrestrial, inland waters, and coastal and marine ecosystems
- Reduce to near zero the loss of areas of high biodiversity importance, including ecosystems of high ecological integrity
- Cut global food waste in half and significantly reduce over consumption and waste generation
- Reduce by half both excess nutrients and the overall risk posed by pesticides and highly hazardous chemicals
- Progressively phase out or reform by 2030 subsidies that harm biodiversity by at least \$500 billion per year, while scaling up positive incentives for biodiversity's conservation and sustainable use

- Mobilize by 2030 at least \$200 billion per year in domestic and international biodiversity-related funding from all sources – public and private
- Raise international financial flows from developed to developing countries, in particular least developed countries, small island developing States, and countries with economies in transition, to at least US\$ 20 billion per year by 2025, and to at least US\$ 30 billion per year by 2030
- Prevent the introduction of priority invasive alien species, and reduce by at least half the introduction and establishment of other known or potential invasive alien species, and eradicate or control invasive alien species on islands and other priority sites
- Require large and transnational companies and financial institutions to monitor, assess, and transparently disclose their risks, dependencies and impacts on biodiversity through their operations, supply and value chains and portfolios

Without such actions, there will be a further acceleration in the global rate of species extinction, which is already at least tens to hundreds of times higher than it has averaged over the past 10 million years.

The Kunming-Montréal Global Biodiversity Framework has four overarching global goals, and 23 targets.

#### **GOALA**

The integrity, connectivity and resilience of all ecosystems are maintained, enhanced, or restored, substantially increasing the area of natural ecosystems by 2050.

Human induced extinction of known threatened species is halted, and, by2050, extinction rate and risk of all species are reduced tenfold, and the abundance of native wild species is increased to healthy and resilient levels.

The genetic diversity within populations of wild and domesticated species, is maintained, safeguarding their adaptive potential.

# GOAL B

Biodiversity is sustainably used and managed and nature's contributions to people, including ecosystem functions and services, are valued, maintained and enhanced, with those currently in decline being restored, supporting the achievement of sustainable development, for the benefit of present and future generations by 2050.

#### **GOAL C**

The monetary and non-monetary benefits from the utilization of genetic resources, and digital sequence information on genetic resources, and of traditional knowledge associated with genetic resources, as applicable, are shared fairly and equitably, including, as appropriate with indigenous peoples and local communities, and substantially increased by 2050, while ensuring traditional knowledge associated with genetic resources is appropriately protected, thereby contributing to the conservation and sustainable use of biodiversity, in accordance with internationally agreed access and benefit-sharing instruments.

#### **GOAL D**

Adequate means of implementation, including financial resources, capacity-building, technical and scientific cooperation,

and access to and transfer of technology to fully implement the Kunming-Montreal global biodiversity framework are secured and equitably accessible to all Parties, especially developing countries, in particular the least developed countries and small island developing States, as well as countries with economies in transition, progressively closing the biodiversity finance gap of \$700 billion per year, and aligning financial flows with the Kunming-Montreal Global Biodiversity Framework and the 2050 Vision for Biodiversity.

#### **Conflicts of Interest**

The author declares that he has no conflict of interest related to the publication of this manuscript.

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# Fishes from the Colombian Amazonia region: species composition from the river systems within the rainforest biome

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Abstract: The Colombian Amazon region is part of the Neotropical rainforest (humid forest biome) covering an area of 483,163 km<sup>2</sup> and includes tributaries of both the Amazon and Orinoco River basins. The aquatic ecosystems found there include: rivers and alluvial plains originating in Andean headwaters, on eroded soils of tropical forests in the lowlands, and Guiana Shield formations, comprising a dense fluvial drainage network in the lowlands, with Paleogene/Neogene geological formations (terra firme streams in higher places that don't usually flood) and Paleozoic (shield streams); and Andean and Guiana Shield streams above 200–250 m a.s.l. We present here an exhaustive compilation of published information, supported by fish collections, consisting of a list of 1104 species distributed in 375 genera, 53 families, and 16 orders. We include occurrence data of these species in each subbasin. The presence/absence species matrix was analyzed using a dendrogram and non-metric multidimensional scaling (NMDS) analysis to identify patterns of similarity between basins and sub-basins. We evaluated species composition between basins and among the different geological origins using PERMANOVA. The dendrogram shows co-occurrences of 404 species in the two basins. It also shows two clear groupings of the sub-basins of the Amazon (except Guainía-Negro drainages) and those of the Orinoco. Within the Amazon Basin, there are two nodes according to the geological origin: systems of Andean origin and those of the lowlands. The dendrogram results are consistent with the NMDS analysis, which shows a clear grouping according to the connectivity of the basins; the Guainía-Negro is included in the Amazon basin. Species distribution patterns were supported by the PERMANOVA, and differed significantly between basins (F = 4.3, R = 0.26, P = 0.003) and geological origin (F = 3.6, R = 0.23, P = 0.003). The number of species in this study represents almost a fifth of the ichthyofauna of the Neotropics and about a third of that of the Amazon River basin; clearly supporting Colombia's status among the countries with the greatest diversity of freshwater fish species of the planet. We include here a significant number of new records (75 spp), provide a first approximation of the distribution patterns, and a framework for future biogeographical studies.

Keywords: Amazon; distribution pattern; freshwater fishes; Neotropics; Orinoco.

# Peces de la región de la Amazonía Colombiana: composición de especies de los sistemas fluviales del bioma de selva húmeda

**Resumen:** La región de la Amazonía colombiana hace parte del bosque húmero neotropical (bioma de selva húmeda) abarcando un área de 483.163 km<sup>2</sup> e incluye afluentes de las cuencas del Amazonas y Orinoco. Los

ecosistemas acuáticos encontrados allí incluyen: ríos y llanuras aluviales, originándose en cabeceras andinas, en suelos erosionados de bosques tropicales en tierras bajas y en formaciones de escudos; conformando una densa red fluvial en tierras bajas con formaciones geológicas paleógenas-neógenas (arroyos de terra firme en sitios elevados que usualmente no se inundan) y paleozoicas (arroyos de escudo); y arroyos andinos y del escudo Guayanés por encima de 200-250 m s.n.m. Presentamos aquí una recopilación exhaustiva de información publicada, sustentada por colecciones ictiológicas, consistiendo en una lista de 1104 especies distribuidas en 375 géneros, 53 familias y 16 órdenes. Incluimos datos de estas especies en cada subcuenca. La matriz de presencia/ausencia de especies fue analizada usando un dendrograma y un análisis de escalamiento multidimensional no métrico (NMDS) para identificar patrones de similitud entre cuencas y subcuencas. Se evaluó la composición de especies entre cuencas y entre los diferentes orígenes geológicos usando PERMANOVA. El dendrograma refleja coocurrencia de 404 especies en las dos cuencas. También muestra dos agrupaciones claras de las subcuencas del Amazonas (excepto Guainía-Negro) y las del Orinoco. Dentro de la cuenca amazónica existen dos nodos según el origen geológico: los sistemas de origen andino y los de tierras bajas. Los resultados del dendrograma son consistentes con el análisis NMDS, el cual muestra una clara agrupación según la conectividad de las cuencas; el Guainía-Negro está incluido en la cuenca del Amazonas. Los patrones de distribución de especies fueron respaldados por el PERMANOVA y difirieron significativamente entre cuencas (F = 4.3, R = 0.26, P = 0.003) y origen geológico (F = 3.6, R = 0.23, P = 0.003). El número de especies en este estudio representa casi la quinta parte de la ictiofauna del Neotrópico y alrededor de un tercio de la de la cuenca del río Amazonas; soportando el estatus de Colombia entre los países con mayor diversidad de especies de peces de agua dulce del planeta. Incluimos aquí un número importante de nuevos registros (75 spp), brindamos una aproximación de los patrones de distribución y un marco para futuros estudios biogeográficos.

Palabras clave: Amazonas; Orinoco; patrones de distribución; peces de agua dulce; región neotropical.

#### Introduction

The Amazon region has been defined following the combination of several hydrological, geological, biological, and even political concepts (Albert et al. 2018). From a hydrogeographic perspective, the region is defined as that drained by the Amazon River basin, with 6.3 million km<sup>2</sup> (Sioli 1984) - henceforth termed the Amazon. A much broader biogeographical region proposed is the Greater Amazonia, which includes the Amazon and Orinoco River basins and several independent river systems from the Guianas (Albert et al. 2018, van der Sleen & Albert 2018). The Greater Amazonia comprises a myriad of upland and terra firme streams (non-flooding systems), as well as small and deep channel rivers that flow under closed forest canopy or drain broad sunlit floodplains (see Figure 1 in van der Sleen & Albert for delimitation of the area). Another comprehensive definition including hydrogeographic and biogeographic concepts includes all affluents of the Amazon and Orinoco River basins and coastal rivers in Guiana, that drain an area historically covered by forest (Olson et al. 2001) - for heuristic purposes, henceforth referred to as the Amazonia region. This Amazonia region encompasses an area of 6.7 million km<sup>2</sup> containing the rainforest shared by eight countries (Colombia, Brazil, Bolivia, Ecuador, Guyana, Peru, Suriname, and Venezuela).

The Amazonia region primarily comprises lowland habitats and is the major component of the Neotropics (Leite & Rogers 2013). The region encompasses a vast variety of landscapes that have originated over its long geological history. These landscapes include the enigmatic *tepuis* in the North, the wide tracts of rainforest in the lowlands (below 200–250 m below sea level), and the forest slopes at the foothills of the Andes, along the western fringe (Hoorn & Wesselingh 2010). The aquatic ecosystems, on the other hand, include upland Andean and streams draining shield areas (van der Sleen & Albert 2018). The rivers draining the lowlands of the Amazon are characterized by a dense network of Paleogene-Neogene geological formations

http://www.scielo.br/bn

(*terra firme* streams) and Pre-Cambrian geological formations (shield streams) (Lundberg *et al.* 1998). Additionally, the aquatic systems are also inclusive of river-floodplain systems belonging to three distinct biogeochemical water types that are related to river system origin: nutrient-poor, humic-stained 'blackwaters' of lowland forest origin; nutrient-poor 'clearwaters' of shield origin; and nutrient-rich 'whitewaters' of Andean origin (Sioli 1984).

The Amazonia region is well recognized for its remarkable biodiversity and endemics (Mittermeier *et al.* 2003, Tisseuil *et al.* 2013). Specifically, the Amazonian lowlands contain the world's largest biodiversity (Gentry 1988, Wilson 1992) in both terrestrial and aquatic faunas (Myers *et al.* 2000). Amazonia hosts about 17% and 10% of all known vascular plants and vertebrate species, respectively (Lundberg *et al.* 2000, Myers *et al.* 2000). In particular, the aquatic ecosystems of the Amazon basin host the most diverse freshwater ichthyofauna in the world (Val & de Almeida 1995, Tisseuil *et al.* 2013), with over 2700 species recorded so far (Dagosta & de Pinna, 2019). Of the total valid species, they represent ~15% of all freshwater fish species currently described in the world (Jézéquel *et al.* 2020).

The high diversity of Amazonian fishes has been associated with ecological and evolutionary processes, coupled with a complex geomorphological history (Vari & Weitzman 1990, Lundberg 2001, Hubert & Renno 2006, Albert & Reis 2011, Lima & Ribeiro, 2011, Dagosta & de Pinna 2017). The origins of most fish species predate the origin of the whole system, which took place during the Cretaceous and Early Cenozoic (Lundberg *et al.* 2010). Thus, most Amazonian fish lineages are not restricted to a single river basin but are widespread across other basins of tropical South America (Schaefer 1997, Willis *et al.* 2007, Lima & Ribeiro, 2011, Ferraris *et al.* 2017). However, the Amazon has served as an area where lineages have accumulated and cladogenesis has occurred (Lundberg *et al.* 1998, Albert & Reis 2011). The freshwater fishes have had the opportunity to adapt to the



Figure 1. Outline map of the Amazonia region in Colombia. Black dots = main collection sites. Leticia (1), Florencia (2), San José del Guaviare (3), Puerto Leguízamo (4), Puerto Inírida (5), and Mitú (6).

diverse environmental conditions of the Amazon over long periods of geological time; ultimately resulting in distinct taxonomic composition at the species level (Albert & Reis 2011), reflected by the high *gamma* diversity (regional species richness).

Although progress has been made in understanding the spatial distribution of the ichthyofauna in the Colombian Amazon, there are still unexplored basins (Jézéquel *et al.* 2020a). High values of fish richness have been identified; species with high levels of irreplaceability, representativeness, and degree of vulnerability, allow for defining conservation priorities of specific areas in the basin (Jézéquel *et al.* 2020a, b; Frederico *et al.* 2021). In this sense, threats to freshwater ecosystems in the Amazonia should be ranked among the highest conservation priorities (Jézéquel *et al.* 2020 a, b; Albert *et al.* 2021). In the Colombian Amazonia region, there are areas that are part of the *National System of Protected Areas*, even so, deforestation continues to increase (Ayram *et al.* 2020, Clerici *et al.* 2020), that is, management and protection policies are inefficient by focusing on human security and not on ecological integrity (Jézéquel *et al.* 2020b).

Ichthyological studies in Colombian Amazonia are not different from the general pattern of the research done in the whole Amazonia region in South America (Bogotá-Gregory & Maldonado-Ocampo 2006). Most research on fishes has occurred within proximity of the largest populations centers such as Leticia (Amazonas Department), Florencia (Caquetá Department), Puerto Leguízamo (Putumayo Department), San José del Guaviare (Guaviare Department), Puerto Inírida (Guainía Department), and Mitú (Vaupés Department), where access facilities and research institutions as the Amazonian Scientific Research Institute SINCHI and the Universidad Nacional de Colombia facilities are located (Figure 1). The research initiatives have been focused in different areas (e.g. biology, ecology, fisheries) and most of the specimens collected are deposited in national scientific collections, mainly CIACOL (Colección Ictiológica de la Amazonía Colombiana, Instituto Amazónico de Investigaciones Científicas SINCHI Leticia, Amazonas), CZUT-IC (Colección Zoológica de la Universidad del Tolima, sección Ictiología), ICN-MHN (Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia,

Bogotá), IAvH-P (Colección de Peces de Agua Dulce del Instituto de Investigación de Recursos Biológicos Alexander von Humboldt), and MPUJ (Museo Javeriano de Historia Natural "Lorenzo Uribe Uribe, S.J.", Pontificia Universidad Javeriana, Bogotá).

Although the Colombian Amazon is little represented from a geographical perspective, DoNascimiento *et al.* (2021) reported 764 species for the basin. This update is part of the very few studies done to document species composition from the region (Mojica 1999, Bogotá-Gregory & Maldonado-Ocampo 2006, Maldonado-Ocampo *et al.* 2008, DoNascimiento *et al.* 2017). Furthermore, no single study has yet sought to document the species from the Colombian Amazonia region, *i.e.* all affluents of the Amazon and Orinoco River basins flowing under areas historically covered by rainforest cover.

The Amazon Institute for Scientific Research-SINCHI is a scientific research entity that promotes the generation of knowledge and dissemination of information about the biological reality of the Amazonia region in Colombia. In this sense, a list of the fish species distributions within the Colombian Amazonia region is presented here, following the delimitation described above and adopted by the SINCHI Institute. The information presented here is based on ichthyological research studies in the area and information associated with material deposited in reference scientific collections. This detailed knowledge of the distribution of species in the basin and its main affluents is essential for their conservation. Ongoing climate change, deforestation, mining, dam construction, and overfishing threaten the aquatic systems of the Amazon (Oberdorff et al. 2015, Castello & Macedo 2016), and management and conservation plans still lack basic information, that is of great importance for sustainable development processes (Castello & Macedo 2016, Abell et al. 2008).

The species composition list we present here includes a preliminary dissimilarity analysis among the sub-basin/river systems level. Here we evaluate the questions: do river systems draining the same basin exhibit higher species similarity? If so, do river systems draining different basins exhibit lower species similarity? Which river systems present higher overlapping fish faunas within basins? The complementary analysis we include is an approach based on the simple principle that the freshwater fish species are restricted to the sub-basin they live in. This approach recognizes species distribution patterns and provides a framework for additional biogeographical studies. This type of study is the first of its kind for the Colombian territory and serves as a guide for determining a work plan for study programs and research institutes (e.g. SINCHI Institute), to document the biodiversity and prioritize conservation areas in the Colombian Amazonia region.

# **Materials and Methods**

The Amazonia region in Colombia corresponds to 42.3% of the continental territory (483.163 km<sup>2</sup>), which encompasses the limit of the basin in the west, defined by the watershed; in the north, as far as the Amazon Forest cover reaches; and in the south and east it corresponds to the international political borders with Ecuador, Perú, Brazil, and Venezuela. According to this delimitation, the Colombian Amazonia region is composed of a forested area below 500 m above sea level, equivalent to 80.9% and the remaining territory corresponds to a montane area within the Andean forests.

http://www.scielo.br/bn

Within a hydrographic context, the Colombian Amazonia region includes all systems that drain into the Amazon River and part of the systems that drain into the Orinoco River. In the Orinoco basin, the delimitation starts from the mouth of the Vichada River to the main channel of the Orinoco River, following its course upstream along the south bank. It continues to the southwest, through the sources of the Uvá, Iteviare, and Siare rivers until reaching the mouth of the Jabón Stream in the Guaviare River, continuing to the Ariari River upstream to the mouth of the Güejar River. From this point, it continues upstream to the source of the Sanza River which derives from the Barrialosa Stream and the Peñas River. Then, the delimitation goes in a straight line to the west up to the Guayabero River following its source to the Triunfo mountain (Figure 1). Major river systems included in this region are the Amazonas, Putumayo, Caquetá, Apaporis, Vaupés, and Guainía-Negro, draining the Amazon River basin, and Inírida, Atabapo, Orinoco (in part), Guaviare, and Matavén draining the Orinoco River basin.

The list presented here corresponds to an exhaustive review of published qualified information supported by records documented in the catalogs and species vouchers of scientific reference collections from different institutions (see Supplementary Appendix 1 for a complete list of the biodiversity collections holding fish specimens from the Amazonia region in Colombia). The records considered only include those with exact locations. Records that simply denote political divisions or basins (e.g., Amazonas, Putumayo, Caquetá, Guaviare) are not included. The information presented here follows strict criteria that were applied for selecting the data that were included to provide a reliable and carefully structured list. A considerable number of the species included in the taxonomic list are supported by unpublished literature. Those citations can be consulted in Bogotá-Gregory and Maldonado-Ocampo (2006).

The list follows the classification adopted by Fricke *et al.* (2022). The same source was used to confirm the validity of the species. The list includes the distribution for each basin (*i.e.* Amazon/Orinoco) and the corresponding river system/sub-basin. For this, the hydrogeographic classification proposed by IDEAM (2004) was followed. In addition, information is included, regarding whether or not each species corresponds to a migratory species *sensu* Usma *et al.* (2009), human use, and information about threatened species according to Mojica *et al.* (2012).

The final matrix of presence and absence data was subjected to different analyses: dendrogram and non-metric multidimensional scaling (NMDS), both based on the Kulczynski index, to identify patterns of similarity between sub-basins. The Kulczynski is one of the indices that performs well in detecting underlying gradients (e.g. ecological) (Faith & Minchin 1987), where values close to one denote different systems and zero indicates similarity between them (i.e. co-occurring taxa). Finally, we use PERMANOVA to test for differences in species composition between basins and geological origin. All analyses were done using the package Vegan for the R environment (Oksanen et al. 2015, R Core Team 2016). For the analyses described in this section, we added data from three outgroup river systems of the Orinoco basin (i.e. Bita, Tomo, and Ventuari) (Lasso et al. 2006, Villa-Navarro et al. 2017, Mesa S. et al. 2019). The addition of systems outside the Amazonia region served as an outgroup or reference to elucidate possible similarities among systems of the ingroup (i.e. Amazonia region). The criteria for selection of the outgroup systems are based on two

#### Fishes from the Colombian rainforest biome



Figure 2. a) Percentage of species per order. b) Number of species per family.



Figure 3. a) Number of species per basin and shared between basins. b) Number of species per sub-basin.

aspects: 1) river systems nearby our area of analysis (Amazonia region), and 2) relatively well-studied systems. Therefore, the three systems added are considered representative of those in the Orinoco basin.

#### Results

Based on databases of species vouchers from scientific reference collections and peer-reviewed studies, 1104 species, 375 genera, 53 families, and 16 taxonomic orders are reported for the Colombian Amazonia region (Table 1). Characiformes (515 species, 46.6%) and Siluriformes (391 species, 35.4%) contain more than 80% of the species (Figure 2a and Table S1). The families Characidae (242 species, 21.9%), Loricariidae (123 species, 11.1%), Cichlidae (88 species, 8%), and Doradidae (53 species, 4.8%) have the highest number of species and comprise almost half of species (Figure 2b and Table S1).

We recorded 887 species for the Colombian Amazon basin, which represents an increase of 16.1% according to the latest estimates for this area (DoNascimiento *et al.* 2021). Of these 887 species, 404 (45.5%) are also present in Orinoco tributaries that are included here as part of the Amazonia region, and 217 species are only present in the Orinoco systems that are part of the rainforest biome (Figure 3a). The Amazon River system presents the highest number of species (579), followed by the Caquetá and Putumayo River systems with 490 and 472 species, respectively (Figure 3b). The lowest numbers of species are recorded for the Matavén River system (129 species) and the Guainía-Negro River system (174 species) in the Orinoco basin and Amazon basin, respectively. Disparities between basins could reflect differences in drainage area (Oberdorff *et al.* 2019), combined with intrinsic differences in species richness between basins, e.g. the number of species in nutrient-rich whitewaters compared to nutrient-poor blackwaters (Saint-Paul *et al.* 2000, Bogotá-Gregory *et al.* 2020). Nevertheless, the species numbers at the river systems level could also reflect sampling effort, e.g. number of species of the Amazon River compared to the ones in the Guainía-Negro River.

Of the species reported here (Table 1), 75 are newly recorded for Colombia (DoNascimiento *et al.* 2017, Bogotá-Gregory *et al.* 2020, 2022), 19 are categorized as threatened (Mojica *et al.* 2012), 82 are classified as migratory (Usma *et al.* 2009), and 426 species have commercial importance (88 for human consumption and 365 of commercial significance in the ornamental trade). We included in the list 17 undetermined species. Indisputable taxonomic identification for these species could not be reached and further studies are required to review their specific identities. We expect that most of these undetermined species may eventually be documented as undescribed.

Dendrogram branches of the systems of the Amazonia region plus the three outgroup systems (*i.e.* Bita, Tomo, and Ventuari), at *ca*. 0.5

Taxa	Amazonas	Putumavo	Caquetá	Ananoris	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Interdo	Custian	Orinoco	Matavén	Orinoco Basin	Collee	ections	is Citations		Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Order Myliobatiformes					_															
Family Potamotrygonidae																				
Heliotrygon gomesi Carvalho & Lovejoy 2011	x						х							CIA	COL	Donascimiento et al. 2017, Lasso et al. 2013				
Paratrygon aiereba (Müller & Henle 1841)	x	х					x							CIACOL, IAvHP,	, CP-IIAP, MSUM	Donascimiento et al. 2017, Lasso et al. 2013, Lasso et al. 2009, Ortega-Lara 2016			orn	VU (A2a,d)
Plesiotrygon iwamae Rosa, Castello & Thorson 1987	x	x					х							CIACOL ICNN	L, IAvHP, MHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			orn	
Plesiotrygon nana Carvalho & Ragno 2011	x	x					х							CIACOL	L, IAvHP	Donascimiento et al. 2017, Lasso et al. 2013			orn	
Potamotrygon constellata (Vaillant 1880)	, x	х	х				х							IAvHP, I	CNMHN	Bogotá-Gregory & Maldonado- Ocampo 2005, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a			orn	
Potamotrygon motoro (Müller & Henle 1841)	х	х	х	х			х	x	,		х	x	х	CIACOL ICNMH1	L, IAvHP, N, MPUJ	Donascimiento et al. 2017, Galvis et al. 2006, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			orn	(NT)
Potamotrygon orbignyi (Castelnau 1855)	x					x	х	х	,		х	£	x	CIACOL, IAVHP, I	CZUT-IC, ICNMHN	Donascimiento et al. 2017, Lasso et al. 2013, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	(NT)
Potamotrygon schroederi Fernández-Yépes 1958				x			x	x		,	х	i.	x	ICNN	MHN	Correa 2003, Correa 2008, Donascimiento <i>et al.</i> 2017, Kullander 2004, Lasso <i>et al.</i> 2009, Villa-Navarro <i>et al.</i> 2021			orn	VU (A4d)
Potamotrygon scobina Garman 1913	x						x			>	Х	í.	x	CIACOI	L, IAvHP	Acosta-Santos 2016, Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2013, Villa-Navarro <i>et al.</i> 2021				
Order Osteoglossiformes																				
Family Osteoglossidae																				
Osteoglossum bicirrhosum (Cuvier 1829)	x	х	х	х			х							CIACOL, CZUT-IC ICNMH1	, CP-IIAP, C, IAvHP, N, MPUJ	Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006			con, orn	VU (A2d)
Family Arapaimidae																				
Arapaima gigas (Schinz 1822)	x	x	х	х			х							CIACOL, IAvHP, I	CZUT-IC, CNMHN	Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006			con	VU (A2d)
Order Clupeiformes																				
Family Pristigasteridae																				
Ilisha amazonica (Miranda-Ribeiro 1920)	х						х							CIACOL,	ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Pellona castelnaeana Valenciennes 1847	х	х	х	х			х	х		,			х	CIACOL, IAvHP, IO MP	CZUT-IC, CNMHN, PUJ	Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Santos 2000, Vejarano 2000		х	con	
Pellona flavipinnis (Valenciennes 1837)	x	x	х				х			>	i.			CIACOL ICNN	L, IAvHP, MHN	Calderón & Hincapié 2001, Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021		х	con	
Pristigaster cayana Cuvier 1829	x	x	х				х							CIACOL ICNN	L, IAvHP, MHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000				
Family Engraulidae																				
Amazonsprattus scintilla Roberts 1984						х	х	х	,		х	x	х	CZUT-IC	C, IAVHP	Villa-Navarro et al. 2021				
Anchoviella guianensis (Eigenmann 1912)		х	х				х	х	,		X	x	х	CIACOL 1 IAv	1913, 1919, vHP	Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Ortega-Lara 2016, Villa-Navarro et al. 2021				
Anchoviella jamesi (Jordan & Seale 1926)	х	x					х		,	:	х	í.	x	CIACOI 21824,	L, IAvHP , 25896	Kullander & Ferraris 2003				
Jurengraulis juruensis (Boulenger 1898)	x	x					x							ICNMH	IN, UCO	Donascimiento <i>et al.</i> 2017, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Santos 2000, Vejarano 2000				
Lycengraulis batesii (Günther 1868)	x	x	x				x			,	х		x	CZUT-IC ICNMH1	C, IAvHP, N, MPUJ	Calderón & Hincapié 2001, Donascimiento et al. 2017, Mojica et al. 2005, Villa-Navarro et al. 2021				

**Table 1.** List of fish species from the Amazonia region in Colombia and distribution in the major river systems. See Supplementary Appendix S5 for a complete list of references "Citations". con = human consumption. orn = ornamental trade.

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Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Matavén	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Order Characiformes																		
Family Crenuchidae																		
Ammocryptocharax elegans Weitzman & Kanazawa 1976				x		x	x	x	х		х	x	CIACOL, CZUT-IC, IAvHP, FMNH, USNM	Donascimiento et al. 2017, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Ammocryptocharax minutus Buckup 1993	x					x	x	x	x			x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005				
Characidium boehlkei Géry 1972			x				x						CIACOL 2681, 2682		х			
Characidium chupa Schultz 1944						x	x		x	x		x	CZUT-IC, IAvHP, MPUJ					
Characidium crandelli Stendachner 1915				x	x		x						CIACOL, IAvHP	Bogotá-Gregory et al. 2020				
Characidium etheostoma Cope 1872	x	x	x				x		x			х	CIACOL, CZUT-IC, ICNMHN, MPUJ	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005				
Characidium geryi (Zarske 1997)			x				x						CIACOL 1923		x			
<i>Characidium longum</i> Taphorn, Montaña & Buckup 2006					x	x	x	x	x	x		x	CIACOL, CZUT-IC, ICNMHN	Lasso <i>et al.</i> 2009, Villa-Navarro <i>et al.</i> 2021				
Characidium pellucidum Eigenmann 1909	x	x	x	х	х	x	x	x	х	x		х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Prieto 2000, Villa-Navarro et al. 2021			orn	
Characidium pteroides Eigenmann 1909	x	x	x		х	x	x	x				х	CIACOL, CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017, Maldonado-Ocampo et al. 2008, Villa-Navarro et al. 2021			orn	
Characidium roesseli Géry 1965	x		x				x						ICNMHN, MPUJ	Donascimiento et al. 2017, Mojica et al. 2005				
Characidium steindachneri Cope 1878		x	х		x		х		x	x		x	CIACOL, CZUT-IC, CAS/SU, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Galvis et al. 2007b, Lasso et al. 2009			orn	
Characidium zebra Eigenmman 1909	x	x	x		x		x		x	x		x	CIACOL, CAS/SU, CIACOL, CZUT-IC, IAVHP, ICNMHN, MPUJ	Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn	
Characidium sp.			x				x						CIACOL 2103					
Crenuchus spilurus Günther 1863	x	x	x				x	x	x		x	x	CIACOL, IAvHP, ICNMHN, ROM, UF	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007b, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn	
<i>Elachocharax geryi</i> Weitzman & Kanazawa 1978				x		х	x		x			x	IAvHP, ICNMHN	Villa-Navarro et al. 2021				
Elachocharax junki (Géry 1971)	x			x			x						CIACOL 1094, 3127		x			
Elachocharax mitopterus Weitzman 1986					х	x	x						CZUT-IC, MPUJ	Donascimiento et al. 2017				
Elachocharax pulcher Myers 1927	x	x	x	x	x	x	x	x	x			х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b Lasso et al. 2009, Mojica et al. 2005, Prieto 2000, Weitzman & Kanazawa 1978	,		orn	
Klausewitzia sp.	x						x						ICNMHN	Arbeláez et al. 2004, Donascimiento et al. 2017				
Melanocharacidium dispilomma Buckup 1993	x		x		x	x	x		x	x		x	CZUT-IC, ICNMHN, MPUJ	Villa-Navarro et al. 2021				
Melanocharacidium melanopteron Buckup 1993					x		x						CZUT-IC 12309					
Melanocharacidium pectorale Buckup 1993	x		x		x	x	x		x			x	CZUT-IC, ICNMHN	Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Villa-Navarro et al. 2021				
Microcharacidium gnomus Buckup 1993	x	x					x				х	x	CIACOL, IAvHP					

Continue...

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				_														
Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Microcharacidium weitzmani Buckup 1993	x	x				x	x						CZUT-IC, ICNMHN	Arroyave 2005				
Odontocharacidium aphanes (Weutzman & Kanazawa 1977)	x						x						IAVHP, ICNMHN	Arbeláez et al. 2008, Buckup 1993, Donascimiento et al. 2017, Mojica et al. 2005, Prieto 2000				
Poecilocharax weitzmani Géry 1965	x			x	x	x	x	x	x		хх	x	CIACOL, CZUT-IC, IAvHP, MPUJ, NRM, SMF	Donascimiento et al. 2017, Géry 1965, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Family Erythrinidae																		
<i>Erythrinus</i> <i>erythrinus</i> (Bloch & Schneider 1801)	x	x	x	x	x		x		x	x		x	CIACOL, CZUT-IC, ICNMHN, MPUJ, ROM	Arroyave 2005, Correa 2003, Donascimiento et al. 2017, Lasso et al. 2009, Ortega et al. 2006, Villa-Navarro et al. 2021				
Hoplerythrinus unitaeniatus (Spix & Agassiz 1829)	x	x	x	x	x		х	x	x	x	х	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM, ROM	Bejarano <i>et al.</i> 2006, Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b, Lasso <i>et al.</i> 2009, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro <i>et al.</i> 2021			con, orn	
Hoplias aimara (Valenciennes 1847)										x		х	MPUJ 11022					
Hoplias curupira Oyakawa & Mattox 2009									x			x	IAvHP 2274					
Hoplias malabaricus (Bloch 1794)	x	x	x	x	x	х	x	x	х	x	хх	x	ANSP, CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM, ROM, UF	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Bejarano et al. 2006, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			con, orn	
Family Parodontidae																		
Parodon apolinari Myers 1930										x		х	IAvHP, MPUJ	Galvis et al. 2007b, Lasso et al. 2009			orn	
Parodon buckleyi Boulenger 1887		x	x				x			x		x	CIACOL, CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017				
Parodon pongoensis (Allen 1942)	x	x	x				x			x		x	ANSP, CIACOL, CZUT-IC, IAvHP	Donascimiento et al. 2017, Fowler 1945, Galvis et al. 2007a				
Family Cynodontidae																		
Cynodon gibbus (Spix & Agassiz 1829)	x	x	x	x			x		x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MCZ, ROM	Bejarano et al. 2006, Donascimiento et al. 2017, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007b, Mojica et al. 2005, Ortega et al. 2006, Toledo-Piza 2000a		x	con, orn	
Hydrolycus armatus (Jardine 1841)		x	x				x	x	x	x	хх	x	CZUT-IC, IAvHP, ICNMHN	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Galvis et al. 2007b, Villa-Navarro et al. 2021		х	con	
Hydrolycus scomberoides (Cuvier 1819)	х	х	х	х		x	х		x	x		х	CIACOL, CZUT-IC, IAvHP, ICNMHN, UF	Bejarano et al. 2006, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000		x	con	
Hydrolycus tatauaia Toledo-Pizza Menezes & Santos 1999		x	x				x	x	x	x	х	x	CZUT-IC, IAvHP, ICNMHN	Lasso <i>et al.</i> 2009, Villa-Navarro <i>et al.</i> 2021		х	con	
<i>Hydrolycus wallacei</i> Toledo-Piza, Menezes & Santos 1999			x	x	x		x	x	x	x		x	CZUT-IC, IAvHP	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021		x	con	
Rhaphiodon vulpinus Spix & Agassiz 1829	x	x	x				x	x	x	x	x	х	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UF	Bejarano et al. 2006, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021		x	con	
Family Serrasalmidae																		
Catoprion mento (Cuvier 1819)		x	x				x	x	x	x		x	ICNMHN, MPUJ	Bejarano et al. 2006, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007b, Lasso et al. 2009				
Colossoma macropomum (Cuvier 1816)	x	x	x				x			x	х	х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Bejarano et al. 2006, Contreras 1999, Correa 2003, Correa 2008, Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		x	con	(NT)
Metynnis argenteus Ahl 1923	x	x	x			x	x	x	x	x		x	ICNMHN, MPUJ	Bejarano et al. 2006, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009		x	orn	
Metynnis guaporensis Eigenmann 1915		x					x						CICAOL 495		x			
Metynnis hypsauchen (Müller & Trsochel 1844)	x	x	x	x	x	x	x		x	x		x	CIACOL, CZUT-IC, IAvHP, MPUJ	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021		x	orn	

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Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Matavén Orinoco Basin		Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Metynnis lippincottianus (Cope 1870)		x	x				x		x			x	c	CZUT-IC, IAvHP	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Villa-Navarro et al. 2021		x		
Metynnis longipinnis Zarske & Géry 2008									х			х	C.	CIACOL 1458		х			
<i>Metynnis luna</i> Cope 1878	x	x	x	x			x		x	x	x	х	¢.	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b, Lasso <i>et al.</i> 2009, Villa-Navarro <i>et al.</i> 2021		x	orn	
Metynnis maculatus (Kner 1858)	x		x				x							CIACOL 559, ICNMHN 579		x		orn	
Myleus setiger Müller & Troschel 1844		x	x	x	x		x			x		х	C.	CIACOL, CZUT-IC, IAvHP	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017				
<i>Myloplus asterias</i> (Müller & Troschel 1844)	x	х	х	х	x		x							CIACOL, CZUT-IC, IAVHP, ICNMHN	Correa 2003, Correa 2008, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009			orn	
Myloplus lobatus (Valenciennes 1850)		x					x							CZUT 14779		х			
Myloplus rubripinnis (Müller & Troschel 1844)	x	x	x	x	x		x		x	x	x	x x	£	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Bejarano et al. 2006, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021		х	con, orn	
Myloplus schomburgkii (Jardine 1841)	x	x	x	x			x		x		x	х	£	CZUT-IC, IAvHP, ICNMHN	Correa 2003, Correa 2008, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009		x	orn	
Myloplus torquatus (Kner 1858)	x	x	x	x			x	x	x			х	C.	CIACOL, CZUT-IC, MPUJ	Donascimiento et al. 2017, Lasso et al. 2009				
Mylossoma albiscopum (Cope 1872)	x	x	x	x			x	х	x	x		х	<b>,</b>	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UF	Villa-Navarro <i>et al</i> . 2021	х			
Mylossoma aureum (Spix & Agassiz 1829)	x	x	x		x		x		x	x		х	د ا	CIACOL, CZUT-IC, IAvHP, ICNMHN, UF	Bejarano et al. 2006, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021		x	con	
Piaractus brachypomus (Cuvier 1818)	x	x	x				x		x	x		х	د ا	CIACOL, CZUT-IC, IAvHP, ICNMHN, UF	Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000		x	con	
Piaractus orinoquensis Escobar L., Ota, Machado-Allison, Andrade-López, Farias & Hrbek 2019										x		х	C.		Villa-Navarro <i>et al.</i> 2021				
Prosomyleus rhomboidalis (Cuvier 1818)		x					x		x			х	C.	CZUT-IC, IAvHP, ICNMHN	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009				
Pygocentrus cariba (Humboldt 1821)	x						x	x	x	x	x	x x	C.	CIACOL, CZUT-IC, IAvHP	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			con	
Pygocentrus nattereri Kner 1858	x	x	х				x			x		x x	C.	CIACOL, CZUT-IC, IAvHP, ICNMHN	Calderón & Hincapié 2001, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Santos 2000, Vejarano 2000			con	
Pygopristis denticulata (Cuvier 1819)								x	х	x		x x	C.	CZUT-IC, IAvHP	Galvis et al. 2007b, Lasso et al. 2009				
Serrasalmus altuvei Ramírez 1965	x	x	х	x			x		х	x		х	C.	IAvHP, ICNMHN	Calderón & Hincapié 2001, Correa 2003, Donascimiento <i>et al.</i> 2017, Villa-Navarro <i>et al.</i> 2021				
Serrasalmus aureus Spix & Agassiz 1829		x	х				x							IAvHP, ICNMHN	Bejarano et al. 2006, Donascimiento et al. 2017				
Serrasalmus calmoni Steindachner 1908	x	x	х	x			x			x	x	х	C.	CIACOL, CZUT-IC, IAvHP, ICNMHN	Bejarano et al. 2006, Correa 2003, Donascimiento et al. 2017, Mojica et al. 2005, Santos 2000, Vejarano 2000				
Serrasalmus careospinus (Fink & Machado- Allison 1992)		x	x				x	x				х	£	CZUT-IC, IAvHP	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Lasso et al. 2009				
Serrasalmus compressus Jégu, Leão & Santos 1991	x	x					x							CIACOL, ICNMHN, UCO	Donascimiento et al. 2017, Galvis et al. 2007a				
Serrasalmus eigenmanni Norman 1929	x		х	x			x							CIACOL, CZUT-IC, MPUJ	Arroyave 2005, Correa 2008, Donascimiento et al. 2017				
Serrasalmus elongatus Kner 1858	x	x	x	x			x		x	x		х	c	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Correa 2003, Correa 2008, Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Santos 2000, Vejarano 2000, Villa-Navarro <i>et al.</i> 2021				

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Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Serrasalmus gouldingi Fink & Machado-Alison 1992		x		x	x		x	x	x		x	x	CIACOL, CZUT-IC, IAvHP	Donascimiento et al. 2017, Lasso et al. 2009				
Serrasalmus hollandi Eigenmann 1915	x		x				x						ICNMHN, UCO	Donascimiento et al. 2017, Mojica et al. 2005, Villa-Navarro et al. 2021				
Serrasalmus irritans Peters 1877								x	х	х		х	CIACOL, ICNMHN, MPUJ	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021				
Serrasalmus maculatus Kner 1858			x				x						MPUJ 12239	Jegú & Dos Santos 2001				
Serrasalmus maculipinnis (Fink & Macahdo- Allison 1992)				x		x	x						CZUT-IC, IAvHP, ICNMHN	Correa 2003, Donascimiento et al. 2017				
Serrasalmus manueli (Fernández-Yépez & Ramírez 1967)	x				x	x	x	x	x	x	х	x	CIACOL, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021				
Serrasalmus medinai Ramírez 1965	x		x	x			x						CIACOL, ICNMHN	Calderón & Hincapié 2001, Correa 2003, Donascimiento <i>et al.</i> 2017, Mojica <i>et al.</i> 2005, Santos 2000, Vejarano 2000				
Serrasalmus nalseni Fernández-Yépez 1969				х			x				х	х	ICNMHN	Correa 2003, Donascimiento et al. 2017, Lasso et al. 2009				
Serrasalmus rhombeus (Linnaeus 1766)	x	x	x	x	x		x	х	x	x	хх	x	CAS/SU, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2004, Bejarano et al. 2006, Calderón & Hincapié 2001, Contreras 1999, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			con	
Serrasalmus sanchezi Géry 1964	x		x				x						CIACOL, CZUT-IC, IAvHP	Donascimiento et al. 2017				
Serrasalmus spilopleura Kner 1858	x						x						ICNMHN	Galvis et al. 2006				
Serrasalmus striolatus Steindachner 1908	x	х	х	x			x	x	х			х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Bejarano et al. 2006, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009				
Family Hemiodontidae																		
Anodus elongatus Agassiz 1829	x	х	х				x		х	х		х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Bejarano et al. 2006, Calderón & Hincapié 2001, Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000				
Anodus orinocensis (Steindachner 1887)						х	x	x	х	х		х	CZUT-IC	Lasso et al. 2009, Villa-Navarro et al. 2021		х		
Argonectes longiceps (Kner 1858)		x	x		x		x	x	x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM	Bejarano <i>et al.</i> 2006, Calderón & Hincapié 2001, Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009, Villa-Navarro <i>et al.</i> 2021				
Bivibranchia fowleri (Steindachner 1908)	x				x		x		x		хх	х	CZUT-IC, IAVHP	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Hemiodus amazonum (Humboldt 1821)				x			x						ICNMHN 17168					
Hemiodus argenteus Pellegrin 1908	x	x	x				x		x	x		х	CIACOL, IAVHP, ICNMHN, MPUJ, ROM	Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Villa-Navarro et al. 2021			orn	
Hemiodus atranalis (Fowler 1940)		х					x						CZUT-IC, IAvHP	Donascimiento et al. 2017				
Hemiodus gracilis Günther 1864	x	x	x		x	x	x	x	x	x	X	x	CIACOL, CZUT-IC, IAVHP, ROM	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Ortega-Lara 2016, Villa-Navarro et al. 2021		x	orn	
Hemiodus immaculatus Kner 1858		x			x		x	x	x	x	X	x	CIACOL, CZUT-IC, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021		x	orn	
Hemiodus microlepis Kner 1858	x	х					x						CIACOL, CZUT-IC, ICNMHN	Arbeláez et al. 2004, Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000				
Hemiodus semitaeniatus Kner 1858		x	x	x	x	x	x	x	x	x		x	CIACOL, CZUT-IC, NRM	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009			orn	
Hemiodus thayeria Böhlke 1955					x	x	x		x			x	CIACOL, CZUT-IC, IAVHP, ICNMHN, CAS/SU	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Hemiodus unimaculatus (Bloch 1794)	x	x	x	x	x		x	x	x	x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Bejarano et al. 2006, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Hemiodus vorderwinkleri (Géry 1964)	x						x						MHNG	Donascimiento <i>et al.</i> 2017, Gutiérrez 2003				

### Fishes from the Colombian rainforest biome

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Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Family Anostomidae																		
Abramites hypselonotus (Günther 1868)	x	x	x				x	x	х	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, USNM	Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Anostomoides atrianalis Pellegrin 1909			x		x		x						CIACOL, ICNMHN					
Anostomus anostomus (Linnaeus 1758)	x	x	x				x	x	x			x	CZUT-IC, IAvHP	Donascimiento et al. 2017, Lasso et al. 2009, Ortega-Lara 2016, Villa-Navarro et al. 2021			orn	
Anostomus ternetzi Fernández-Yépez 1949			x		x		x	x	x		x	x	CZUT-IC, IAvHP, ICNMHN, MPUJ	Calderón & Hincapié 2001, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b, Lasso <i>et al.</i> 2009, Villa-Navarro <i>et al.</i> 2021			orn	
Gnathodolus bidens Myers 1927					x		x						CZUT-IC 12278					
Laemolyta fernandezi Myers 1950								х		x		x	IAvHP	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Laemolyta garmani (Borodin 1931)	x		х		х		х						CIACOL, ICNMHN, MPUJ	Donascimiento et al. 2017, Mojica et al. 2005		x	orn	
Laemolyta proxima (Garman 1890)	x		х	х			х			х		x	CIACOL, CZUT-IC, IAvHP	Correa 2003, Donascimiento et al. 2017				
Laemolyta taeniata (Kner 1858)	x	x	х		x	х	x	x	х			х	CIACOL, CZUT-IC, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006			orn	
Leporellus vittatus (Valenciennes 1850)			х	х			х						CIACOL, IAvHP, ICNMHN				orn	
<i>Leporinus agassizi</i> Steindachner 1876	x	x	x	x	x		x	x	x	x		х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Bejarano et al. 2006, Calderón & Hincapié 2001, Contreras 1999, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		х	con, orn	
Leporinus altipinnis Borodin 1929									x			х	CIACOL	Bogotá-Gregory et al. 2020, Villa-Navarro et al. 2021				
Leporinus amazonicus Santos & Zuanon 2008	x				x		x						CIACOL	Donascimiento et al. 2017				
Leporinus arimaspi Burns, Frable & Sidlauskas 2014									x	x		x	IAvHP 19575	Villa-Navarro <i>et al.</i> 2021				
Leporinus boehlkei Garavello 1988									х	x		х	CIACOL, IAvHP				orn	
Leporinus brunneus Myers 1950		x	x	x	x		x	x	x			х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Bejarano et al. 2006, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009				
Leporinus enyae Burns, Birindelli & Sidlauskas 2017								х			x	х	CIACOL	Burns et al.2017, Villa-Navarro et al. 2021				
Leporinus fasciatus (Bloch 1794)	x	x	x	x	x	x	x	x	x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Bejarano et al. 2006, Contreras 1999, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		х	con, orn	
Leporinus friderici (Bloch 1794)	x	x	x	x	x	х	x	x	x	x		x x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UCO	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Bejarano et al. 2006, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021		x	con	
<i>Leporinus jamesi</i> Garman 1929	x						x						ICNMHN	Donascimiento et al. 2017, Garavello et al. 2014				
Leporinus klausewitzi Géry 1960	x		x	x	x		x						CIACOL, CZUT-IC, IAvHP, ICNMHN	Bejarano <i>et al.</i> 2006, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005				
Leporinus moralesi Fowler 1942	x	x	x				x						CIACOL, CZUT-IC	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Ortega et al. 2006				
Leporinus niceforoi Fowler 1943	x		x				x	x				x	ANSP, CIACOL, MPUJ	Donascimiento et al. 2017, Fowler 1943, Lasso et al. 2009				
Leporinus octomaculatus Garavello 2000										x		x	IAvHP 16191					
Leporinus parae Eigenmann 1907	x	x					х			x		х	CZUT-IC, IAvHP	Donascimiento et al. 2017				
Leporinus striatus Kner 1858		x	х				x						ICNMHN, CAS/SU	Donascimiento et al. 2017, Galvis et al. 2007b, Ortega-Lara 2016			con	

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Mataven	UTINOCO DASIN	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Leporinus subniger Fowler 1943	x	x	x				x							ANSP, IAVHP, ICNMHN	Donascimiento et al. 2017, Fowler 1943				
Leporinus y-ophorus Eigenmann 1922									x	x	x	,	x	CZUT-IC, ICNMHN	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Megaleporinus trifasciatus (Steindachner 1876)	x	x	x				x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000			orn	
Pseudanos trimaculatus (Kner 1858)	x	х		x	x		x	x				3	ĸ	CIACOL, CZUT-IC, ICNMHN, MPUJ, NRM, ROM	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
<i>Pseudanos varii</i> Birindelli, Lima & Britski 2012								x				3	ĸ	FMNH	Birindelli et al. 2012				
Pseudanos winterbottomi Sidlauskas & Santos 2005								x			x	3	ĸ	CAS/SU	Galvis et al. 2007b, Lasso et al. 2009			orn	
Rhytiodus argenteofuscus Kner 1858	x	x					x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006			orn	
Rhytiodus microlepis Kner 1858	x	x	x				x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000				
Schizodon fasciatus Spix & Agassiz 1829	x	x	x	x			x						I	CIACOL, CZUT-IC, AvHP, ICNMHN, UF	Arbelácz <i>et al.</i> 2004, Calderón & Hincapié 2001, Contreras 1999, Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Prieto 2000, Santos 2000, Vejarano 2000		х	con, orn	
<i>Schizodon</i> <i>scotorhabdotus</i> Sidlauskas, Gavello & Jellen 2007								x	x	x	x	3	ĸ	CIACOL, CZUT-IC, IAvHP, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021			con	
Synaptolaemus latofasciatus (Steindachner 1910)					x		x					x 3	ĸ	CZUT-IC	Donascimiento et al. 2017				
Family Chilodontidae																			
Caenotropus labyrinthicus (Kner 1858)	x	x	х		x		x	x	x	x		2	x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Caenotropus maculosus (Eigenmann 1912)											x	,	x		Villa-Navarro et al. 2021				
Caenotropus mestomorgmatos Vari, Castro & Raredon 1995		x	x		x	x	x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Bejarano et al. 2006, Donascimiento et al. 2017				
<i>Chilodus gracilis</i> Isbrücker & Nijssen 1988		x	x		x		х							CIACOL, CZUT-IC, ICNMHN, USNM	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Chilodus punctatus Müller & Trosche 1844	x	x	x		x	x	x	x	x	х		3	ĸ	CZUT-IC, IAvHP, ICNMHN, MPUJ, ROM	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn	
Family Curimatidae																			
Curimata aspera Günther 1868	х	х	х				х							CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM	Calderón & Hincapié 2001, Donascimiento <i>et al.</i> 2017, Vari 1989, Ortega <i>et al.</i> 2006		х		
Curimata cisandina (Allen 1942)	x	x					х							CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Santos 2000, Vejarano 2000				
Curimata cyprinoides (Linnaeus 1766)	x	х					х	x	х			,	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Lasso et al. 2009, Prieto 2000, Villa-Navarro et al. 2021		x		
Curimata incompta Vari 1984	x	x					х		х	x		,	ĸ	CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021				
Curimata knerii Steindachner 1876	x						х							CIACOL 402, 831		х			
<i>Curimata ocellata</i> Eigenmman & Eigenmman 1889	x	x	x	x			x							CZUT-IC, IAvHP, ICNMHN	Bejarano <i>et al.</i> 2006, Correa 2003, Donascimiento <i>et al.</i> 2017, Mojica <i>et al.</i> 2005, Santos 2000, Vejarano 2000				
Curimata roseni Vari 1989	x	x	x				x			x		,	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Bejarano et al. 2006, Galvis et al. 2007a, Prieto 2000				

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Matavén	<b>Orinoco Basin</b>	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Curimata vittata (Kner 1858)	x	x	x	x			x		x	x			x	CIACOL, CZUT-IC, IAvHP, ICNNHM, MCZ	Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b, Lasso <i>et al.</i> 2009, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Prieto 2000, Santos 2000, Vari 1989, Vejarano 2000, Villa-Navarro <i>et al.</i> 2021		x	con	
Curimatella alburnus (Müller & Troschel 1844)	x	x	x	x			x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vari 1992, Vejarano 2000		x		
Curimatella dorsalis (Eigenmann & Eigenmann 1889)	x	x	x		x		x	x	x	x	x		x	CZUT-IC, ICNMHN, IMCN, MPUJ, ROM, UCO	Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Vari 1992				
Curimatella immaculata (Fernández-Yépez 1948)	x	x	x		x		x		x	x	x		x	AMNH, CIACOL, CZUT-IC, IAvHP, MPUJ, NRM	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Vari 1992, Villa-Navarro et al. 2021				
Curimatella meyeri (Steindachner 1882)	x	x	x	x	x		x							CIACOL, CZUT-IC, IAvHP, ICNMHN, UCO	Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Santos 2000, Vari 1992, Vejarano 2000				
Curimatopsis cryptica Vari 1982				x	x		x	x	x	x			x	CIACOL, ICNMHN, MPUJ, NRM	Lasso et al. 2009, Villa-Navarro et al. 2021				
Curimatopsis evelynae Géry 1964		x			x	x	x	x	x	x		x	x	CIACOL, IAvHP, CZUT-IC, ICNMHN, MPUJ	Galvis et al. 2007a, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Curimatopsis macrolepis (Steindachner 1876)	x	x	х	x	x	x	x	x	х	х	x	х	x	AMNH, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM, ROM, UF, USNM	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Vari 1982, Villa-Navarro et al. 2021				
Curimatopsis microlepis Eigenmann & Eigenmann 1889	x					x	x							CZUT-IC, ICNMHN	Donascimiento et al. 2017				
Cyphocharax abramoides (Kner 1858)								x	x	x			x	NRM	Lasso et al. 2009, Villa-Navarro et al. 2021				
Cyphocharax festivus Vari 1992		x			x	x	x		x	x			x	CIACOL, CZUT-IC, MPUJ, NRM	Donascimiento et al. 2017				
Cyphocharax leucostictus Eigenmann & Eigenmann 1889					x		x	x						CIACOL, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Villa-Navarro et al. 2021				
Cyphocharax multilineatus (Myers 1927)					x		x	x	x				x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Cyphocharax nigripinnis Vari 1992	x	x	x				x							CIACOL, CZUT-IC, AMNH, IAvHP	Donascimiento et al. 2017, Galvis et al. 2007a, Vari 1992		x		
Cyphocharax notatus (Steindachner 1908)		x	x				x							CZUT-IC	Donascimiento et al. 2017				
Cyphocharax oenas Vari 1992									x	x	x		x	ICNMHN, MPUJ	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021				
<i>Cyphocharax</i> <i>pantostictos</i> Vari & Barriga Salazar 1990	x	x	x				x							CZUT-IC, IAvHP, NRM	Arbeláez et al. 2008, Donascimiento et al. 2017, Ortega et al. 2006, Vari 1992				
Cyphocharax plumbeus (Eigenmann & Eigenmann 1889)	х	x			x		x		x				х	CIACOL 206, 398, 399, 443, 953, 1495, ICNMHN 15993- 15995		х			
Cyphocharax spiluropsis (Eigenmann & Eigenmann 1889)	x	x	x	x	x		x							CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Ortega et al. 2006, Prieto 2000, Vejarano 2000				
Cyphocharax spilurus (Günther 1864)	x	x	x		x	x	x	x	x	x			x	CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM, UF	Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Santos 2000, Villa-Navarro et al. 2021			orn	
Potamorhina altamazonica (Cope 1878)	x	x	x	x			x	x	x	x	x		x	ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN, MCZ, MPUJ, NRM	Calderón & Hincapié 2001, Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vari 1984, Vejarano 2000, Villa-Navarro et al. 2021		x	con	
Potamorhina latior (Spix & Agassiz 1829)	x	x	x	x			x			x			x	ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, ROM, UCO	Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Santos 2000, Vari 1984, Vejarano 2000			con	

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Orinoco Basin		Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Potamorhina pristigaster (Steindachner 1876)	x		x	x			x							CZUT-IC, IAvHP, ICNMHN, MPUJ	Correa 2003, Donascimiento et al. 2017				
Psectrogaster amazonica Eigenmann & Eigenmann 1889	x	x	x				x						C	CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM, ROM, UCO	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000				
Psectrogaster ciliata (Müller & Troschel 1844)	x						x			x	x	x	0	CIACOL, CZUT-IC, IAvHP, MPUJ	Vari 1989, Villa-Navarro et al. 2021		x		
Psectrogaster essequibensis (Günther 1864)	x		x	x			x						C	CIACOL, CZUT-IC, ICNMHN	Cipamocha 2002, Donascimiento <i>et al.</i> 2017, Mojica <i>et al.</i> 2005, Santos 2000, Vejarano 2000				
Psectrogaster rhomboides Egenmann & Eigenmann 1889	x		x	x			x						C	CIACOL, CZUT-IC, IAvHP, ICNMHN	Correa 2003, Donascimiento <i>et al.</i> 2017, Mojica <i>et al.</i> 2005, Prieto 2000, Santos 2000, Vejarano 2000				
Psectrogaster rutiloides (Kner 1858)	x	x			x		x		x	x		x	0	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000		x		
Steindachnerina argentea (Gill 1858)	х	x	х				x		x	x		x	. (	CIACOL, CZUT-IC, IAvHP, ICNMHN, IMCN, MPUJ	Lasso et al. 2009				
Steindachnerina bimaculata (Steindachner 1876)	x		x				x						C	ANSP, CIACOL, ZUT-IC, ICNMHN, NRM, ROM	Donascimiento et al. 2017, Mojica et al. 2005, Prieto 2000, Santos 2000, Vari 1991, Vejarano 2000				
Steindachnerina dobula (Günther 1868)		x	x				x							ANSP, CIACOL, ICNMHN, USNM	Donascimiento et al. 2017, Fowler 1943, Galvis et al. 2007a, Vari 1991, Ortega et al. 2006				
Steindachnerina guentheri (Eigenmann & Eigenmann 1889)	x	x	x	x	x		x		x	x	x	x	. (	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021				
Steindachnerina hypostoma (Boulenger 1887)	x	x					x			x		x		CZUT-IC, IAvHP, ICNMHN	Donascimiento <i>et al.</i> 2017, Mojica <i>et al.</i> 2005, Vari 1991, Ortega <i>et al.</i> 2006				
Steindachnerina leucisca (Günther 1868)	x						x							CIACOL 112, 201, ICNMHN 13385, 13665		х			
<i>Steindachnerina</i> <i>planiventris</i> Vari & Williams Vari 1989		x	x				x							ICNMHN, UCO	Ortega-Lara 2016				
Steindachnerina pupula Vari 1991								x	x	x	x	x		IAvHP, CZUT-IC, MPUJ	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021				
Family Prochilodontidae																			
Prochilodus mariae Eigenmann 1922					х		х		x	x	х	х	0	CIACOL, CZUT-IC, IAvHP, MPUJ	Galvis et al. 2007b, Lasso et al. 2009		х	con	
Prochilodus nigricans Spix & Agassiz 1829	x	x	x	x			х						C	ANSP, CAS/SU, CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM, USNM	Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000		х	con	
Prochilodus rubrotaeniatus Jardine 1841	x	x	x				x							CZUT-IC, IAvHP, ICNMHN, UF	Donascimiento et al. 2017		x		
Semaprochilodus insignis (Jardine 1841)	х	x	x				x		x			x		ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UMMZ, UF	Arbeláez <i>et al.</i> 2008, Arbeláez <i>et al.</i> 2004, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Gutiérrez 2003, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Prieto 2000, Santos 2000, Vejarano 2000		x	orn	
Semaprochilodus kneri (Pellegrin 1909)	x	x		x			x	x	x	x	3	K X	0	CIACOL, CZUT-IC, ICNMHN, ROM	Correa 2003, Correa 2008, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b, Lasso <i>et al.</i> 2009		x	con, orn	
Semaprochilodus laticeps (Steindachner 1879)									x	x	3	K X	0	CIACOL, CZUT-IC, IAvHP	Galvis et al. 2007b, Lasso et al. 2009		x	con, orn	
Semaprochilodus taeniurus (Valenciennes 1817)	x		x	x			x							IAvHP, ICNMHN	Correa 2003, Correa 2008, Donascimiento et al. 2017		x		
Family Lebiasinidae																			
Copeina guttata (Steindachner 1876)	x	х			x		х		x			x		CIACOL, IAvHP, NMW, NRM	Arbeláez et al. 2008, Donascimiento et al. 2017, Ortega et al. 2006			orn	

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Copella callolepis (Regan 1912)		x	x				x						(	CIACOL 4598, 4599, 4601		x			
Copella compta (Myers 1927)					x		x						3	CIACOL 2415, 8019-3024, CZUT-IC 7881, ICNMHN 14057-14060				orn	
Copella eigenmanni (Regan 1912)		x		x	x	x	x	x	x	x		,	¢,	CIACOL, CZUT-IC, IAvHP, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Copella nattereri (Steindachner 1876)	x	x		x	x	x	x	х	х	x		,	¢ I	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Arbeláez et al. 2004, Donascimiento et al. 2017, Lasso et al. 2009, Ortega et al. 2006, Piorski et al. 2008, Villa-Navarro et al. 2021			orn	
Copella vilmae Géry 1963	x						x							IAvHP, CZUT-IC, ICNMHN, SMF	Donascimiento et al. 2017, Galvis et al. 2007a, Géry 1965, Mojica et al. 2005			orn	
Lebiasina elongata (Boulenger 1887)		x	x				x							CIACOL, CZUT-IC, FMNH, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017				
Nannostomus digrammus (Fowler 1913)		x	x			x	x							CIACOL, CZUT-IC, IAvHP	Donascimiento et al. 2017				
Nannostomus eques Steindachner 1876	x	x	x		x	x	x	x	x	x	x	х У	¢ I	CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM, USNM	Bejarano et al. 2006, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Prieto 2000, Villa-Navarro et al. 2021			orn	
Nannostomus marginatus Eigenmann 1909	x	x	х	x	x	x	x		х			,	¢	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM, ROM, USNM	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn	
Nannostomus marilynae Weitzman & Stanley 1975						x	x	x	x	x		,	ĸ	CAS, CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017, Lasso et al. 2009, Weitzman & Cobb, 1975, Villa-Navarro et al. 2021				
Nannostomus trifasciatus Steindachner 1876	x	x	x		x	x	x	x	x			,	¢ I	CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM, USNM	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn	
Nannostomus unifasciatus Steindachner 1876	x	x				x	x	x	x	x		хУ	¢ i	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Donascimiento et al. 2017, Lasso et al. 2009, Ortega-Lara 2016			orn	
Pyrrhulina beni Pearson 1924	x						x							CZUT-IC 14118		х			
Pyrrhulina brevis Steindachner 1876	x	x	x	x	x	х	x		x	x		,	¢ I	CIACOL, CZUT-IC, ICNMHN, MPUJ, NRM	Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009, Ortega <i>et al.</i> 2006			orn	
Pyrrhulina eleanorae Fowler 1940										х		,	ĸ	IAvHP	Lasso et al. 2009				
Pyrrhulina laeta (Cope 1872)	x	x	x		x		x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000			orn	
Pyrrhulina lugubris Eigenmann 1922	x	x	x	x	x		x		x	x	x	,	¢ I	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UF	Calderón & Hincapié 2001, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Pyrrhulina obermulleri Myers 1926	x		x				x							ICNMHN, MPUJ	Donascimiento et al. 2017, Mojica et al. 2005				
Pyrrhulina semifasciata Steindachner 1876	x						x							ROM, USNM	Donascimiento et al. 2017				
Pyrrhulina zigzag Zarske & Géry 1997	x						x							CZUT-IC 14250		x			
Family Ctenoluciidae																			
Boulengerella cuvieri (Spix & Agassiz 1829)	x	x	x	x	x		x			x		х >	¢ I	CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM	Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Lasso et al. 2009, Vari 1995, Villa-Navarro et al. 2021				
Boulengerella lateristriga (Boulenger 1895)	x			x		x	x	x	x			х У	¢ I	CIACOL, CZUT-IC, IAvHP, MPUJ	Correa 2003, Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Boulengerella lucius (Cuvier 1816)			x		x	x	x	x	x	x		x >	C I	CIACOL, CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021				

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Boulengerella maculata (Valenciennes 1850)	x	x	x	x	x	x	x	x	x	x		1	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM, UF	Arbelácz et al. 2004, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Vari 1995			orn	
Boulengerella xyrekes Vari 1995		x	x	x		x	x		x			1	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Lasso et al. 2009, Ortega-Lara 2016			orn	
Family Acestrorhynchidae																			
Acestrorhynchus abbreviatus (Cope 1878)	x	x	x				x							CIACOL, ICNMHN	Galvis et al. 2007a, Donascimiento et al. 2017, Mojica et al. 2005				
Acestrorhynchus falcatus (Bloch 1794)	x	х	x	x	x	x	x	x	х	x	x	1	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Bejarano et al. 2006, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Ortega et al. 2006, Prieto 2000				
Acestrorhynchus falcirostris (Cuvier 1819)	x	x	x		x	x	x	x	x	x	x	1	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Arbeláez et al. 2004, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021				
Acestrorhynchus grandoculis Menezes & Géry 1983								х			x	3	x	IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
Acestrorhynchus heterolepis (Cope 1878)	x	x	x			x	x		x	x	x	1	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Bejarano et al. 2006, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Ortega et al. 2006, Villa-Navarro et al. 2021				
Acestrorhynchus microlepis (Jardine 1841)	x	x	x		x	x	x	x	x	x	x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Arbeláez et al. 2004, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			orn	
Acestrorhynchus minimus Menezes 1969						х	х	х	x	х		x	x	CZUT-IC, IAvHP, ICNMHN, NRM	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021				
Acestrorhynchus nasutus Eigenmann 1912					x	x	x	x	x			x	x	CIACOL, CZUT-IC, MPUJ	Lasso <i>et al.</i> 2009				
Gnathocharax steindachneri Fowler 1913	x		х			x	x	x	x	x		1	x	CIACOL, CZUT-IC, ICNMHN, MPUJ, NRM	Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Villa-Navarro et al. 2021			orn	
Heterocharax leptogrammus Toledo-Piza 2000									x			1	x	IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
Heterocharax macrolepis Eigenmann 1912	x					x	x	x	x			x	x	CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Lasso et al. 2009, Toledo-Piza 2000b				
Heterocharax virgulatus Toledo-Piza 2000								х	x			3	x	CZUT-IC, IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
Hoplocharax goethei Géry 1966									x			x	x	IAvHP, MPUJ					
Lonchogenys ilisha Myers 1927		х				х	х	х	x			1	x	CAS, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007b, Lasso et al. 2009, Myers 1927, Ortega et al. 2006, Villa-Navarro et al. 2021				
Priocharax ariel Weitzman & Vari 1987								x	x			1	x		Villa-Navarro et al. 2021				
Priocharax pygmaeus Weitzman & Vari 1987	x						x							NRM, USNM	Donascimiento et al. 2017, Weitzman & Vari 1987				
Roestes molossus (Kner 1858)	х	х	х				x							CIACOL, ICNMHN, MPUJ	Donascimiento et al. 2017, Prieto 2000				
Roestes ogilviei (Fowler 1914)		х					х							ICNMHN	Galvis et al. 2007b				
Family Characidae																			
Acestrocephalus boehlkei Menezes 1977	х	х	х		х		x			х		1	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Ortega-Lara 2016				
Acestrocephalus sardina (Fowler 1913)			х		x		x		x	x		3	х	CIACOL, CZUT-IC, IAvHP	Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021				
Aphyocharax colifax Taphorn & Thomerson 1991						x	х							CZUT-IC 4271	Donascimiento et al. 2017				
Aphyocharax erythrurus Figenmann 1912		x	x				x			x		3	x	ICNMHN, MPUJ	Donascimiento et al. 2017, Galvis et al. 2007a, Villa-Navarro et al. 2021			orn	

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Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negr	Amazon Basi	Atabapo	Inírida	Guaviare	Orinoco	Orinoco Basin		Collections	Citations	New record fo Colombia	Migratory	Use	Threatened species (Moji <i>et al.</i> 20012)
Aphyocharax pusillus Günther 1868	x	x	x		x		x	x	x	x	x	x x	ĸ	ANSP, CIACOL, CZUT-IC, FMNH, ICNMHN, IAvHP, MPUJ, UF	Calderón & Hincapié 2001, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b, Lasso <i>et al.</i> 2009, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Villa-Navarro <i>et al.</i> 2021			orn	
Astyanax anterior Eigenmann 1908	x	x	x	x	x		x		x	x		х	¢ I	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Donascimiento et al. 2017				
Astyanax bimaculatus (Linnaeus 1758)	x	x	x				x		x	x		х	¢	ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN, IMCN, MPUJ	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b, Lasso <i>et al.</i> 2009, Ortega-Lara 2016				
Astyanax fasciatus (Cuvier 1819)		x	x				x			x		х	¢	ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN	Bejarano et al. 2006, Donascimiento et al. 2017, Fowler 1943, Lasso et al. 2009, Ortega et al. 2006			con	
Astyanax integer Myers 1930			x				x		x	x		х	ĸ	CZUT-IC, IAvHP, ICNMHN, MPUJ	Lasso et al. 2009				
Astyanax maximus (Steindachner 1876)		х	x				x		x	x		х	¢	CIACOL, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017				
Astyanax metae Eigenmann 1914										x		х	c	ICNMHN	Galvis et al. 2007b, Lasso et al. 2009				
Astyanax myersi (Fernández-Yépez 1950)						x	x							NRM 26420		x			
Astyanax siapae Garutti 2003									x	x		х	¢.	MPUJ 11570, 11453					
Astyanax superbus Myers 1942									x	x		х	¢	CIACOL					
Astyanax symmetricus Eigenmann 1908			x				x							ICNMHN 6044					
Astyanax venezuelae Schultz 1944										x		х	ĸ	CZUT-IC, IAvHP, MPUJ	Lasso et al. 2009				
Astyanax villwocki Zarske & Géry 1999			x				x							IUQ	Ruiz-C. et al. 2018				
Atopomesus						x	x							CAS	Myers 1927				
Axelrodia riesei Géry 1966									x			х	¢	IAvHP, MPUJ	Villa-Navarro <i>et al</i> . 2021			orn	
Axelrodia stigmatias (Fowler 1913)	x	x	x				x							IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000				
Bario steindachneri (Eigenmann 1893)	x	х					x							ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006				
Boehlkea fredcochui Géry 1966	x		x				x							ANSP, CIACOL	Donascimiento et al. 2017, Géry 1965			orn	
Brachychalcinus copei (Steindachner 1882)	x	x	x		x		x							ICNMHN, MPUJ	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Prieto 2000				
Brachychalcinus nummus Böhlke 1958	x	x	x				x							CAS/SU, CIACOL, CZUT-IC, IAvHP	Arbeláez et al. 2008, Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017				
Brittanichthys						x	x		x			х	ĸ	CZUT-IC 4210	Villa-Navarro <i>et al.</i> 2021				
Brittanichthys myersi Géry 1965									x			х	¢	IAvHP 2297	Villa-Navarro <i>et al</i> . 2021				
Bryconamericus carlosi Román-Valencia 2003		x	x				x							IUQ, STRI	Donascimiento et al. 2017, Román-Valencia 2003b				
Bryconamericus cismontanus Eigenmann 1914					x		x			x	x	K X	¢	CZUT-IC, IAvHP, MPUJ	Lasso et al. 2009				
Bryconamericus diaphanus (Cope 1878)		х	x		x		x						(	CIACOL 1294, 2371, ICNMHN 5056		x			
Bryconamericus macarenae Román- Valencia, García-Alzate, Ruiz-C. & Taphorn 2010									x	x		х	¢	CIACOL, IAvHP					

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Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Ormoco Matavén	<b>Orinoco Basin</b>	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Bryconamericus macrophthalmus Román- Valencia 2003						x	x						CZUT-IC	Donascimiento et al. 2017				
Bryconamericus orinocoensis Román- Valencia 2003					x	х	x			x		x	CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017				
Bryconamericus pachacuti Eigenmann 1927		x					x						ICNMHN 11152		x			
Bryconella pallidifrons (Fowler 1946)	x	x	x	х			х						CIACOL, CZUT-IC, IAvHP, MPUJ, SMF	Donascimiento et al. 2017, Géry 1965, Géry 1977, Ortega et al. 2006				
Ceratobranchia sp. Eigenmann 1927			x				x						ANSP, CZUT-IC, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017				
Charax apurensis Lucena 1987									x			x	MPUJ 11433		x			
Charax condei (Géry & Knöppel 1876)	x					x	x	x	x		x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Villa-Navarro et al. 2021			orn	
Charax delimai Menezes & Lucena 2014					х		х						CIACOL 2375					
Charax metae Eigenmann 1922								x	x	x		х	CZUT, IAvHP, ICNMHN, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Charax michaeli Lucena 1989	x	x	x	х	х		х						CIACOL, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005				
Charax niger Lucena 1989	х						х						CZUT-IC, ICNMHN	Donascimiento et al. 2017				
Charax pauciradiatus (Günther 1864)					x		x						CIACOL 1414, 4786					
Charax tectifer (Cope 1870)	x	x	x		x		x		x	x		x	CAS/SU, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000				
Cheirodontops geayi Schultz 1944										x		x	CZUT-IC, IAvHP, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021				
Chrysobrycon guahibo Vanegas-Ríos, Urbano- Bonilla & Azpelicueta 2015					x		x		x	x		x	CIACOL, IAvHP, MPUJ	Vanegas-Ríos et al. 2015				
Chrysobrycon hesperus (Böhlke 1958)	х	x					x						CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Vanegas-Ríos et al. 2013				
Chrysobrycon mojicai Vanegas-Ríos & Urbano- Bonilla 2017	x						x						CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Vanegas-Rios & Urbano-Bonilla 2017				
Chryssobrycon sp.			x				x						MPUJ 13877-13880					
Corynopoma riisei Gill 1858										х		х	CZUT-IC, IAvHP	Lasso <i>et al.</i> 2009			orn	
Creagrutus amoenus Fowler 1943		x	x				x						ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM, USNM	Donascimiento et al. 2017, Fowler 1943, Galvis et al. 2007a, Ortega et al. 2006				
Creagrutus andaki Albornoz-Garzón, Acosta-Santos, Bogotá- Gregory & Agudelo- Córdoba 2020			х				x						CIACOL	Albornoz-Garzón et al. 2020				
<i>Creagrutus barrigai</i> Vari & Harold 2001			x				х						CZUT-IC	Donascimiento et al. 2017				
Creagrutus bolivari Schultz 1944										x		x	IAvHP	Lasso <i>et al.</i> 2009				
<i>Creagrutus calai</i> Vari & Harold 2001									x	x		x	CIACOL, IAvHP, MPUJ					
Creagrutus cochui Géry 1964	х	x	x				х						CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Vari & Harold 2001				

### Fishes from the Colombian rainforest biome

## ...Continuation

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupės	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
<i>Creagrutus flavescens</i> (Vari & Harold 2001)	x	x	x				x						ANSP, CAS, CIACOL, ICNMHN, MPUJ, NRM	Donascimiento et al. 2017, Vari & Harold 2001				
Creagrutus gyrospilus Vari & Harold 2001										x		x	CZUT-IC, IAvHP	Bogotá-Gregory et al. 2020				
<i>Creagrutus kunturus</i> Vari, Harold & Ortega 1995			x				x						ICNMHN 14118		х			
Creagrutus maculosus Román- Valencia, García-Alzate, Ruiz-C. & Taphorn 2010										x		x	CZUT-IC, IAvHP, MPUJ					
Creagrutus maxillaris (Myers 1927)					x	x	x	х	x		х	x	CAS, CZUT-IC, IAvHP	Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009, Vari & Harold 2001, Villa-Navarro <i>et al.</i> 2021				
Creagrutus melasma Vari, Harold & Taphorn 1994									x	x		x	CZUT-IC, MPUJ					
Creagrutus muelleri (Günther 1859)		x	x				x						ICNMHN 9331, 9345		х			
<i>Creagrutus ortegai</i> Vari & Harold 2001		x					x						ICNMHN 11034		х			
Creagrutus phasma Myers 1927									x			x	ICNMHN	Galvis et al. 2007b, Lasso et al. 2009			orn	
Creagrutus runa Vari & Harold 2001						x	x						CZUT-IC	Donascimiento et al. 2017				
<i>Creagrutus taphorni</i> Vari & Harold 2001										x		x	IAvHP	Lasso <i>et al.</i> 2009				
<i>Creagrutus tuyuka</i> Vari & Lima 2003			х		x		x						MPUJ, MZUSP	Donascimiento et al. 2017, Vari & Lima 2003				
Creagrutus vexillapinnus Vari & Harold 2001									x	x		x	CIACOL, MPUJ					
Creagrutus zephyrus Vari & Harold 2001										x		x		Villa-Navarro et al. 2021				
Creagrutus sp.1				x			x						CIACOL 3160, 3167		х			
Creagrutus sp.2			х				x						CIACOL 2121					
Ctenobrycon hauxwellianus (Cope 1870)	x	x	x				x						CIACOL 21, 202, 269, 276, 278, 301, 1102, 1838, 1924, 1946, 1965, CZUT-IT 14663, ICNMH 10547, 10554, 10559,		х		orn	
Ctenobrycon oliverai Benine, Lopes & Ron 2010										x		x	CZUT-IC, IAvHP, MPUJ					
Ctenobrycon spilurus (Valenciennes 1850)	x	x	x				x		x	x		x	CAS/SU, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM, UF	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			orn	
Cynopotamus amazonum (Günther 1868)	x	x	x				x						CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Ferraris & Vari 2000, Ortega et al. 2006, Prieto 2000				
Cynopotamus bipunctatus Pellegrin 1909										x	x	x	IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
Exodon paradoxus Müller & Troschel 1844										x		x	MPUJ 1997-2015				orn	
Galeocharax gulo (Cope 1870)	x	x	x				x			x		x	CIACOL, IAvHP, ICNMHN, UCO, UF	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006				
Gephyrocharax valencia Eigenmann 1920										х		x	CZUT-IC 7243					

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Orinoco Basin		Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
<i>Grundulus cochae</i> Román-Valencia, Paepke & Pantoja 2003		x					x							CZUT-IC, IAvHP, IMCN, IUQ	Donascimiento et al. 2017				
Gymnocorymbus bondi (Fowler 1911)									х	х	x	х	(	CIACOL, CZUT-IC, IAvHP, MPUJ	Villa-Navarro et al. 2021			orn	
Gymnocorymbus thayeri Eigenmamm 1908	x	x	x		x		x		х	x	x	х	(	CIACOL, CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017			orn	
Hemibrycon galvisi (Román-Valencia 2000)		x	x				x							CZUT-IC, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Román-Valencia 2003a, Román-Valencia 2000				
Hemibrycon jelskii (Steindachner 1876)		x	x				х						(	CIACOL, CZUT-IC, IAvHP, ICNMHN, UCO	Donascimiento et al. 2017				
Hemibrycon metae Myers 1930										x		х		IAvHP, MPUJ	Galvis et al. 2007b				
Hemibrycon mikrostiktos Bertaco & Malabarba 2010			x				x						1	CZUT-IC 12038, 2048, 12052, MPUJ 11072, 11068, 11065		х			
Hemibrycon polyodon (Günther 1864)			x				х						2	CIACOL 1391-1393, 156-2158, ICNMHN 9347		х			
Hemigrammus aguaruna Lima, Correa & Ota 2016	x						x								Donascimiento et al. 2017, Lima et al. 2016				
Hemigrammus amacayacu Albornoz- Garzón, Méndez-López, DoNascimiento & Lima 2019	x						x						A	ANSP. IAvHP, ZUEC					
Hemigrammus analis Durbin 1909	x	x	x	x	x	x	x	x	x	x	x	K X	. (	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Bejarano et al. 2006, Correa 2003, Donascimiento et al. 2017, Gutiérrez 2003, Mojica et al. 2005, Prieto 2000, Villa-Navarro et al. 2021				
<i>Hemigrammus</i> <i>barrigonae</i> Eigenmann & Henn 1914	x	x			x		x		x	x	x	х	. (	CIACOL, CZUT-IC, IAvHP, MPUJ	Galvis et al. 2007b, Lasso et al. 2009, Miller-Hurtado et al. 2009			orn	
Hemigrammus bellottii (Steindachner 1882)	x	x	x	x	x	х	х	х	x	x	2	K X	(	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2004, Correa 2003, Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021				
<i>Hemigrammus</i> bleheri Géry & Mahnert 1986									x			х		CZUT-IC, IAvHP	Villa-Navarro et al. 2021			orn	
Hemigrammus coeruleus Durbin 1908	x	x	x				x		x			х		CZUT-IC, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Villa-Navarro et al. 2021				
Hemigrammus cupreus Durbin 1918			x				x		x			х	I	CNMHN 2786, 9291, 9373, MPUJ 1053		х			
Hemigrammus elegans (Steindachner 1882)											x	х			Villa-Navarro et al. 2021			orn	
Hemigrammus geisleri Zarske & Géry 2007		x					x		x	x		х	(	CIACOL, CZUT-IC, IAvHP	Donascimiento et al. 2017, Villa-Navarro et al. 2021				
Hemigrammus hyanuary Durbin 1918	x					х	x	x	x	х		х	(	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b, Lasso <i>et al.</i> 2009, Villa-Navarro <i>et al.</i> 2021			orn	
Hemigrammus levis Durbin 1908	x	x	x	x			x	x	x			х	(	CIACOL, CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017				
Hemigrammus luelingi Géry 1964	x	х	x	x	x		x		x	х		х	(	CIACOL, ICNMHN, MPUJ, NRM	Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000			orn	
Hemigrammus lunatus Durbin 1918	x		x				x							ICNMHN, MPUJ	Donascimiento et al. 2017, Mojica et al. 2005				
Hemigrammus melanochrous Fowler 1913		x	x	x			x						(	CZUT-IC, ICNMHN	Bejarano et al. 2006, Correa 2003, Donascimiento et al. 2017				

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Orinoco Basin	Collections	Citations	New record for Colombia	wingratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Hemigrammus micropterus Meek 1907	x		x	x			x	x	x	x	x	( x	IAvHP, ICNMHN, MPUJ, NRM	Arbeláez et al. 2008, Correa 2003, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Hemigrammus microstomus Durbin 1918	x	x	x		x		x	x	x	x		х	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Bejarano et al. 2006, Calderón & Hincapié 2001, Donascimiento et al. 2017, Lasso et al. 2009, Ortega et al. 2006				
Hemigrammus mimus Böhlke 1955					x		x		x	x		x	CZUT-IC, MPUJ	Villa-Navarro et al. 2021				
Hemigrammus newboldi (Fernández-Yépez 1949)		x	х		х		x			х		х	CIACOL, CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017				
Hemigrammus ocellifer (Steindachner 1882)	x	x	x	x	x		x		x			х	CIACOL, CZUT-IC, ICNMHN, NRM, USNM	Arbeláez <i>et al.</i> 2004, Donascimiento <i>et al.</i> 2017, Gutiérrez 2003, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Prieto 2000			orn	
Hemigrammus orthus Durbin 1909	x	х		x	x		x		x	x		х	CIACOL 672, 1047, 1048, 1050, 1053, 1657, 3098, 3100, 3105, 3110, 3157, 3431					
Hemigrammus pretoensis Géry 1965	x						x						ICNMHN, USNM	Donascimiento et al. 2017				
Hemigrammus pulcher Ladiges 1938	x	x					x						CZUT-IC, ICNMHN, ROM, UF, USNM	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000		,	orn	
Hemigrammus schmardae (Steindachner 1882)	x	x	x		x	x	x	x	x	x	3	K X	CIACOL, CZUT-IC, IAvHP, ICNMHN, MUPJ	Bejarano et al. 2006, Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021				
Hemigrammus stictus (Durbin 1909)								x	x	x	3	K X	CIACOL, IAvHP, ICNMHN, NRM	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Hemigrammus unilineatus (Gill 1858)	х	x	х	x			x	х	x	х	3	x x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Ortega-Lara 2016			orn	
Hemigrammus vorderwinkleri Géry 1963		x	x	x	x	x	x	x	x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Bejarano et al. 2006, Correa 2003, Donascimiento et al. 2017, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Hemigrammus xaveriellus Lima, Urbano-Bonilla & Prada- Pedreros 2020					х		x						FMNH, MPUJ, ZUEC					
Hemigrammus yinyang Lima & Sousa 2009					x	x	x			x		х	CIACOL, CZUT-IC, MPUJ	Donascimiento et al. 2017				
Hemigrammus sp.				x			x						CIACOL 3174					
Hyphessobrycon acaciae García-Alzate, Román-Valencia & Prada-Pedreros 2010									х	x		х	CZUT-IC, IAvHP, MPUJ					
Hyphessobrycon agulha Fowler 1913	x	x	x	x	x	x	x						CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, USNM	Arbeláez et al. 2008, Arroyave 2005, Donascimiento et al. 2017, Ortega et al. 2006				
Hyphessobrycon amaronensis García- Alzate, Román-Valencia & Taphorn 2010		x				x	x		x			x	CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017				
Hyphessobrycon bayleyi Lima, Bastos, Rappy- Daniel & Ota 2022	x	x	x	x			x						ICNMHN, MPUJ	Lima <i>et al.</i> 2020				
Hyphessobrycon bentosi Durbin 1908	x	x	x		x		x		x			х	CIACOL, CZUT-IC, IAvHP, USNM	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Hyphessobrycon chiribiquete Garcia- Alzate, Lima, Taphorn, Mojica, Urbano-Bonilla & Teixeira 2020			x	x			x						CZUT-IC, IAvHP, ICNHMHN, MPUJ					
Hyphessobrycon copelandi Durbin 1908	x	x	x		x	x	x		x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021		,	orn	
Hyphessobrycon diancistrus Weitzman 1977								х	x		2	K X	IAvHP	Donascimiento et al. 2017, Villa-Navarro et al. 2021				

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	Orinoco Basin	Collections	Citations	New record for Colombia	MIGratory		I hreatened species (Mojica <i>et al.</i> 20012)
Hyphessobrycon dorsalis Zarske, 2014					x		x	x	x			x	CIACOL, CZUT-IC, IAvHP	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021				
Hyphessobrycon epicharis Weitzman & Palmer 1997						x	x						CZUT-IC	Donascimiento et al. 2017				
Hyphessobrycon gracilior Géry 1964			x				x						ICNMHN	Bejarano et al. 2006, Donascimiento et al. 2017				
Hyphessobrycon klausanni García-Alzate, Urbano-Bonilla & Taphorn 2017			x				x			x		x	CIACOL 3107, 3367, MPUJ 14034-14051					
Hyphessobrycon loretoensis Ladiges 1938	х	х	x				x						CZUT-IC, ICNMHN, MPUJ, USNM	Donascimiento et al. 2017, Ortega-Lara 2016				
Hyphessobrycon mavro García-Alzate, Román- Valencia & Prada- Pedreros 2010									x			x		Villa-Navarro et al. 2021				
Hyphessobrycon metae Eigenmann & Henn 1914			x		x		x	x	x	x	х	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Galvis et al. 2007b, Villa-Navarro et al. 2021		01	n	
Hyphessobrycon minimus Durbin 1909								x	x	x	x	x		Villa-Navarro et al. 2021				
Hyphessobrycon niger García-Alzate, Román-Valencia & Prada-Pedreros 2010						x	x						CZUT-IC, IAvHP					
Hyphessobrycon oritoensis García-Alzate, Román-Valencia & Taphorn 2008		x	x				x						CIACOL, IUQ, MBUCV, MCNG	García-Alzate et al. 2008, Donascimiento et al. 2017				
Hyphessobrycon otrynus Benine & Lopes 2008									x	x		x	CZUT-IC, IAvHP, MPUJ					
Hyphessobrycon peruvianus Ladiges 1938	x	x	x	x			x			x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006		01	n	
Hyphessobrycon rheophilus Ohara, Teixeira, Albornoz- Garzón, Mirande & Lima 2019						x	x				x	x	ANSP, CZUT-IC					
Hyphessobrycon sweglesi (Géry 1961)	i	x			x		x	x	x	x	х	x	CIACOL, CZUT-IC, IAvHP, MPUJ, USNM	Galvis et al. 2007a, Galvis et al. 2007b, Géry 1961, Lasso et al. 2009, Villa-Navarro et al. 2021		01	n	
Hyphessobrycon taguae García-Alzate, Román- Valencia & Taphorn 2010	x	x	x				x		x			х	CZUT-IC, IAvHP, IUQ, MPUJ	Donascimiento <i>et al.</i> 2017, García-Alzate & Román-Valencia 2010, García-Alzate <i>et al.</i> 2008				
Hyphessobrycon tropis Géry 1963			x				x		x			x	MPUJ 14052	Villa-Navarro et al. 2021				
Hyphessobrycon tukunai Géry 1965		x	x				x						ICNMHN	Bejarano et al. 2006, Donascimiento et al. 2017				
Jupiaba abramoides (Eigenmann 1909)					x	х	х			x		х	CIACOL, ICNMHN, MPUJ					
Jupiaba anteroides (Géry 1965)	x	x	x	x	x	x	x	x	x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Prieto 2000				
Jupiaba asymmetrica (Eigenmann 1908)		x	x				x		x	x		x	ANSP, CIACOL, ICNMHN, MPUJ	Donascimiento et al. 2017, Fowler 1945	:	x		
Jupiaba atypindi Zanata 1997									x			x		Villa-Navarro et al. 2021				
<i>Jupiaba poekotero</i> Zanata & Lima 2005					x	x	x			x		х	CIACOL, CZUT-IC					
Jupiaba polvlepis (Günther 1864)										x		х	IAvHP, MPUJ					

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Mafavén	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Jupiaba scologaster (Weitzman & Vari 1986)				x	x		x	x				x	IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007b				
Jupiaba zonata (Eigenmann 1908)	x	x	x	x	x		x		x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Ortega-Lara 2016, Villa-Navarro et al. 2021		x		
Knodus alpha (Eigenmann 1914)			x				x		x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Lasso <i>et al.</i> 2009				
Knodus breviceps Eigenmann 1908	x	x	x				x		x	x		x	CIACOL, CZUT-IC, IAvHP, FMNH	Arbeláez et al. 2008, Donascimiento et al. 2017, Ortega-Lara 2016				
Knodus caquetae Fowler 1945			x				x						CIACOL, UCO					
Knodus delta Géry 1972		x					x						ICNMHN 11011		х			
Knodus deuterodonoides (Eigenmann 1914)								x		x		x	CZUT-IC, IAvHP					
Knodus gamma Géry 1972	x		x				x						CZUT-IC, MPUJ	Donascimiento et al. 2017				
Knodus heteresthes (Eigenmann 1908)	x		x		x		x						CZUT-IC, IUQ, MPUJ	Donascimiento et al. 2017, Román-Valencia 2003a				
Knodus hypopterus (Fowler 1943)	x	x	x				x		x	x		x	ANSP, CIACOL, CZUT-IC, IAvH, IUQ, MPUJ	Fowler 1943, Román-Valencia 2003a				
Knodus megalops Myers 1929		x					x						ICNMHN 11014		x			
Knodus orteguasae (Fowler 1943)		x	x				x						ANSP, CZUT-IC, IUQ	Donascimiento et al. 2017, Fowler 1943, Román-Valencia 2003a				
Knodus tiquiensis Ferreira & Lima 2006					x		x						CIACOL, CZUT-IC	Donascimiento et al. 2017				
Knodus sp.			x				x						CIACOL 2416					
Leptobrycon jatuaranae Eigenmann 1915											х	x	IAvHP 20296		x			
Makunaima guianensis (Eigenmann 1909)		x	x		x	x	x			x		х	CIACOL 1041, 3762–3765	Donascimiento et al. 2017, Marinho et al. 2015				
Markiana geayi (Pellgrin 1909)	x		x				x				хх	x	CZUT-IC, IAvHP, ICNMHN	Bogotá-Gregory & Maldonado-Ocampo 2005, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b				
Microgenys lativirgata Pearson 1927			x				x						CZUT-IT 12039, 12034		х			
Microschemobrycon callops Böhlke 1953					x		x		х	x		х	CIACOL, IAvHP, ICNMHN, MPUJ	Villa-Navarro <i>et al.</i> 2021				
Microschemobrycon casiquiare Böhlke 1953					x	х	x	x	x	x	хх	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021				
Microschemobrycon geisleri Géry 1973	x		x	x	x	x	x						CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Prieto 2000				
Microschemobrycon melanotus (Eigenmann 1912)								x	x			х	MPUJ	Donascimiento et al. 2017, Villa-Navarro et al. 2021				
Moenkhausia agnesae Géry 1965				x			x						ICNMHN 17158		х			
Moenkhausia ceros Eigenmann 1908			x		x		x				х	x	CZUT-IC, IAvHP					
Moenkhausia chrysargyrea (Günther 1864)	x	x	x				x	x	x	x	х	x	CIACOL, CP-IIAP, CZUT-IC, IAvHP, MPUJ	Arbeláez et al. 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Ortega-Lara 2016, Villa-Navarro et al. 2021				
Moenkhausia collettii (Steindachner 1882)	x	x	x	x	x	x	x	x	x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007b, Lasso et al. 2009, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Moenkhausia comma Eigenmann 1908	x	x	x	x	x		x		x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000			orn	

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Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Moenkhausia copei (Steindachner 1882)	x	x	x				x	x	x	x	х	x	CZUT-IC, IAvHP, ICNMHN	Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009, Ortega-Lara 2016, Villa-Navarro <i>et al.</i> 2021				
Moenkhausia cotinho Eigenmann 1908	x	x	x	x	x	x	x	x	x		х	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Calderón & Hincapié 2001, Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021		x		
Moenkhausia dichroura (Kner 1858)	x	x	x	x			x		x	x		x	CAS, CIACOL, CZUT- IC, IAvHP, ICNMHN, MPUJ, UCO	Arbeláez et al. 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			orn	
Moenkhausia diktyota Lima & Toledo-Piza, 2001					x		x						CIACOL 1020, 1023	Bogotá-Gregory et al. 2020				
Moenkhausia gracilima Eigenmann 1908		x	х				х		x	x		x	CIACOL, IAvHP, MPUJ	Bogotá-Gregory et al. 2020, Villa-Navarro et al. 2021				
Moenkhausia grandisquamis (Müller & Troschel 1845)	x	x	x		x		x	x	x	x	хх	х	CIACOL, ICNMHN, MPUJ	Donascimiento et al. 2017, Lasso et al. 2009				
Moenkhausia hemigrammoides Géry 1965									x	x		x		Villa-Navarro et al. 2021				
Moenkhausia intermedia Eigenmann 1908	x	x	x				x	x		x		x	CIACOL, ICNMHN	Arroyave 2005, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009				
Moenkhausia jamesi Eigenmann 1908		x					x			x		x	CZUT-IC, ICNMHN					
Moenkhausia lata Eigenmann 1908					x		x						CIACOL	Bogotá-Gregory et al. 2020				
<i>Moenkhausia latissima</i> Eigenmann 1908	x						х						IAvHP	Donascimiento et al. 2017				
Moenkhausia lepidura (Kner 1858)	x	x	x	x	x	x	x	x	x	x	x	x	CIACOL, CZUT-IC, FMNH, IAvHP, ICNMHN, MPUJ, USMN	Arbeláez et al. 2008, Arbeláez et al. 2004, Bejarano et al. 2006, Calderón & Hincapié 2001, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000		х	orn	
Moenkhausia margitae Zarske & Géry 2001			х				х						MPUJ 14032		х			
Moenkhausia megalops (Eigenmann 1907)	x	x	x	x			х		x	х	хх	х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005				
<i>Moenkhausia melogramma</i> Eigenmann 1908	x	x	x				x						CIACOL, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2004, Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000				
Moenkhausia metae Eigenmann 1922										x		x	MPUJ 10466					
<i>Moenkhausia mikia</i> Marinho & Langeani 2010	x	x	x	x	x	x	x		x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Villa-Navarro et al. 2021				
Moenkhausia oligolepis (Günther 1864)	x	x	x	x	x	x	x	x	x	x	x	x	CIACOL, CZUT-IC, ANSP, IAvHP, ICNMHN, MPUJ, NRM, UF	Arbeláez et al. 2008, Arroyave 2005, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Moenkhausia orteguasae Fowler 1943			x		x		х						ANSP, MPUJ	Donascimiento et al. 2017, Fowler 1943				
Moenkhausia ovalis (Günther 1868)			х				х						ICNMHN 6032		x			
Moenkhausia robertsi Géry 1964			x				х						ICNMHN	Cipamocha 2002, Donascimiento et al. 2017				
Moenkhausia tridentata Holly 1929	x						х						IAvHP	Arbelåez et al. 2008				
Odontostilbe euspilurus (Fowler 1945)			x				x						CIACOL	Fowler 1945				
Odontostilbe fugitiva Cope 1870	x	x	x		x		х						ANSP, CAS, CIACOL, CZUT-IC, ICNMHN, NRM, UF, USNM	Bührnheim & Malabarba 2006, Donascimiento et al. 2017, Fowler 1943, Galvis et al. 2007a, Ortega et al. 2006				
Odontostilbe pulchra (Gill 1858)			x				х	x	x	x		x	CIACOL, CZUT-IC, IAvHP, MPUJ	Lasso <i>et al</i> . 2009				

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	vaupes	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Mataven	Urinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Odontostilbe splendida Bührnheim & Malabarba 2007										x		;	x	CZUT-IC, IAvHP, MPUJ	Villa-Navarro et al. 2021				
Oxybrycon parvulus Géry 1964						x	x							CZUT-IC	Donascimiento et al. 2017				
Paracheirodon axelrodi (Schultz 1956)								x	x	x	x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Paracheirodon innesi (Myers 1936)	x	x	x				x	x	x			3	x	IAvHP, ICNMHN, MPUJ, NRM, USNM	Donascimiento et al. 2017, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Paracheirodon simulans (Géry 1963)						x	x	x	x			3	x	CZUT-IC, IAvHP, NRM	Villa-Navarro et al. 2021				
Paragoniates alburnus Steindachner 1876	x	x	x				x							CAS/SU, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007b, Mojica et al. 2005, Ortega et al. 2006			orn	
Parapristella georgiae Géry 1964						x	х	x	x			x	x	IAvHP, MPUJ	Villa-Navarro et al. 2021				
Parecbasis cyclolepis Eigenmann 1914	x						x							CIACOL	Donascimiento et al. 2017				
Petitella bleheri (Géry & Mahnert 1986)				3	x		x							CZUT-IC 4174					
Petitella georgiae Géry & Boutière 1964	x		x				x							CIACOL, ICNMHN	Galvis et al. 2007a, Donascimiento et al. 2017, Lasso et al. 2009			orn	
Petitella rhodostomus (Ahl 1924)	x					x	x	x	x			x	x	CIACOL, CZUT-IC, IAvHP, NRM	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Phenacogaster maculoblonga Lucena & Malabarba									x	x		1	x	IAvHP 19698	Villa-Navarro <i>et al.</i> 2021				
Phenacogaster napoatilis Lucena & Malabarba 2010		x					x							CZUT-IC	Donascimiento et al. 2017				
Phenacogaster pectinata (Cope 1870)	x	x	x	3	ĸ	x	x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000				
Phenacogaster prolata Lucena & Malabarba 2010									x	x		1	x	CIACOL, CZUT-IC	Villa-Navarro <i>et al.</i> 2021				
Poptella brevispina Reis 1989	x						x							ICNMHN 13820					
Poptella compressa (Günther 1864)	x	x		1	ĸ		x		x	x		1	x	IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021				
Poptella longipinnis (Popta 1901)										x	x	3	x	IAvHP, ICNMHN, MPUJ	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021				
Prionobrama filigera (Cuvier 1870)	x	x	x				x							CAS, CIACOL, IAvHP, ICNMHN, ROM	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000			orn	
Protocheirodon pi (Vari 1978)	x						x							CAS	Donascimiento et al. 2017				
Rhinobrycon negrensis Myers 1944.								x	x			3	x	CZUT-IC 5081	Villa-Navarro et al. 2021				
Roeboides affinis (Günther 1868)	x	x	x				x		x	x	x	3	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UCO, UF	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			orn	
Roeboides araguaito Lucena 2003										x		3	x	IAvHP 21434					
Roeboides myersii Gill 1870	x	x					x				x	3	x	CIACOL, IAvHP, ICNMHN	Arbelácz et al. 2008, Arbelácz et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lucena 2003, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000				
Scopaeocharax rhinodus (Böhlke 1958)			x				x					1		CIACOL	Bogotá-Gregory et al. 2020				

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Matavén Orinoco Rasin		Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Stethaprion erythrops Cope 1870	x	x	x	x			x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005				
Stichonodon insignis (Steindachner 1876)	x						х							CIACOL, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Santos 2000, Vejarano 2000				
Tetragonopterus argenteus Cuvier 1816	x	x	x				x	x	х	x	x	хх	C .	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, MLS, ROM, UCO, UF	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021		x	orn	
Tetragonopterus chalceus Spix & Agassiz 1829	x	x	x	x	x	х	х		х	х	x	хх	£	ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN	Calderón & Hincapié 2001, Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b, Lasso <i>et al.</i> 2009, Ortega <i>et al.</i> 2006, Villa-Navarro <i>et al.</i> 2021			orn	
<i>Thayeria obliqua</i> Eigenmann 1908		x	x	x		x	x	x	x			х	C.	IAvHP, ICNMHN, NRM	Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Ortega-Lara 2016, Villa-Navarro et al. 2021		x	orn	
Thrissobrycon pectinifer Böhlke 1953								x	x			х	C.	IAvHP, NRM	Lasso <i>et al.</i> 2009				
Trochilocharax ornatus Zarske 2010	x						х							IAvHP 8271-8279		x			
Tyttobrycon dorsimaculatus Géry 1973	x						x							CIACOL, ICNMHN	Mojica <i>et al.</i> 2005				
Tyttobrycon hamatus Géry 1873	x						x							ICNMHN 8271		x			
Tyttobrycon xeruini Géry 1973									x			х	Ľ		Villa-Navarro et al. 2021				
Tyttocharax cochui (Ladiges 1949)	x		x	x	x		x							CIACOL, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Gutiérrez 2003, Mojica et al. 2005				
Tyttocharax madeirae Fowler 1913	x		x	x			x							CIACOL, ICNMHN, MPUJ	Arroyave 2005, Donascimiento et al. 2017, Prieto 2000				
<i>Tyttocharax</i> <i>metae</i> Román-Valencia, García-Alzate, Ruiz-C. & Taphorn 2012									х	x		х	t	CZUT-IC, IAvHP, MPUJ					
Xenagoniates bondi Myers 1942										x		х	Ľ	MPUJ 5970				orn	
Xenurobrycon heterodon Weitzman & Fink 1985			x				х							USNM	Donascimiento et al. 2017				
Family Gasteropelecidae																			
Carnegiella marthae Myers 1927	x	x	x		x	x	x	x	x	x		х		CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Carnegiella myersi Fernández-Yépez 1950	x	x					x							NRM, USNM	Donascimiento et al. 2017, Ortega-Lara 2016			orn	
Carnegiella schereri Fernández-Yépez 1950	x	x					x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			orn	
Carnegiella strigata (Günther 1864)	x	x	x	x	x		x	x	х	x	x	х	:	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM, ROM, USNM	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Géry 1977, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn	
Gasteropelecus sternicla (Linnaeus 1758)	x	x	x				x							CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Donascimiento et al. 2017, Galvis et al. 2007a, Ortega-Lara 2016			orn	
Thoracocharax securis De Filippi 1853	x	x					x							ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000			orn	
Thoracocharax stellatus (Kner 1858)	x	x	x				x	x	x	x		х		CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UCO	Calderón & Hincapié 2001, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Galvis <i>et al.</i> 2007b, Lasso <i>et al.</i> 2009, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Villa-Navarro <i>et al.</i> 2021			orn	

Таха	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Matavén	<b>Urinoco Basin</b>	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Family Bryconidae																			
Brycon amazonicus (Spix & Agassiz 1829)	x	x	x	x			x	x	x				x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Correa 2003, Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro <i>et al.</i> 2021		х	con	
Brycon falcatus Müller & Troschel 1844		x	x	x	x		x	x	x	x		x	x	CIACOL, IAvHP, ICNMHN, MPUJ	Bejarano et al. 2006, Calderón & Hincapié 2001, Donascimiento et al. 2017, Lasso et al. 2009, Lima 2017, Villa-Navarro et al. 2021		x		
Brycon hilarii (Valenciennes 1850)	x	x		x			х							IAvHP, NRM	Donascimiento et al. 2017, Lima 2017				
Brycon melanopterus (Cope 1872)	x	x	x	x			x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Bejarano et al. 2006, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007b, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000		x		
Brycon pesu Müller & Troschel 1845			x	x	x	x	x	x	x			x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021		x	orn	
Brycon polylepis Moscó Morales 1988										х			х	CIACOL 3725					
Brycon whitei Myers & Weitzman 1960										x			x	CZUT-IC, IAvHP, MPUJ	Lasso et al. 2009		x		
Salminus hilarii Valenciennes 1850	x	x	x				x			x			x	ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN	Calderón & Hincapié 2001, Donascimiento et al. 2017, Ortega et al. 2006		x	con	
Family Triportheidae																			
Agoniates anchovia Eigenmann 1914	x	x	x	x	x		х							CIACOL, ICNMHN	Bejarano et al. 2006, Calderón & Hincapié 2001, Correa 2003, Donascimiento et al. 2017, Mojica et al. 2005, Santos 2000, Vejarano 2000				
Agoniates halecinus Müller & Troschel 1845		x		x			x							IAvHP	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017				
Triportheus albus Cope 1872	x	x	x	x	x		x							CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UCO, UF	Bejarano <i>et al.</i> 2006, Calderón & Hincapié 2001, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Santos 2000, Vejarano 2000		x		
Triportheus angulatus (Spix & Agassiz 1829)	x	x	x	x	x		x			x			х	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UCO, UF	Arbeláez et al. 2008, Arbeláez et al. 2004, Bejarano et al. 2006, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000		x	con	
Triportheus auritus (Valenciennes 1850)	x	x	x	x			x	x	x	x			x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UF	Bejarano et al. 2006, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021				
Triportheus brachipomus (Valenciennes 1850)											x		x		Villa-Navarro et al. 2021			orn	
Triportheus culter (Cope 1872)	x		x	x			x							CIACOL, CZUT-IC, ICNMHN	Donascimiento et al. 2017				
Triportheus orinocensis Malabarba 2004									x	x	x	x	x	CIACOL, IAvHP, ICNMHN	Lasso et al. 2009, Miller-Hurtado et al. 2009				
Triportheus pictus (Garman 1890)	x	x		x			x							IAvHP, ICNMHN	Arbeláez et al. 2008, Correa 2003, Correa 2008, Donascimiento et al. 2017				
Triportheus rotundatus (Jardine 1841)	x	x	x				х							CZUT-IC, IAvHP	Donascimiento et al. 2017				
Triportheus venezuelensis Malabarba 2004								x	х	x	x		x	CZUT-IC, IAvHP, ICNMHN	Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021		x	orn	
Family Iguanodectidae																			
Bryconops affinis (Günther 1864)		x	x			x	x		x	x			x	IAvHP, ICNMHN	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009				
Bryconops alburnoides Kner 1858		x	x		х	x	х		х	х		x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Bejarano et al. 2006, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Villa-Navarro et al. 2021				
Bryconops caudomaculatus (Günther 1864)	x	x	х	x	x	x	x	x	x	x	x	х	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Bejarano et al. 2006, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Bryconops collettei Chernoff & Machado- Allison 2005	x	x			x		x							CIACOL, IAvHP, MPUJ	Donascimiento et al. 2017				

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Matavén	<b>Orinoco Basin</b>	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Bryconops giacopinii (Fernández-Yépez 1950)	x	x	x	x	x	x	x	x	x	x			x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Bejarano et al. 2006, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Bryconops humeralis Machado-Allison, Chernoff & Buckup 1996					x	x	x	x	x	x			x	CIACOL, CZUT-IC, IAvHP, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021				
<i>Bryconops inpai</i> Knöppel, Junk & Géry 1968	x	x	x	x	x		x		х				x	CIACOL, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006				
Bryconops magoi Chernoff & Machado- Allison 2005						x	x		х	x			x	CZUT-IC, MPUJ	Donascimiento et al. 2017				
Iguanodectes adujai Géry 1970						х	x	x	x		x	x	x	CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Iguanodectes geisleri Géry 1970			x			x	x	x	x			x	x	CIACOL, CZUT-IC, ICNMHN, MPUJ	Donascimiento et al. 2017, Galvis et al. 2007b, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Iguanodectes gracilis Géry 1993								x					x	,	Villa-Navarro et al. 2021				
Iguanodectes purusii (Steindachner 1908)	x		x		x		x							CIACOL, ICNMHN,	Donascimiento et al. 2017, Mojica et al. 2005				
Iguanodectes spilurus (Günther 1864)	x	x	x		x	x	x	x	x	x		x	x	CAS/SU, CIACOL, CZUT-IC, IAvHP, ICNMHN, UF	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Prieto 2000, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Family Chalceidae																			
Chalceus epakros Zanata & Toledo-Piza 2004	х	х	х	х	х		х		х	х			х	CIACOL, CZUT-IC, IAvHP	Donascimiento et al. 2017, Villa-Navarro et al. 2021			orn	
Chalceus erythrurus (Cope 1870)	x	x	x				x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000			orn	
Chalceus macrolepidotus Cuvier 1817	x	x	x	x	x	x	x	x	x	x	x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Galvis et al. 2007b, Lasso et al. 2009, Ortega et al. 2006, Villa-Navarro et al. 2021		x	orn	
Order Gymnotiformes																			
Family Apteronotidae																			
Adontosternarchus balaenops (Cope 1878)	х						х							ICNMHN	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Maldonado-Ocampo & Albert 2003, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Santos 2000, Vejarano 2000			orn	
Adontosternarchus clarkae Mago-Leccia, Lundberg & Baskin 1985	х						х							FMNH	Donascimiento et al. 2017, Lundberg & Akama 2005, Mago-Leccia et al. 1985, Maldonado-Ocampo & Albert 2003				
Apteronotus albifrons (Linnaeus 1766)	x		x		x		x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Arroyave 2005, Galvis et al. 2007a, Mojica et al. 2005			orn	
Apteronotus bonapartii (Castelnau 1855)	x	x		х			x			х			x	CIACOL, ICNMHN, IAvHP	Donascimiento et al. 2017, Galvis et al. 2007a, Maldonado- Ocampo & Albert 2003, Mojica et al. 2005, Ortega et al. 2006			orn	
Apteronotus galvisi de Santana, Maldonado- Ocampo & Crampton 2007										x			x	IAvHP, MPUJ				orn	
Apteronotus macrolepis (Steindachner 1881)	x						x							FMNH	Donascimiento et al. 2017				
Apteronotus magoi de Santana, Castillo & Taphorn 2006						x	x			x			x	CZUT-IC, IAvHP					
Parapteronotus hasemani (Elis 1913)	x						x							FMNH, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Maldonado- Ocampo & Albert 2003, Moiica et al. 2005			orn	
Platyurosternarchus macrostomus (Gunther 1870)	x	x					x							IAvHP, ICNMHN	Donascimiento <i>et al.</i> 2017, Maldonado-Ocampo & Albert 2003, Mojica <i>et al.</i> 2005				
Sternarchella schotti (Steindachner 1868)	x						x							ICNMHN	Donascimiento et al. 2017, Evans et al. 2017, Galvis et al. 2007a, Maldonado-Ocampo & Albert 2003, Moiica et al. 2005			orn	
Sternarchogiton nattereri (Steindachner 1868)	x						x							ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Maldonado- Ocampo & Albert 2003, Moiica et al. 2005, Santos 2000 Veiarano 2000			orn	
Sternarchorhamphus muelleri	x						x							IAvHP, ICNMHN	Donascimiento <i>et al.</i> 2017, Maldonado-Ocampo & Albert 2003, Mojica <i>et al.</i> 2005				
Sternarchorhynchus mormyrus (Steindachner 1868)	x						x							ICNMHN	Donascimiento et al. 2017, Maldonado-Ocampo & Albert 2003			orn	

### Fishes from the Colombian rainforest biome

...Continuation

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Family Sternopygidae																		
Distocyclus conirostris (Eigenmann & Allen 1942)	x						x						CZUT-IC, ICNMHN	Donascimiento <i>et al.</i> 2017, Maldonado-Ocampo & Albert 2003, Mojica <i>et al.</i> 2005				
<i>Eigenmannia limbata</i> (Schreiner & Miranda Ribeiro 1903)	x	x		x	x		x	x		x	x	x	CAS, CIACOL, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Maldonado-Ocampo & Albert 2003, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000			orn	
Eigenmannia macrops (Boulenger 1897)		х			x		x	x	х	x	x	x	CIACOL, CZUT-IC, IAvHP	Lasso et al. 2009, Ortega-Lara 2016, Villa-Navarro et al. 2021				
Eigenmannia nigra Mago-Leccia 1994	x	х					x				x		CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017				
Rhabdolichops eastwardi Lundberg & Mago-Leccia 1986					x		x		x			x	CIACOL, CZUT-IC	Donascimiento et al. 2017				
Rhabdolichops nigrimans Correa, Crampton & Albert 2006					x		x						CIACOL 878		x			
Rhabdolichops stewarti Lundberg & Mago-Leccia 1986					x		x		x			x	IAvHP 1338, CZUT- IC 3642, 3987		x			
Rhabdolichops troscheli (Kaup 1856)						x	x						ICNMHN	Donascimiento et al. 2017, Maldonado-Ocampo & Albert 2003				
Sternopygus macrurus (Bloch & Schneider 1801)	x	x	x	x	x	x	x	x	x	x		x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Maldonado- Ocampo & Albert 2003, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000			con, orn	
Sternopygus obtusirostris Steindachner 1881					x		x						CIACOL 2670					
Family Gymnotidae																		
Electrophorus electricus (Linnaeus 1766)	x	x	x				x	x	x	x	хх	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Maldonado-Ocampo & Albert 2003, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021				
<i>Gymnotus anguillaris</i> Hoedeman 1962			x		x		x			x		x	CIACOL, CZUT-IC, ICNMHN	Galvis et al. 2007a, Lasso et al. 2009, Ortega-Lara 2016			orn	
<i>Gymnotus carapo</i> Linnaeus 1758	x	x	x	x	x	x	x	x	x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, FMNH, ROM	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Maldonado- Ocampo & Albert 2003, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
<i>Gymnotus cataniapo</i> Mago-Leccia 1994					x		x						CIACOL 2520, 2521				orn	
Gymnotus coropinae Hoedeman 1962	x	x	x	x	x		x		x	x		x	CIACOL, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Maldonado-Ocampo & Albert 2003			orn	
<i>Gymnotus javari</i> Albert, Crampton & Hagedorn 2003	x				x		x						CZUT-IC, IAvHP, ICNMHN	Albert & Crampton 2003, Arbeláez et al. 2008, Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Gymnotus pedanopterus Mago-Leccia 1994	x						x			x		x	IAvHP, ICNMHN, ROM	Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Maldonado- Ocampo & Albert 2003, Mojica et al. 2005, Prieto 2000				
Gymnotus stenoleucus Mago-Leccia 1994	x						x		x	x		x	IAvHP	Donascimiento et al. 2017, Lasso et al. 2009, Maldonado-Ocampo & Albert 2003, Villa-Navarro et al. 2021				
Gymnotus tigre Albert & Crampton 2003	x						x						IAvHP, ICNMHN	Donascimiento et al. 2017, Maldonado-Ocampo & Albert 2003, Mojica et al. 2005				
<i>Gymnotus tiquie</i> Maxime, Lima & Albert 2011					x		x						CIACOL	Bogotá-Gregory et al. 2020				
Family Hypopomidae																		
Brachyhypopomus batesi Crampton, de Santana, Waddell & Lovejoy 2016					x		x						CIACOL	Crampton et al. 2016, Donascimiento et al. 2017				
Brachyhypopomus beebei (Schultz 1944)	x	х	x	х	x		x		х			x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Gutiérrez 2003, Lasso et al. 2009, Maldonado-Ocampo & Albert 2003, Mojica et al. 2005				
Brachyhypopomus benjamini Crampton, de Santana, Waddell & Lovejoy 2017				x			x						CIACOL 3295		x			

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Mataven Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Brachyhypopomus bennetti Sullivan, Zuanon & Cox Fernandes 2013	x						x						FMNH	Donascimiento et al. 2017, Sullivan et al. 2013				
Brachyhypopomus brevirostris (Steindachner 1868)	x	x	x	x			x	x	x	x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Correa 2003, Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009, Maldonado-Ocampo & Albert 2003, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Prieto 2000, Villa-Navarro <i>et al.</i> 2021			orn	
Brachyhypopomus bullocki Sullivan & Hopkins 2009					x	x	x	x		x	x	x	ANSP, MCNG	Donascimiento et al. 2017, Sullivan & Hopkins 2009				
Brachyhypopomus flavipomus Crampton, de Santana, Waddell & Lovejoy 2017	x						x						USNM	Crampton et al. 2016, Donascimiento et al. 2017				
Brachyhypopomus hamiltoni Crampton, de Santana, Waddell & Lovejoy 2017					x		x						CIACOL 2480, 2668					
Brachyhypopomus sullivani Crampton, de Santana, Waddell & Lovejoy 2017				x			x		х	x		x	CIACOL, IAvHP	Villa-Navarro <i>et al.</i> 2021				
Microsternarchus bilineatus Fernández- Yépez 1968					x		x	x	x	x		x	CIACOL, CZUT-IC, IAvHP, NRM	Villa-Navarro et al. 2021				
Microsternarchus sp.					x		x						CIACOL 2485, 2505, 2508-2510, 2518, 2530, 2531, 2533, 2537, 2539, 2541, 2543, 2544, 2548, 2550, 2553, 2562- 2566, 2655, 2656, 2880, 3761					
Family Rhamphichthydae																		
Gymnorhamphichthys hypostomus Ellis 1912		x	x	x	x	x	x	x		x		x	CAS/SU, CZUT-IC, ICNMHN, MPUJ	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009, Maldonado-Ocampo & Albert 2003				
Gymnorhamphichthys rondoni (Miranda Ribeiro 1920)	х	x	х	х	x	x	x	x	x	х		x x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Lasso et al. 2009, Maldonado-Ocampo & Albert 2003, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021				
Hypopygus lepturus Hoedeman 1962	x	x	x	х	x	х	x	x	x	х		х	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Maldonado-Ocampo & Albert 2003, Mojica et al. 2005, Villa-Navarro et al. 2021			orn	
Hypopygus neblinae Mago-Leccia 1994	x						x	x		x		x	ICNMHN, MPUJ	Donascimiento et al. 2017, Galvis et al. 2007a, Villa-Navarro et al. 2021				
Rhamphichthys apurensis (Fernández- Yépez 1968)										x		x	IAvHP 19414					
Rhamphichthys drepanium Triques 1999											x	x		Villa-Navarro et al. 2021				
Rhamphichthys rostratus (Linnaeus 1766)	x	x	x		x	x	x						CIACOL, IAvHP, ICNMHN	Calderón & Hincapié 2001, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Maldonado-Ocampo & Albert 2003, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Prieto 2000			orn	
Steatogenys duidae (La Monte 1929)	x			x	x	x	x	x				x	CIACOL, ICNMHN, MPUJ	Donascimiento et al. 2017, Lasso et al. 2009, Maldonado-Ocampo & Albert 2003			orn	
Steatogenys elegans (Steindachner 1880)	x	x	х		x		x		x		x	x x	CIACOL, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Maldonado-Ocampo & Albert 2003, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn	
Steatogenys ocellatus Crampton, Thorsen & Albert 2004		x					x						CIACOL	Bogotá-Gregory et al. 2018				
Order Siluriformes																		
Family Trichomycteridae																		
Ammoglanis sp.		х					х						CIACOL 4414					
																	Co	ntinue

Taxa	Amazonas	Putumavo	Caquetá	Ananoris	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	<b>Orinoco Basin</b>	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Haemomaster venezuelae Myers 1927									x			x	IAvHP 14103	Lasso et al. 2009, Villa-Navarro et al. 2021				
Henonemus punctatus (Boulenger 1887)	x	x					x						CIACOL, CZUT-IC, ICNMHN, UCO	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006				
Henonemus triacanthopomus DoNascimiento & Provenzano 2006											x	x		Villa-Navarro <i>et al.</i> 2021				
Ituglanis guayaberensis (Dahl 1960)									x	x		x	CIACOL, CZUT-IC, ICNMHN, IAvHP	Lasso et al. 2009				
Malacoglanis gelatinosus Myers & Weitzman 1966			х				x						CAS/SU	Donascimiento et al. 2017, Myers & Weitzman 1960				
Megalocentor echthrus de Pinna & Britski 1991			х				x						IAvHP 5995	Donascimiento et al. 2017				
Ochmacanthus alternus Myers 1927									x	x	x x	x	CZUT-IC, IAvHP, ICNMHN, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021				
Ochmacanthus orinoco Myers 1927								x	x	x		x	IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021				
Ochmacanthus reinhardtii (Steindachner 1882)	x	х	x		х		x						CIACOL, CZUT-IC, ICNMHN, MPUJ	Arbeláez et al. 2004, Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006				
Paracanthopoma sp.									х			x	ICNMHN	Lasso et al. 2009				
Paravandellia sp.	x						x						CIACOL 429					
Potamoglanis hasemani (Eigenmann 1914)*				x			x						CIACOL 3218		x			
Pseudostegophilus haemomyzon (Myers 1942)										x		x	IAvHP, MPUJ					
Pseudostegophilus nemurus (Günther 1869)	x	x	x				x			x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, UCO	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Villa-Navarro <i>et al.</i> 2021				
Schultzichthys gracilis Dalh 1960										x		x	CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017				
<i>Stauroglanis gouldingi</i> de Pinna 1989*					x		х						CIACOL 2677					
Stegophilus septentrionalis Myers 1927										x		x	CZUT-IC, ICNMHN	Lasso et al. 2009				
Trichomycterus migrans (Dalh 1960)										х		х	ICNMHN, MPUJ	Lasso et al. 2009				
Tridens sp.	x	x					x						CIACOL 4544-4549					
Tridentopsis pearsoni Myers 1925	х						x						CZUT-IC 17989, 18069	Donascimiento et al. 2017				
Vandellia beccarii Di Caporiacco 1935									x	x		x	CIACOL, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021				
Vandellia cirrhosa Valenciennes 1846	х	х	х				x			х		х	CIACOL, CZUT-IC, IAvHP, ICNMHN, UF	Arbeláez et al. 2008, Donascimiento et al. 2017, Lasso et al. 2009, Ortega-Lara 2016				
Gen. nv.									x			x	CIACOL 2678					
Family Callichthyidae																		
Callichthys callichthys (Linnaeus 1758)	x	x	x	х	x	x	x		x	x		x	CIACOL, CAS, CZUT-IC, IAvHP, ICNMHN, UF	Arroyave 2005, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn	
Callichthys serralabium Lehmann A. & Reis 2004				x	x		x						CIACOL	Bogotá-Gregory et al. 2020				
Corydoras aeneus (Gill 1858)			x				x		x	x	x	x	CZUT-IC, IAvHP, MPUJ	Lasso et al. 2009			orn	
Corydoras agassizii Steindachner 1876	х	х					x						IAvHP, ICNMHN, UBJTLMM	Donascimiento et al. 2017, Galvis et al. 2007a, Ortega-Lara 2016			orn	

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupės	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	<b>Orinoco Basin</b>	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Corydoras ambiacus Cope 1872	x	x	x				x						CIACOL, CZUT-IC, IAvHP, ICNMHN, UBJTLMM	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			orn	
Corydoras arcuatus Elwin 1938	x	x	x	x			x						CIACOL, CZUT-IC, IAvHP, ICNMHN, UBJTLMM	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Tencatt et al. 2019			orn	
Corydoras armatus (Günther 1868)	x	x					x						CZUT-IC, ICNMHN	Bogotá-Gregory et al. 2020			orn	
Corydoras axelrodi Rössel 1962										x		x	IAvHP 19665				orn	
Corydoras benattii Espíndola, Tencatt, Pupo, Villa-Verde & Britto 2018	x						x						MPUJ 13263		х			
Corydoras concolor Weitzman 1961									x	x	х	х	CZUT-IC	Villa-Navarro et al. 2021			orn	
Corydoras crypticus Sands 1995					х		x						CZUT-IC, IMCN	Donascimiento et al. 2017			orn	
Corydoras delphax Nijssen & Isbrücker 1983								x	x	x	х	х	CZUT-IC, IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
<i>Corydoras elegans</i> Steindachner 1876	x	x	x				x						CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM, UBJTLMM	Arbeláez <i>et al.</i> 2008, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Nijssen & Isbrücker 1983, Ortega <i>et al.</i> 2006			orn	
Corydoras evelynae Rössel 1963	x						x						ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			orn	
Corydoras fowleri Böehlke 1950	x						x						NRM	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Corydoras gomezi Castro 1986	x						x						CZUT-IC, UBJTLMM	Donascimiento et al. 2017			orn	
Corydoras granti Tencatt, Lima & Britto 2019	x						x						ICNMHN, MCZ	Tencatt et al. 2019				
Corydoras julii Steindachner 1906			x				x						MPUJ 13997		x			
Corydoras leopardus Myers 1933			x				x						CIACOL 3452, MPUJ 14155		x			
Corydoras leucomelas Eigenmann & Allen 1942	x	x	x		х	x	x						ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM, UBJTLMM, USMN	Donascimiento <i>et al.</i> 2017, Fowler 1943, Galvis <i>et al.</i> 2007a, Nijssen & Isbrücker 1983, Ortega <i>et al.</i> 2006			orn	
Corydoras loxozonus Nijssen & Isbrücker 1983										x		x	CIACOL, IAvHP, ICNMHN, MPUJ	Lasso <i>et al.</i> 2009			orn	
Corydoras melanistius Regan 1912								x	x	x	х	х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Corydoras melanotaenia Regan 1912										x		x		Villa-Navarro et al. 2021			orn	
Corydoras melini Lönnberg & Rendahl 1930	x		x		x		x		x	х		x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM, UBJTLMM	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009, Nijssen & Isbrücker 1983			orn	
Corydoras napoensis Nijssen & Isbrücker 1986		x	x				x						ICNMHN 14733, MPUJ 14004		х		orn	
Corydoras ortegai Britto, Lima & Hidalgo 2007		x			x		x						CIACOL 4507	Lasso et al. 2009, Miller-Hurtado et al. 2009				
Corydoras osteocarus Bölhke 1951								x	x			x	ICNMHN				orn	
Corydoras pastazensis Weitzman 1963	x	x	x				x						CIACOL, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000			orn	
Corydoras pygmaeus Knaack 1966	x						x						CZUT-IC, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			orn	
<i>Corydoras rabauti</i> La Monte 1941	x	x					x						CIACOL, IAvHP, ICNMHN, UBJTLMM	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000			orn	

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	<b>Orinoco Basin</b>	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Corydoras reticulatus Fraser-Brunner 1938	x		x				x						CIACOL, ICNMHN, UBJTLMM	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Corydoras reynoldsi Myers & Weitzman 1960			x				x						CAS, MPUJ, ZMA	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Myers & Weitzman 1960, Nijssen & Isbrücker 1983			orn	
Corydoras semiaquilus Weitzman 1964	x						x						IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Gutiérrez 2003, Mojica et al. 2005				
Corydoras sodalis Nijssen & Isbrücker 1986	х	x	x				x						CIACOL, CZUT-IC, IAvHP, ICNMHN, UBJTLMM	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a			orn	
Corydoras splendens (Castelnau 1855)	x	x	x				x						CIACOL, CZUT-IC, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000				
Corydoras trilineatus Cope 1872	x	x	x				x						CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UBJTLMM	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Nijssen & Isbrücker 1983, Ortega <i>et al.</i> 2006			orn	
Corydoras zygatus Eigenmann & Allen 1942	x	x	x				x						ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005			orn	
Corydoras sp.					x		x						CIACOL 811, 833					
Dianema longibarbis Cope 1872	x	x					x						CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000			orn	
Hoplosternum littorale (Hancock 1828)	x	x	х		х		x			x		х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2004, Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000			con, orn	
Lepthoplosternum altamazonicum Reis 1997	х	x					x						CZUT-IC, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Megalechis picta (Müller & Troschel 1849)	x				x		x		x	x		x	CIACOL, CZUT-IC, IAvHP	Donascimiento et al. 2017, Villa-Navarro et al. 2021			orn	
Megalechis thoracata (Valenciennes 1840)	x	х	x		x		x	x	x	x		x	CAS/SU, CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM, ROM	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Bogotá-Gregory & Maldonado-Ocampo 2005, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Reis 1997, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			orn	
Family Scoloplacidae																		
Scoloplax baileyi Rocha, Lazzarotto & Rapp Py- Daniel 2012	x						x						CIACOL	Albornoz-Garzón et al. 2018				
Scoloplax dicra Bailey & Baskin 1976	x						x						CZUT-IC	Albornoz-Garzón et al. 2018				
Family Astroblepidae																		
Astroblepus caquetae Fowler 1943			х				х						ANSP, CIACOL, CZUT-IC, MPUJ	Donascimiento et al. 2017, Fowler 1943				
<i>Astroblepus</i> <i>putumayoensis</i> Ardila Rodriguez 2015		x	x				x						IAvHP, MPUJ	Ardila Rodríguez 2015, Donascimiento et al. 2017				
Family Loricariidae																		
Acanthicus hystrix Spix & Agassiz 1829	x						x			x		x	IAvHP	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Lasso et al. 2009			orn	
Acestridium colombiense Retzer 2005								x	x		x	x	FMNH, IAvHP, INHS, USNM	Lasso et al. 2009, Retzer 2005, Villa-Navarro et al. 2021			orn	
Acestridium dichromum Retzer, Nico & Provenzano 1999						x	x		x		x x	x	CZUT-IC, IAvHP, NRM	Donascimiento et al. 2017				
Acestridium martini Retzer, Nico & Provenzano 1999								x	x		х	x	IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Ancistrus dolichopterus Kner 1854					x		х						CIACOL 838, 839		x		orn	
Ancistrus malacops (Cope 1872)	x		x				x		x	x			CIACOL, CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017				

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Mataven Orinoco Basin	UTINOCO DASIN	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Ancistrus macrophthalmus (Pellegrin 1912)						x	x			x		,	x	CZUT-IC	Lasso et al. 2009			orn	
Ancistrus triradiatus Eigenmann 1918									x	x		,	x	CIACOL, CZUT-IC, IAvHP, MPUJ				orn	
Andeancistrus platycephalus (Boulenger 1898)			x				x							ICNMHN					
Aphanotorulus ammophilus Armbruster & Page 1996									x	x	x	х >	x	CZUT-IC, IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Aphanotorulus emarginatus (Valenciennes 1840)	x	x	x				x			x	x	,	x	CAS, CZUT-IC, FMNH, ICNMHN, IAvHP, MCZ	Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009, Ray & Armbruster 2016, Villa-Navarro <i>et al.</i> 2021			orn	
Aphanotorulus horridus (Kner 1854)	x						x							FMNH	Donascimiento et al. 2017, Ray & Armbruster 2016				
Aphanotorulus unicolor (Steindachner 1908)	x	x	x				x							CAS, CIACOL, ICNMHN, MLS	Cipamocha 2002, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Santos 2000, Vejarano 2000			orn	
Baryancistrus beggini Lujan, Arce H. & Armbruster 2009	č.										x	x >	x	IAvHP 7045	Villa-Navarro et al. 2021			orn	
Baryancistrus demantoides Werneke, Sabaj Pérez, Lujan & Armbruster 2005											x	,	x		Villa-Navarro et al. 2021			orn	
Chaetostoma anale (Fowler 1943)		x	x				x							ANSP, CIACOL, IAvHP, ICNMHN, ICNMHN, MLS	Donascimiento et al. 2017, Fowler 1943, Galvis et al. 2007a				
Chaetostoma breve Regan 1904		х	x				x							IAvHP, MPUJ	Urbano-Bonilla & Ballen 2021				
Chaetostoma chimu Urbano-Bonilla & Ballen 2021										x		,	ĸ	MPUJ	Urbano-Bonilla & Ballen 2021				
Chaetostoma dorsale Eigenmann 1922	2									x		,	ĸ	MPUJ 9942				orn	
Chaetostoma formosae Ballen 2011										x		,	ĸ	IAvHP, ICNMHN, MPUJ				orn	
Chaetostoma joropo Ballen, Urbano- Bonilla & Maldonado- Ocampo 2016										x		,	x	MPUJ	Ballen et al. 2016				
Chaetostoma platyrhynchus (Fowler 1943)		x	x				x			x		,	x	ANSP, CIACOL, CZUT-IC, IAvHP, FMNH, MPUJ, USNM	Donascimiento et al. 2017, Fowler 1943				
Dekeyseria amazonica Rapp Py-Daniel 1985	x						x							CIACOL, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Dekeyseria picta (Kner 1854)						x	x	x	x			х У	ĸ	CIACOL, CZUT-IC, IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Dekeyseria scaphirhynchus (Kner 1854)						x	x	x	x	x		x >	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Dolichancistrus fuesslii (Steindachner 1911)			x				x							MPUJ 13455,13462, 13465				orn	
Farlowella amazonum (Günther 1864)	x	x	x				x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Ortega et al. 2006, Mojica et al. 2005, Prieto 2000, Santos 2000, Vejarano 2000				
Farlowella colombiensis Retzer & Page 1997										x		,	x	MPUJ	Lasso et al. 2009			orn	
Farlowella gracilis Regan 1904			x				x							BMNH, CAS, CIACOL, MLS	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Farlowella mariaelenae Martín Salazar 1964									x	x		,	x	CIACOL, IAvHP				orn	

### Fishes from the Colombian rainforest biome

#### ...Continuation

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
<i>Farlowella</i> <i>mitoupibo</i> Ballen, Urbano-Bonilla & Zamudio 2016					x		x			x		x	MPUJ	Ballen et al. 2016				
Farlowella nattereri Steindachner 1910	x		x				x						CIACOL, CZUT-IC, IAvHP, ICNMHN, FMNH	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Farlowella oxyrrhyncha (Kner 1853)	x	x	x				x						CIACOL, FMNH, IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			orn	
Farlowella smithi Fowler 1913	x	x	x				x						CIACOL, ICNMHN, IAvHP	Calderón & Hincapié 2001, Donascimiento <i>et al.</i> 2017, Prieto 2000, Ortega <i>et al.</i> 2006				
Farlowella vittata Myers 1942										x		x	CIACOL, IAvHP, ICNMHN, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Furcodontichthys novaesi Rapp Py-Daniel 1981		x					x						CIACOL 4625		x			
Hemiancistrus guahiborum Werneke, Armbruster, Lujan & Taphorn 2005									x	x	x	x	ICNMHN, NRM	Villa-Navarro <i>et al.</i> 2021			orn	
Hemiancistrus subviridis Werneke, Sabaj Pérez, Lujan & Armbruster 2005					x		x			x	x	x	CZUT-IC 4830	Villa-Navarro <i>et al.</i> 2021			orn	
Hemiodontichthys acipenserinus (Kner 1853)	x		x				x						CIACOL, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Hypancistrus contradens Armbruster, Lujan & Taphorn 2007									x		x	x	ICNMHN 11917-18	Villa-Navarro <i>et al.</i> 2021			orn	
<i>Hypancistrus</i> <i>debilittera</i> Armbruster, Lujan & Taphorn 2007								x	x	x	x	х	IAvHP, ICNMHN	Lasso et al. 2009			orn	
Hypancistrus furunculus Armbruster, Lujan & Taphorn 2007								х			x	x	IMCN	Lasso et al. 2009			orn	
Hypancistrus inspector Armbruster 2002					x		x		x		x	x	CIACOL, CZUT-IC	Lasso et al. 2009			orn	
Hypoptopoma bianale Aquino & Schaefer 2010	x						x						FMNH	Aquino & Schaefer 2010, Donascimiento et al. 2017				
Hypoptopoma brevirostratum Aquino & Schaefer 2010	x						x						FMNH	Aquino & Schaefer 2010, Donascimiento et al. 2017				
Hypoptopoma gulare Cope 1878	x		x				x						CIACOL, FMNH, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Hypoptopoma machadoi Aquino & Schaefer 2010										x		x	CZUT-IC 9881	Villa-Navarro et al. 2021				
Hypoptopoma psilogaster Fowler 1915	x						x						CIACOL 4634		x			
Hypoptopoma spectabile (Eigenmann 1914)											x	x		Villa-Navarro et al. 2021			orn	
Hypoptopoma steindachneri Boulenger 1895	x						x						CZUT-IC, USNM	Aquino & Schaefer 2010, Donascimiento et al. 2017			orn	
Hypoptopoma thoracatum Günther 1868	x		x	x			x						CIACOL, IAvHP, ICNMHN, CAS/SU	Aquino & Schaefer 2010, Donascimiento et al. 2017				
Hypostomus carinatus (Steindachner 1881)	x						x						IAvHP	Donascimiento et al. 2017				
Hypostomus hemicochliodon Armbruster 2003	x		x		x		x		x			x	IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017			orn	

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Hypostomus niceforoi (Fowler 1943)		x	x				x			x		x	ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Fowler 1943, Galvis et al. 2007a			orn	
Hypostomus oculeus (Fowler 1943)	x	x	x		x		x						ANSP, CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Fowler 1943, Mojica et al. 2005, Prieto 2000				
Hypostomus plecostomoides (Eigenmann 1922)			x				x			x		x	CZUT-IC, IAvHP	Donascimiento et al. 2017, Lasso et al. 2009			con, orn	
Hypostomus plecostomus (Linnaeus 1758)										x		x	ICNMHN	Lasso et al. 2009			con, orn	
Hypostomus pyrineusi (Miranda Ribeiro 1920)	x		x				x			x		х	CIACOL, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			con, orn	
Hypostomus sculpodon Armbruster 2003									x	x		х	MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021			con, orn	
Hypostomus varimaculosus (Fowler 1945)			x	x			x						CIACOL, ANSP	Fowler 1945, Donascimiento et al. 2017				
Lamontichthys llanero Taphorn & Lilyestrom 1984										x		x	IAvHP 19355, 19397, 19487, 19611, 19715, 19769, 22525	Donascimiento et al. 2017			orn	
Lasiancistrus schomburgkii (Günther 1864)			x				x						ANSP, IAvHP, ICNMHN	Armbruster 2005, Donascimiento et al. 2017, Fowler 1945, Galvis et al. 2007a			orn	
Lasiancistrus tentaculatus Armbruster 2005										x		x	IAvHP, MPUJ				orn	
<i>Leporacanthicus</i> galaxias Isbrücker & Nijssen 1989											x	x	IAvHP 7041				orn	
Leporacanthicus triactis Isbrücker, Nijssen & Nico 1992										x	x	x	IAvHP 8564	Villa-Navarro et al. 2021			orn	
Leptotocinclus ctenistus Delapieve, Lehmann A & Reis 2018	x						x						ICNMHN	Delapieve et al. 2017				
Limatulichthys griseus (Eigenmann 1909)	x	x	x			x	x			x	x x	х	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UCO	Arbeláez et al. 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Lithoxancistrus orinoco Isbrücker, Nijssen & Cala 1988								x		x	x	x	ICNMHN, ZMA, ZMUL	Lasso et al. 2009, Villa-Navarro et al. 2021				
Loricaria cataphracta Linnaeus 1758	x	x	x		x	x	x		x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Ortega-Lara 2016			orn	
Loricaria nickeriensis Isbrücker 1979	x		x				x						CIACOL, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Loricariichthys acutus (Valenciennes 1840)		x					x						CZUT-IC 14699		х			
Loricariichthys brunneus (Hancock 1828)								x	x	x	x	x	CZUT-IC, IAvHP, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Loricariichthys hauxwelli Fowler 1915	i x						x						IAvHP 12562	Donascimiento et al. 2017				
Loricariichthys stuebelii (Steindachner 1882)	x						x						IAvHP 651		х			
Nannoptopoma spectabile (Eigenmann 1914)	x		x				x			x		x	CIACOL	Donascimiento et al. 2017, Lasso et al. 2009			orn	
Nannoptopoma sternoptychum Scheafer 1996	x						x						USNM	Donascimiento et al. 2017, Schaefer 1996				
Otocinclus batmani Lehmann A. 2006	x		x	x			x						ICNMHN	Donascimiento et al. 2017, Lehmann 2006				
Otocinclus huaorani Schaefer 1997	x				x		x		x	x		x	CIACOL, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Galvis et al. 2007a			orn	

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Otocinclus macrospilus Eigenmann & Allen 1842	x	x	x				x						CAS, CZUT-IC, ICNMHN, USNM	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006			orn	
Otocinclus vestitus Cope 1872	x				x		x						CIACOL, ICNMHN, MPUJ	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Prieto 2000			orn	
Otocinclus vittatus Regan 1904									x	x		x	CIACOL, CZUT-IC, MPUJ	•			orn	
<i>Oxyropsis acutirostra</i> Miranda Ribeiro 1951								x	x		x	x	IAvHP, ICNMHN, MNRJ	Lasso et al. 2009, De Miranda Ribeiro 1951			orn	
Oxyropsis carinata (Steindachner 1879)	x						x						CAS, CZUT-IC, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
<i>Oxyropsis wrightiana</i> Eigenmann & Eigenmann 1889	x	x	x	x	x		x						CZUT-IC, IAvHP, ICNMHN, FMNH, USNM	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Panaqolus albomaculatus (Kanazawa 1958)			х				x						ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Panaqolus maccus (Schaefer & Stewart 1993)										x	x	x	CZUT-IC, IAvHP, MPUJ	Lasso et al. 2009			orn	
Panaque nigrolineatus (Peters 1877)								x	x	x	x	x	CAS, CIACOL, IAvHP, ICNMHN	Lasso et al. 2009, Lujan et al. 2010			orn	
Panaque titan Lujan, Hidalgo & Stewart 2010			x				x						CIACOL, IMCN	Donascimiento et al. 2017			orn	
Parotocinclus eppleyi Schaefer & Povenzano 1993									x		хх	x	IAvHP, NRM	Lasso et al. 2009, Miller-Hurtado et al. 2009			orn	
Parotocinclus longirostris Garavello 1988					x		x						CZUT-IC 4048		х			
Parotocinclus variola Lehmann Schvambach & Reis 2015	x						x						ICNMHN	Donascimiento et al. 2017, Lehmann et al. 2015				
Peckoltia brevis (La Monte 1935)	x		x				x						CZUT-IC, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005			orn	
Peckoltia furcata (Fowler 1940)	х						x						CIACOL 1566		х			
Peckoltia lineola Armbruster 2008									x			x	ICNMHN	Donascimiento et al. 2017				
<i>Peckoltia</i> <i>lujani</i> Armbruster, Werneke & Tan 2015										x		х	IAvHP	Donascimiento et al. 2017				
Peckoltia vittata (Steindachner 1881)	x						x		х	x	x	х	ICNMHN	Donascimiento et al. 2017, Villa-Navarro et al. 2021			orn	
Peckoltichthys bachi (Boulenger 1898)	х		х				х						CIACOL, ICNMHN	Cipamocha 2002, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005			orn	
Pseudancistrus sidereus Armbruster 2004											x	x		Villa-Navarro et al. 2021			orn	
Pseudohemiodon unillano Rojas-Molina, Provenzano & Ramírez- Gil 2019										x	x	x	IAvHP 28429					
Pseudolithoxus anthrax (Armbruster & Provenzano 2000)									x			x	ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Pseudolithoxus nicoi (Armbruster & Provenzano 2000)						x	x						CZUT-IC 5132		x			
Pseudolithoxus tigris (Armbruster & Provenzano 2000)									x			x	CZUT-IC 11821					
Pseudorinelepis genibarbis (Valenciennes 1840)	x						x		x	x	x	x	CZUT-IC, ICNMHN	Donascimiento et al. 2017, Lasso et al. 2009, Ortega-Lara 2016			orn	
Pterygoplichthys gibbiceps (Kner 1854)								x	x	x	x	x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	

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Pterygoplichthys lituratus (Kner 1854)	x						x						(	CIACOL, ICNMHN	Donascimiento <i>et al.</i> 2017, Mojica <i>et al.</i> 2005, Prieto 2000, Santos 2000, Vejarano 2000				
Pterygoplichthys pardalis (Castelnau 1855)	s x	х					x						C	CIACOL, CZUT-IC, FMNH, IAvHP, ICNMHN, UF	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006			con, orn	
Pterygoplichthys scrophus (Cope 1874)	x	x					x							CZUT-IC 14445, 14758		х		orn	
Pterygoplichthys weberi Armbruster & Page 2006	х		x				x							CZUT-IC, FMNH, IAvHP, ICNMHN	Armbruster & Page 2006, Donascimiento et al. 2017				
<i>Rineloricaria castroi</i> Isbrücker & Nijssen 1984	x						x							IAvHP, ICNMHN	Arbelácz et al. 2008, Arbelácz et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Prieto 2000			orn	
<i>Rineloricaria daraha</i> Rapp Py-Daniel & Fichberg 2008					x		x							CIACOL	Bogotá-Gregory et al. 2016, Donascimiento et al. 2017				
Rineloricaria eigenmanni (Pellegrin 1908)	i							x	x	x	x	x	C	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Villa-Navarro <i>et al.</i> 2021			orn	
<i>Rineloricaria formosa</i> Isbrücker & Nijssen 1979	)							x	x	x	x	x x		CIACOL, IAvHP, ICNMHN	Bogotá-Gregory & Maldonado-Ocampo 2005, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
<i>Rineloricaria jurupari</i> Londoño- Burbano & Urbano- Bonilla 2018					x		x							MPUJ	Londoño-Burbano & Urbano-Bonilla 2018				
Rineloricaria lanceolata (Günther 1868)	x		x				x							CIACOL, CAS, FMNH, IAvHP, ICNMHN, USNM	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Mojica et al. 2005, Prieto 2000			orn	
Rineloricaria morrowi Fowler 1940	х	x					x						C	IACOL 4489, 4624, CZUT-IC 14728		х			
<i>Rineloricaria</i> phoxocephala (Eigenmann & Eigenmann 1889)		х					x							CZUT-IC 14728		x			
Rhadinoloricaria rhami (Isbrücker & Nijssen 1983)	x						x							ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Spatuloricaria euacanthagenys Isbrücker 1979		x	х		x		x						C	ANSP, CIACOL, ZUT-IC, ICNMHN, IMCN	Donascimiento et al. 2017, Fowler 1943, Fowler 1945, Galvis et al. 2007a				
Spatuloricaria terracanticum Londoño- Burbano, Urbano- Bonilla, Rojas-Molina, Ramírez-Gil & Prada- Pedreros 2018										x		х		IAvHP	Londoño-Burbano et al. 2018				
Sturisoma guentheri (Regan 1904)		x					x							CZUT-IC 14729		х			
Sturisoma nigrirostrum Fowler 1940	x	x	x				x						CI I	ACOL 2269, CZUT- C 14729, ICNMHN 1210, 2655, UCO 1360		x			
Sturisoma tenuirostre (Steindachner 1910)										x		x		CZUT-IC, IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Sturisomatichthys caquetae (Fowler 1945)			x		x		x							ANSP, CZUT-IC	Fowler 1945, Donascimiento et al. 2017				
Family Cetopsidae																			
Cetopsidium morenoi (Fernández- Yépez 1972)											x	x x		IAvHP 26050	Donascimiento et al. 2017				
Cetopsis candiru Spix & Agassiz 1829	х	x	x				x						(	CAS/SU, CIACOL, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000				
Cetopsis coecutiens (Lichtenstein 1819)	x	x	х		x		x			x	x	x	(	ANSP, CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MHNG	Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009, Mojica <i>et al.</i> 2005, Vari <i>et al.</i> 2005			orn	
Cetopsis montana Vari, Ferraris & de Pinna 2005			x				x			x		х	C	IACOL 1543, 2247, 2898		х			

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Cetopsis orinoco (Schultz 1944)										x		x	MPUJ	Donascimiento et al. 2017				
Denticetopsis seducta Vari, Ferraris & de Pinna 2005	x		x		x		x						CIACOL 857, 1544, 3064, 3613					
Helogenes castaneus (Dahl 1960)									х	х		x	IAvHP, MPUJ	Lasso et al. 2009, Miller-Hurtado et al. 2009				
Helogenes marmoratus Günther 1863	x	x	x	x	x		x	x	x	x	х	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, ROM	Arbeláez et al. 2008, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Prieto 2000, Villa-Navarro et al. 2021			orn	
Family Aspredinidae																		
Amaralia hypsiura (Kner 1855)			x				x						USNM	Friel & Carvalho 2016, Donascimiento et al. 2017				
Bunocephalus aleuropsis Cope 1870	x						x						CIACOL, IAvHP, ICNMHN, FMNH, USNM	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Bunocephalus aloikae Hoedeman 1961									x	x	х	x	IAvHP, MPUJ	Donascimiento et al. 2017, Villa-Navarro et al. 2021				
Bunocephalus coracoideus (Cope 1874)	х	х			х		x						CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Prieto 2000			orn	
Bunocephalus knerii Steindachner 1882			х	х	х		x						CIACOL, USNM	Donascimiento et al. 2017				
Bunocephalus verrucosus (Walbaun 1792)	х	х					x						CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Bogotá-Gregory & Maldonado- Ocampo 2005			orn	
Hoplomyzon papillatus Stewart 1985	х						x						ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			orn	
Pseudobunocephalus amazonicus (Mees 1989)	x						x						CZUT-IC, UF, USNM	Friel 2008, Donascimiento et al. 2017				
Pseudobunocephalus bifidus (Eigenmann 1942)	х						x						ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Pterobunocephalus depressus (Haseman 1911)	x						x			x		x	CIACOL, IAvHP	Donascimiento et al. 2017				
Xyliphius melanopterus Orcés V. 1962		x	x				x						ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Ortega-Lara 2016				
Family Auchenipteridae																		
Ageneiosus inermis (Linnaeus 1766)	x	x	x	x	x		x	x	x	x	хx	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Agudelo Córdoba et al. 2000, Correa 2003, Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		x	con	
Ageneiosus lineatus Ribeiro, Rapp Py-Daniel & Walsh 2017	x						x	x					CIACOL 451, IAvHP 23357	Villa-Navarro <i>et al.</i> 2021				
Ageneiosus polystictus Steindachner 1915					x		x						CIACOL	Bogotá-Gregory et al. 2020				
Ageneiosus ucayalensis Castelanu 1855	x	x			x	x	x						CZUT-IC, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005				
Ageneiosus vittatus Steindachner 1908	x	x	x				x						ICNMHN	Donascimiento et al. 2017, Ortega et al. 2006, Santos 2000, Vejarano 2000				
Asterophysus batrachus Kner 1858									х			x	CIACOL, CZUT-IC	Lasso et al. 2009			orn	
Auchenipterichthys coracoideus (Eigenmann & Allen 1942)	x	x	x	x	x		x						CIACOL, CZUT-IC, IAvHP	Donascimiento et al. 2017, Galvis et al. 2007b				
Auchenipterichthys longimanus (Günther 1864)		x	x		x	x	x	x	x	x	x	x	CZUT-IC, IAvHP, ICNMHN, MPUJ	Bejarano et al. 2006, Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Auchenipterichthys punctatus (Valenciennes 1840)		x				x	x		x		х	x	CZUT-IC, IAvHP	Donascimiento et al. 2017, Villa-Navarro et al. 2021				
Auchenipterus ambyiacus Fowler 1915	x		x				x			x		x	CIACOL, ANSP, IAvHP, ICNMHN	Donascimiento et al. 2017, Ferraris & Vari 1999, Mojica et al. 2005				
Auchenipterus brachyurus (Cope 1878)	x	x					x						CZUT-IC 14314, 14357, ICNMHN 7803–7808, 14021, 14022		х		orn	

	zonas	mayo	uetá	poris	ipės	a-Negro	n Basin	bapo	rida	viare	noco	aven o Baein		Collections	Citations	cord for mbia	atory	se	atened (Mojica 20012)
	Ama	Putu	Caq	Apa	Vai	Guainí	Amazo	Ata	Ìní	Gua	ii 0	Orinoo		Concentions	Сниција	New re Colo	Migr	n	Thre species et al.
Auchenipterus britskii Ferraris & Vari 1999	x		x				x							CIACOL	Bogotá-Gregory et al. 2020				
Auchenipterus nuchalis (Spix & Agassiz 1829)	x	x	x				x			x	x	,	¢	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021				
Centromochlus existimatus Mees 1974	x	х	x				х							IAvHP, ICNMHN, UCO	Calderón & Hincapié 2001, Donascimiento et al. 2017, Mojica et al. 2005				
Centromochlus heckelii (De Filippi 1853)	x	x	x		х		x			x	x	,	¢	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Santos 2000, Vejarano 2000				
Centromochlus macracanthus Soares- Porto 2000					x		x			x		,	¢	IAvHP	Donascimiento et al. 2017				
Duringlanis romani (Mees 1988)									x	x		>	ĸ	IAvHP, MPUJ	Villa-Navarro et al. 2021				
Entomocorus gameroi Mago-Leccia 1984									х			,	¢	IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Epapterus dispilurus Cope 1878	x	x					x							CIACOL, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000				
Liosomadoras morrowi Fowler 1940		х	х			x	х		х		1	K >	ĸ	CZUT-IC, IAvHP, ICNMHN	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017			orn	
Liosomadoras oncinus (Jardine 1841)			x			х	х		х		3	K >	ĸ	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Pseudepapterus cucuhyensis Böhlke 1951						х	х							CAS/SU	Ferraris & Vari 2000, Donascimiento et al. 2017				
Pseudepapterus hasemani (Steindachner 1915)	x						x							ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Tatia altae (Fowler 1945)	x	x	x				x			x		,	¢	ANSP, CIACOL, CZUT-IC, ICNMHN, MPUJ	Donascimiento et al. 2017, Fowler 1945, Galvis et al. 2007a				
Tatia aulopygia (Kner 1858)	x						x				1	<b>x</b> >	ĸ	CZUT-IC, IAvHP, ROM	Donascimiento et al. 2017			orn	
Tatia brunnea Mees 1974	x		x		х		x							CIACOL, CZUT-IC, ICNMHN	Bogotá-Gregory et al. 2020				
Tatia caudosignata DoNascimiento, Albornoz-Garzón & García-Melo 2019	x						x							IAvHP	Donascimiento et al. 2017				
Tatia dunni Fowler 1945	x		x		x		x							ANSP, IAvHP	Donascimiento et al. 2017, Fowler 1945, Sarmento-Soares & Martins-Pinheiro 2008				
Tatia galaxias Mees 1974									х	x	x	,	¢	IAvHP, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Tatia gyrina (Eigenmann & Allen 1942)	x			х	х		х							CIACOL, FMNH	Sarmento-Soares & Martins-Pinheiro 2008, Donascimiento et al. 2017			orn	
Tatia intermedia (Steindachner 1877)	x	x	x		x		x		x	x		,	ĸ	CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Donascimiento et al. 2017, Mojica et al. 2005, Prieto 2000, Sarmento-Soares & Martins-Pinheiro 2008			orn	
<i>Tatia nigra</i> Sarmento- Soares & Martins- Pinheiro 2008					x		x		х	x	1	<b>x</b> >	¢	IAvHP, ICNMHN	Donascimiento et al. 2017, Villa-Navarro et al. 2021				
Tatia perugiae (Steindachner 1882)	x	х		x			х							CIACOL, IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Prieto 2000			orn	
<i>Tatia reticulata</i> Mees 1974	x						x		x	x		,	¢	ICNMHN, MPPUJ	Donascimiento et al. 2017, Mojica et al. 2005			orn	
Tatia strigata Soares- Porto 1995					x		x				1	K >	¢	CZUT-IC, IAvHP	Donascimiento et al. 2017				
<i>Tetranematichthys</i> <i>wallacei</i> Vari & Ferraris 2006	x						x	x	x		x	<b>x</b> >	ĸ	IAvHP, ICNMHN	Donascimiento et al. 2017, Lasso et al. 2009, Vari & Ferraris 2006, Villa-Navarro et al. 2021			orn	
Trachelyichthys decaradiatus Mees 1974								x	x		:	<b>x</b> >	ĸ	CZUT-IC, ICNMHN	Lasso <i>et al.</i> 2009				
Trachelyopterichthys anduzei Ferraris & Fernandez 1987								x	x		1	<b>x</b> >	¢	CZUT-IC, IAvHP, ICNMHN	Lasso et al. 2009			orn	

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Trachelyopterichthys taeniatus (Kner 1858)	x						x	x	x		x	x	x	CIACOL, CAS, IAvHP, ICNMHN	Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Trachelyopterus galeatus (Linnaeus 1766)	x	x	x		x		x	x	x	х	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2004, Bejarano et al. 2006, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			con, orn	
Trachycorystes trachycorystes (Valenciennes 1840)	x					x	x		x		x	x	x	CIACOL, CZUT-IC	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
<i>Tympanopleura</i> atronasus Eigenmann & Eigenmann 1888	x						x							CIACOL, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
<i>Tympanopleura brevis</i> (Steindachner 1881)	х	х					х							ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000				
Tympanopleura piperata Eigenmann 1912	х						х							ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Family Doradidae																			
Acanthodoras cataphractus (Linnaeus 1758)	x		x		x	x	x	x	x				x	CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM	Calderón & Hincapié 2001, Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021		x		
Acanthodoras depressus (Steindachner 1881)					x	x	х							CIACOL, CZUT-IC	Donascimiento et al. 2017				
Acanthodoras spinosissimus (Eigenamnn & Eigenann 1888)	x	x			x	x	x	x	x	x	x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Villa-Navarro et al. 2021			orn	
Agamyxis pectinifrons (Cope 1870)	x	x	x				x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000			orn	
Amblydoras affinis (Kner 1855)	x	х	x	x	x	x	х	x	x	x	x		x	CIACOL, CZUT-IC, IAvHP, MPUJ	Donascimiento et al. 2017, Mojica et al. 2005, Villa-Navarro et al. 2021				
Amblydoras bolivarensis (Fernández-Yépez 1968)								x	x	x		x	x	IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
Amblydoras gonzalezi (Fernández-Yépez 1968)					x	x	x			x			x	CZUT-IC, ICNMHN, MPUJ	Villa-Navarro et al. 2021			orn	
Amblydoras monitor (Cope 1872)	x						х							ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Amblydoras nauticus (Cope 1874)	x	x	x		x		x							CIACOL, CZUT-IC, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			orn	
Anadoras grypus (Cope 1872)	х	х					х							CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000				
Anduzedoras oxyrhynchus (Valenciennes 1821)					x		х		х	x			x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Astrodoras sp.	x						x							CIACOL, IAvHP	Roa-Fuentes et al. 2010				
Centrodoras brachiatus (Cope 1872)	x						x							IAvHP, CZUT-IC	Donascimiento et al. 2017				
Centrodoras hasemani (Steindachner 1915)	x						x							CZUT-IC 14832	Donascimiento et al. 2017				
Doras phlyzakion Sabaj & Brindelli 2008				x			x							IAvHP	Donascimiento et al. 2017, Sabaj Pérez & Birindelli 2008				
Doras punctatus Kner 1855	x	x	x				x							CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, ROM	Birindelli & Pérez 2011, Donascimiento et al. 2017, Mojica et al. 2005				
Hassar orestis (Steindachner 1875)	x	x	x		x		x		x	x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, UCO	Donascimiento et al. 2017, Lasso et al. 2009, Santos 2000, Vejarano 2000			orn	
Hemidoras boulengeri Steindachner 1915	x						x		x				x	ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Villa-Navarro et al. 2021				
Hemidoras morrisi Eigenmann 1925	x	x					x							CIACOL, CZUT-IC, ICNMHN	Donascimiento et al. 2017, Ortega et al. 2006, Santos 2000, Vejarano 2000				
Hemidoras stenopeltis (Kper 1855)	х						x							ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				

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Opsodoras stuebelii (Steindachner 1882)	x						x						CIACOL, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Santos 2000, Vejarano 2000				
Oxydoras sifontesi Fernández-Yépez 1968									x			x	IAvHP	Villa-Navarro et al. 2021				
Hypodoras forficulatus Eigenmann 1925	x	x					x						CIACOL, IAvHP, ICNMHN	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Mojica et al. 2005				
Leptodoras acipenserinus (Günther 1868)		x	x				x						IAvHP, ICNMHN	Donascimiento et al. 2017				
Leptodoras copei (Fernández-Yépez 1968)					x		x		x			x	CZUT-IC 12297, ICNMHN 12900					
Leptodoras juruensis Boulenger 1898	x	x					x						ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006				
Leptodoras linnelli Eigenmann 1912				х			x		x			х	CIACOL 3228, ICNMHN 2771	Lasso et al. 2009				
Leptodoras myersi Böhlke 1970			x				x						IMCN 407		х			
Leptodoras nelsoni Sabaj Pérez 2005										x		х	IAvHP	Donascimiento et al. 2017, Sabaj & Arce 2021				
Lithodoras dorsalis (Valenciennes 1840)	x						x						CZUT-IC	Donascimiento et al. 2017				
Megalodoras uranoscopus (Eigenmann & Eigenmann 1888)	x	x	x		x		x						CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006			con	
Nemadoras elongatus (Boulenger 1898)	x	x					x						ICNMHN	Donascimiento et al. 2017, Sabaj Pérez et al. 2014				
Nemadoras hemipeltis (Eigenmann 1925)	x						x						ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Sabaj Pérez et al. 2014, Santos 2000, Vejarano 2000				
Nemadoras humeralis (Kner 1855)	x	x					x						CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Sabaj Pérez et al. 2014				
Nemadoras trimaculatus (Boulenger 1898)	x	x	x				x						IAvHP, ICNMHN, UCO	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Mojica et al. 2005				
Orinocodoras eigenmanni Myer 1927								x			х	x	ICNMHN	Lasso et al. 2009			orn	
Oxydoras niger (Valenciennes 1821)	x	x	x	x			x						CIACOL, CZUT-IC, IAvHP, ICNMHN	Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000		x	con	
<i>Oxydoras</i> <i>sifontesi</i> Fernández- Yépez 1968								x	x	x	x	x	CZUT-IC, IAvHP	Donascimiento et al. 2017, Sabaj & Arce 2021				
Physopyxis ananas Sousa & Rapp Py-Daniel 2005	x			x			x						CIACOL, IAvHP, ICNMHN	Donascimiento et al. 2017				
Physopyxis lyra Cope 1872	х	х					x						CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Platydoras armatulus (Valenciennes 1840)	x	x	x				x		x	x	x	x	IAvHP, ICNMHN	Piorski et al. 2008, Villa-Navarro et al. 2021			orn	
Platydoras hancockii (Valenciennes 1840)					x	x	x	x	x	x	x x	x	CIACOL, CZUT-IC, IAvHP, ICNMH	Villa-Navarro et al. 2021			orn	
Pterodoras granulosus (Valenciennes 1821)	x	x					x		x			x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000			con	
Pterodoras rivasi (Fernández-Yépez 1950)									x			x	ICNMHN	Mojica 1999		x	con	
<i>Rhinodoras</i> <i>boehlkei</i> Glodek, Whitmire & Orcés V. 1976					x		x						CIACOL, CZUT-IC	Donascimiento et al. 2017				
<i>Rhinodoras</i> gallagheri Sabaj Pérez, Taphorn & Castillo G. 2008										x		x	IAvHP	Donascimiento et al. 2017				
Scorpiodoras heckelii (Kner 1855)	x			x	x		x	x	x		x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Correa 2003, Donascimiento et al. 2017, Lasso et al. 2009			orn	
Tenellus cristinae (Sabaj Pérez, Arce H., Souza & Birindelli 2014)	x						x						ICNMHN	Sabaj Pérez <i>et al.</i> 2014				

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Tenellus leporhinus (Eigenmann 1912)	x						x						ICNMHN 4457					
Tenellus ternetzi (Eigenmann 1925)	x		x			x	x						ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Trachydoras microstomus (Eigenmann 1912)	x						x	x	x			x	ICNMHN 6398, IAvHP 22191	Lasso et al. 2009, Villa-Navarro et al. 2021				
Trachydoras nattereri (Steindachner 1881)	x	x			x		x						CIACOL, CZUT-IC, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Trachydoras steindachneri (Perugia 1897)	x						x						CIACOL, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Santos 2000, Vejarano 2000				
Family Heptapteridae																		
Brachyrhamdia meesi Sands & Black 1985	x						x						IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Brachyrhamdia thayeria Slobodian & Bockmann 2013	x						x						ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005				
Cetopsorhamdia insidiosa (Steindachner 1915)			x				x						CIACOL 3318		х		orn	
Cetopsorhamdia orinoco Schultz 1944										x		x	MPUJ 10926				orn	
Cetopsorhamdia hidalgoi Faustino-Fuster & de Souza 2021			x				x						CIACOL, ROM	Faustino-Fuster & De Souza 2021				
Chasmocranus quadrizonatus Pearson 1937			x				x						CIACOL 1608-1610, MPUJ 14193		x			
Gladioglanis conquistador Lundberg, Bornbusch & Mago- Leccia 1991		x		x	x		x						CIACOL, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Ortega-Lara 2016				
Gladioglanis machadoi Ferraris & Mago-Leccia 1989					x	x	x				x x	х	CZUT-IC, IAvHP	Donascimiento et al. 2017				
Goeldiella eques (Müller & Troschel 1849)	x	x		x		x	x	x	x	x	x x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Correa 2003, Donascimiento et al. 2017, Villa-Navarro et al. 2021				
Imparfinis longicauda (Boulenger 1887)			x				x						CIACOL 1862		х			
Imparfinis microps Eigenmann & Fisher 1916										x		х	IAvHP					
Imparfinis pristos Mees & Cala 1989						x	х		x		хх	х	IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
Imparfinis stictonotus (Fowler 1940)	x		x				x						CIACOL, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a				
Imparfinis sp.nv.									x			х	CIACOL 3627					
Mastiglanis asopos Bockmann 1994	х		х	х	x	x	х		х		x	х	CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009			orn	
Myoglanis koepckei Chang 1999	x						x						CIACOL, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a				
Nannoglanis fasciatus Boulenger 1887*				х			х						CIACOL 3236		х			
Nemuroglanis mariai (Schultz 1944)								x	x	х	x	x	CIACOL, IAvHP, ICNMHN, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021				
<i>Nemuroglanis</i> pauciradiatus Ferraris 1988								x			x	x	CIACOL 1689, IAvHP 26052					
Pariolius armillatus Cope 1872	x	x			x		x						CIACOL, IAvHP	Donascimiento et al. 2017				
Phenacorhamdia macarenensis Dahl 1961										х		x	IAvHP	Donascimiento et al. 2017				

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Phenacorhamdia nigrolineata Zarske 1998	x						x						IAvHP	Donascimiento et al. 2017				
Pimelodella buckleyi (Boulenger 1887)			x		x		x						CIACOL 816, 2245		x			
Pimelodella chaparae Fowler 1940										х		x	IAvHP 21921		x			
Pimelodella conquetaensis Ahl 1925		x	x				x						CIACOL, IAvHP, ICNMHN, ZMB	Ahl 1925, Donascimiento et al. 2017, Galvis et al. 2007a				
Pimelodella cristata (Müller & Troschel 1849)	x	x	x	x	x	x	x				x	x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2004, Cipamocha 2002, Contreras 1999, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021				
Pimelodella cruxenti Fernández-Yépez 1950								x	x	х	x	x	CZUT-IC, IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
Pimelodella figueroai Dahl 1961										x	x	x	IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021				
Pimelodella geryi Hoedeman 1961	x	x	х				x			x		x	IAvHP, ICNMHN	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Cipamocha 2002, Donascimiento et al. 2017, Mojica et al. 2005				
Pimelodella megalops Eigenmann 1912		x	x				x			x	x	x	CIACOL, IAvHP 16502, 16640, 19709, ICNMHN 15187, 15190–15192		х			
Pimelodella metae Eigenmann 1917										x		x	IAvHP, ICNMHN, MPUJ	Lasso et al. 2009			orn	
Rhamdia laukidi Bleeker 1858					x		x						CIACOL 799, 800, 822, 863, 864					
Rhamdia muelleri (Günther 1864)					x		x						CZUT-IC 12291		х			
Rhamdia sp.	x	x	x	x	x		x	x	x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, MLS	Donascimiento et al. 2017, Lasso et al. 2009, Prieto 2000			con	
Family Pimelodidae																		
Aguarunichthys inpai Zuanon, Rapp Py-Daniel & Jégu 1993	x	х					x						CIACOL, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005				
Brachyplatystoma filamentosum (Lichtenstein 1819)	x	x	x	x			x		x	x		x	CIACOL, CZUT-IC, ICNMHN	Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Muñoz-Sosa 1999, Muñoz et al. 1996, Ortega et al. 2006, Villa-Navarro et al. 2021		х	con	VU (A2c,d)
Brachyplatystoma juruense (Boulenger 1898)	x	x	x				x		x	х	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Agudelo Córdoba et al. 2000, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		x	con	VU (A2c,d)
Brachyplatystoma platynemum Boulenger 1898	x	x	x				x			x	x	x	CIACOL, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Lundberg & Akama 2005, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		x	con	VU (A2c,d)
Brachyplatystoma rousseauxii (Castelnau 1855)	x	x					x			x		x	CIACOL, ICNMHN	Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		x	con	
Brachyplatystoma tigrinum (Bristki 1981)	х	x	х				x						BMNH, CIACOL, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Lundberg & Akama 2005, Mojica et al. 2005, Ortega et al. 2006		х	con	
Brachyplatystoma vaillanti (Valenciennes 1840)	x	x	x				x		x	x		x	CIACOL, IAvHP, ICNMHN	Agudelo Córdoba et al. 2000, Contreras 1999, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		x	con	VU (A2c,d)
Callophysus macropterus (Lichtenstein 1819)	x	x	x				x		x	x		x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN	Agudelo Córdoba et al. 2000, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021		x	con	
Cheirocerus eques Eigenmann 1917			x				x						CIACOL 107		x			
Cheirocerus goeldii (Steindachner 1908)	x	x					x						ICNMHN, UCO	Donascimiento et al. 2017, Mojica et al. 2005				
Duopalatinus peruanus Eigenmann & Allen 1942										x		x	IAvHP, MPUJ	Donascimiento et al. 2017				
Hemisorubim platyrhynchos (Valenciennes 1840)	x	x	x	x			x	x	x	x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2004, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			con	

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Matavén Orinoco Basin		Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Hypophthalmus edentatus Spix & Agassiz 1829	x	x	x	x			x			x		x	(	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UF	Agudelo Córdoba et al. 2000, Calderón & Hincapié 2001, Contreras 1999, Correa 2008, Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			con	
Hypophthalmus fimbriatus Kner 1858	x						x						0	CZUT-IC, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005		x		
Hypophthalmus marginatus Valenciennes 1840										x	x	x		IAvHP	Donascimiento et al. 2017, Mojica et al. 2005, Villa-Navarro et al. 2021		x		
Hypophthalmus oremaculatus Nani & Fuster de Plaza 1947	x	x					x							IAvHP, ICNMHN					
Leiarius marmoratus (Gill 1870)	x	x	x	x			x		x	x		х	( IA	CIACOL, CZUT-IC, AvHP, ICNMHN, UF	Agudelo Córdoba et al. 2000, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		х	con	
Leiarius pictus (Müller & Troschel 1849)	x		x	x			x			x		х		IAvHP, ICNMHN	Donascimiento et al. 2017, Correa 2003, Correa 2008, Villa-Navarro et al. 2021				
Megalonema orixanthum Lundberg & Dahdul 2008										x		х	Ι	AvHP 22700, 27400					
Megalonema platycephalum Eigenmann 1912					x		x			x		x		CIACOL, IAvHP, ICNMHN	Lasso et al. 2009				
Phractocephalus hemioliopterus (Bloch & Schneider 1801)	x	x	x	x			x	x	x	x	x	х	(	CIACOL, CZUT-IC, IAvHP, ICNMHN	Agudelo Córdoba et al. 2000, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021			con	
Pimelodina flavipinnis Steindachner 1876	x	x	x	x			x		x	x	x	х		CIACOL, IAvHP, ICNMHN, MPUJ	Calderón & Hincapié 2001, Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Santos 2000, Vejarano 2000, Villa-Navarro <i>et al.</i> 2021				
Pimelodus albofasciatus Mees 1974	x	x	x		x		x	х		x		х		CZUT-IC, IAvHP	Lasso et al. 2009			orn	
Pimelodus altissimus Eigenmann & Pearson 1942	x						x							IAvHP 411		x			
Pimelodus blochii Valenciennes 1840	x	x	x	х	x	x	x	x	x	x	х	x x	(	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UCO, UF	Arbeláez et al. 2004, Arroyave 2005, Bejarano et al. 2006, Calderón & Hincapié 2001, Contreras 1999, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021		х	con, orn	
Pimelodus garciabarrigai Dahl 1961									x	x	x	x		CZUT-IC, IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021				
Pimelodus ornatus Kner 1858	x	x	x	x	x		x		x	x	x	х		CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005			orn	
Pimelodus pictus Steindachner 1876	x	x	x				x		x	x		х		CAS, CIACOL, IAvHP, ICNMHN, MLS, USMN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006		x	orn	
Pinirampus pirinampu (Spix & Agassiz 1829)	x	x	x		x		x		x	x	x	x	(	CIACOL, CZUT-IC, IAvHP, ICNMHN	Agudelo Córdoba et al. 2000, Bejarano et al. 2006, Calderón & Hincapié 2001, Contreras 1999, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021		x	con	
Platynematichthys notatus (Jardine 1841)	x	x	x	x			x			x		x	(	CIACOL, CZUT-IC, ICNMHN	Agudelo Córdoba et al. 2000, Bejarano et al. 2006, Calderón & Hincapié 2001, Contreras 1999, Correa 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		x	con	
Platysilurus mucosus (Vaillant 1880)	x		x				x			x	x	x		IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Villa-Navarro et al. 2021			con	
Platystomatichthys sturio (Kner 1858)	x	x	x				x							CIACOL, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006			con	
Pseudoplatystoma metaense Buitrago- Suárez & Burr 2007								x	x	x	x	x x		IAvHP, MPUJ	Lasso <i>et al.</i> 2009		x	con	VU (A2c,d)
Pseudoplatystoma orinocoense Buitrago- Suárez & Burr 2007									x	x		x	(	CZUT-IC, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021		x	con	VU (A2c,d)
Pseudoplatystoma punctifer (Castelnau 1855)	x	x	x				x						(	CIACOL, CZUT-IC, IAvHP	Buitrago-Suárez & Burr 2007, Donascimiento et al. 2017			con	
Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco Matavén	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)	
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Pseudoplatystoma tigrinum (Valenciennes 1840)	x	x	x	x	x		x						CIACOL, ICNMHN	Agudelo Córdoba et al. 2000, Buitrago-Suárez & Burr 2007, Correa 2003, Correa 2008, Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000		x	con	VU (A2c,d)	
Sorubim elongatus Littmann, Burr, Schmidt & Isern 2001	x	x	x	x			x		x	x	x	х	CIACOL, IAvHP, ICNMHN, MCZ, MPUJ	Donascimiento et al. 2017, Galvis et al. 2007a, Littmann 2007, Littmann et al. 2001, Mojica et al. 2005, Villa-Navarro et al. 2021			con		
Sorubim lima (Bloch & Schneider 1801)	x	x	x	x			x	x	x	x	x	x	CIACOL, CZUT-IC, FMNH, IAvHP, ICNMHN, MPUJ, UF	Agudelo Córdoba et al. 2000, Calderón & Hincapié 2001, Contreras 1999, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Littmann 2007, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021		x	con	(NT)	
Sorubim maniradii Littman, Burr & Buitrago-Suárez 2001	x						x						CIACOL, ICNMHN	Donascimiento et al. 2017, Littmann et al. 2001, Mojica et al. 2005			con		
Sorubimichthys planiceps (Spix & Agassiz 1829)	x	x	x				x		x	x		x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN	Agudelo Córdoba et al. 2000, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021		x	con	(NT)	
Zungaro zungaro (Humboldt 1821)	x	x	x				x		x	x		x	CAS, CIACOL, CZUT-IC, FMNH, IAvHP, ICNMHN	Agudelo Córdoba et al. 2000, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Muñoz-Sosa 1999, Muñoz et al. 1996, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021		x	con	VU (A2c,d)	
Family Pseudonimelodidae																			
Batrochoglanis raninus (Valenciennes 1840)	x	x			x	x	x		x			x	CIACOL 1619, CZUT IC 4294, IAvHP, ICNMHN	<ul> <li>Bogotá-Gregory &amp; Maldonado-Ocampo 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005</li> </ul>			orn		
Batrochoglanis villosus (Eigenmann 1912)				x	x		x	x			хх	x	CIACOL 815, 3231, IAvHP, ICNMHN, USNM	Lasso et al. 2009, Villa-Navarro et al. 2021					
Microglanis iheringi Gomes 1946										x	Х	x	IAvHP	Donascimiento et al. 2017, Villa-Navarro et al. 2021			orn		
Microglanis poecilus	x	x	x			x	x	x	x	x	x	x	CZUT-IC, IAvHP,	Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005			orn		
Pseudopimelodus bufonius (Valenciennes 1840)	x				x		x			x		x	CZUT-IC, IAvHP, ICNMHN, MPUJ	Donascimiento et al. 2017			con		
<i>Rhyacoglanis</i> annulatus Shibatta & Vari 2017										x		x	IAvHP	Donascimiento et al. 2017					
Order Batrachoidiformes																			
Family Batrachoididae																			
Thalassophryne amazonica Steindachner 1876	x	x					x						IAvHP, ICNMHN	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Mojica et al. 2005			orn		
Order Gobiiformes																			
Family Eleotridae																			
Microphilypnus ternetzi Myers 1927	х					х	х	х	х		хх	x	CAS, CZUT-IC, IAvHP, ICNMHN	Caires et al. 2011, Donascimiento et al. 2017, Mojica et al. 2005, Villa-Navarro et al. 2021					
Order Synbranchiformes																			
Family Synbranchidae																			
Synbranchus marmoratus Bloch 1795	x	x	x	x	x	x	x	x	х	x	хх	x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, UF, USNM	Arbeláez et al. 2008, Arbeláez et al. 2004, Correa 2003, Calderón & Hincapié 2001, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn		
Order Carangiformes																			
Family Achiridae																			
Apionichthys nattereri (Steindachner 1876)	x						х						IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			orn		
Hypoclinemus mentalis (Günther 1862)	х	х	х				х			x	x	х	CIACOL, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021					

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Order Cichliformes																		
Family Polycentridae																		
<i>Monocirrhus</i> <i>polyacanthus</i> Heckel 1840	x	x	x			x	x	x	x	x	x	х	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Arbeláez et al. 2008, Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn	
Family Cichlidae																		
Acarichthys heckelii (Müller & Troschel 1849)	x	x					x						IAvHP, NMW, NRM	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento <i>et al.</i> 2017, Kullander 1986				
Acaronia nassa (Heckel 1840)		x	x				х						CIACOL, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a				
Acaronia vultuosa Kullander 1989								x	x		x	х	CZUT-IC, IAvHP, ICNMHN, NRM	Kullander 1989, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Aequidens diadema (Heckel 1840)	x	х	х			x	x	x	х	x	2	x	CZUT-IC, IAvHP, ICNMHN, NRM	Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Lasso et al. 2009, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Aequidens metae Eigenmann 1922								x	x	x		x	IAvHP, ICNMHN, MPUJ, NRM	Lasso et al. 2009, Villa-Navarro et al. 2021			con, orn	
Aequidens patricki Kullander 1984	x	x		x	x		x						CZUT-IC 3589, 4522, ICNMHN 14840- 14842, 17246		х			
Aequidens tetramerus (Heckel 1840)	x	x	x	x	x		x	x	x	x	x	x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Villa-Navarro et al. 2021			orn	
Apistogramma agassizii (Steindachner 1875)	x	x					x						CIACOL, IAvHP, ICNMHN, NRM, ROM	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Prieto 2000			orn	
Apistogramma alacrina Kullander 2004			x				х			x		х	IAvHP, MPUJ, NRM	Donascimiento et al. 2017, Kullander 2004, Lasso et al. 2009				
Apistogramma bitaeniata Pellegrin 1936	x	x	x				x						IAvHP, ICNMHN, MNHN, NRM	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Kullander 1980, Mojica et al. 2005, Ortega et al. 2006			orn	
Apistogramma cacatuoides Hoedeman 1951	x	x					x						IAvHP, ICNMHN, NRM, ROM, USNM, ZMA	Donascimiento et al. 2017, Galvis et al. 2007a, Kullander 1980			orn	
Apistogramma cruzi Kullander 1986		x	x				x						CAS	Donascimiento et al. 2017, Ortega-Lara 2016				
Apistogramma diplotaenia Kullander 1987	x						x						IAvHP	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017				
Apistogramma eunotus Kullander 1981	x				x		x						MPUJ, NRM, ROM, UF	Donascimiento et al. 2017				
Apistogramma flabellicauda Mesa S. & Lasso 2011						x	x	x	x	x	3	x	CZUT-IC, IAvHP	Donascimiento et al. 2017, Villa-Navarro et al. 2021				
Apistogramma hoignei Meinken 1965									x	x	x	х	IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
Apistogramma hongsloi Kullander 1979									x	x	x	x	IAvHP, MPUJ	Donascimiento et al. 2017, Villa-Navarro et al. 2021			orn	
Apistogramma iniridae Kullander 1979		x	x		x	x	x	x	x	x		x	CIACOL, CZUT-IC, IAvHP, MPUJ, NRM	Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Apistogramma lineata Mesa S. & Lasso 2011								x				х	IAvHP 11794					
Apistogramma macmasteri Kullander 1979										x		x	ICNMHN, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Apistogramma megaptera Mesa S. & Lasso 2011								x	x	x		x	IAvHP 11714, 24785	Villa-Navarro et al. 2021				
Apistogramma velifera Staeck 2003										x	x	х		Villa-Navarro et al. 2021				
Apistogramma viejita Kullander 1979										x		х	ICNMHN, MPUJ	Donascimiento et al. 2017				

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Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Matavén	<b>Orinoco Basin</b>	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojics <i>et al.</i> 20012)
Apistogrammoides pucallpaensis Meinken 1965	x						x							MCZ	Donascimiento et al. 2017, Kullander 1986				
Astronotus ocellatus (Agassiz 1831)	x	x	x	x			x	x	x	x	x		x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN	Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			con, orn	
Biotodoma cupido (Heckel 1840)	x	x	x	x			x							CIACOL, CZUT-IC, IAvHP, ICNMHN, UF	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Bogotá-Gregory & Maldonado-Ocampo 2005			con, orn	
Biotodoma wavrini (Gosse 1963)	x		x			x	x	x	х		x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM	Arbeláez et al. 2004, Donascimiento et al. 2017, Lasso et al. 2009, Mojica et al. 2005, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			con, orn	
Biotoecus dicentrarchus Kullander 1989									x				x		Villa-Navarro et al. 2021				
<i>Bujurquina cordemadi</i> Kullander 1986	x						x							CZUT-IC 14365		x			
<i>Bujurquina huallagae</i> Kullander 1986										x			x	MPUJ 12996, 12997		х			
Bujurquina mariae (Eigenmann 1922)								x	x	x	x		x	CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Correa 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			con, orn	
Bujurquina moriorum Kullander 1986	x	x	x	x			x			x			x	IAvHP 19331, 19516, 19634, MPUJ, NRM	Donascimiento et al. 2017				
<i>Bujurquina</i> peregrinabunda Kullander 1986	x	x	x				x							ANSP, CIACOL, NRM	Donascimiento et al. 2017				
Bujurquina syspilus (Cope 1872)	x						x							ICNMHN, ROM	Donascimiento et al. 2017				
Caquetaia myersi (Schultz 1944)	x	x	x			x	x							ANSP, CAS, CIACOL, IAvHP, ICNMHN, USNM	Donascimiento et al. 2017, Fowler 1945, Galvis et al. 2007a				
Chaetobranchus flavescens Heckel 1840	x	x	x			x	x		x	x			x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			orn	
Cichla intermedia Machado-Allison 1971									х	х			x	IAvHP	Lasso et al. 2009				
Cichla monoculus Spix & Agassiz 1831	х	x		x			x		x	x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM	Arbeláez et al. 2004, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			con	
Cichla orinocensis Humboldt 1821					x	x	x	x	x	x	x	x	x	CIACOL, CZUT-IC, IAvHP, NRM	Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021		x	con	
Cichla temensis Humboldt 1821		x	x	x	x	x	x	x	x	x	x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009, Villa-Navarro <i>et al.</i> 2021			con	
Cichlasoma amazonarum Kullander 1983	x	x					x							CIACOL, CZUT-IC, IAvHP, ICNMHN	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Kullander 1983, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000			orn	
Cichlasoma orinocense Kullander 1983								x	x				x	ANSP, FMNH, NRM	Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021				
Crenicara punctulata (Günther 1863)	x	x					x							ICNMHN, NRM	Donascimiento et al. 2017, Ortega-Lara 2016				
Crenicichla alta Eiegenmann 1912	x	x	x		x		x	x	x	x			x	CZUT-IC, IAvHP, MPUJ	Arbeláez et al. 2008, Arroyave 2005, Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Villa-Navarro et al. 2021			orn	
Crenicichla anthurus Cope 1872	x	x	x	x	x		х	x	x				x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Correa 2003, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009, Ortega <i>et al.</i> 2006			orn	
Crenicichla cincta Regan 1905	x						х							CIACOL	Bogotá-Gregory et al. 2020				
Crenicichla geayi Pellegrin 1903									x	x			x	IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Crenicichla johanna Heckel 1840	x	x	x	x			x	x	x	x		x	x	CIACOL, IAvHP, ICNMHN, NRM	Arbeláez et al. 2004, Calderón & Hincapié 2001, Donascimiento et al. 2017, Gutiérrez 2003, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			orn	

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Crenicichla lenticulata Heckel 1840	x	x		x	x	x	x	x	x			x	CI I	IACOL, CZUT-IC, AvHP, ICNMHN, NRM	Correa 2003, Correa 2008, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009, Villa-Navarro <i>et al.</i> 2021			con, orn	
Crenicichla lucius Cope 1870			x		x		x							CIACOL 2012, ICNMHN 898		х			
Crenicichla lugubris Heckel 1840		x	x	x	x		x	x	x	x	3	K X	CI I	IACOL, CZUT-IC, AvHP, ICNMHN	Bejarano et al. 2006, Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Ortega et al. 2006				
Crenicichla marmorata Pellegrin 1904		x			x		x						Cl	IACOL, ICNMHN	Bogotá-Gregory et al. 2020			orn	
<i>Crenicichla</i> <i>monicae</i> Kullander & Varella 2015					x		x							NRM	Donascimiento et al. 2017, Kullander & Varella 2015				
Crenicichla proteus Cope 1872	х						x							CIACOL	Bogotá-Gregory et al. 2020				
Crenicichla reticulata (Heckel 1840)	x	x					x						Cl	IACOL, ICNMHN	Donascimiento et al. 2017				
Crenicichla strigata Günther 1862	х		x				х						C	IACOL, ICNMHN	Donascimiento et al. 2017, Calderón & Hincapié 2001				
Crenicichla sveni Ploeg 1991										x	2	K X	1	IAvHP	Donascimiento et al. 2017			orn	
<i>Crenicichla</i> wallacii Regan 1905								x	x			x	. (	CZUT-IC, IAvHP, MPUJ				orn	
<i>Crenicichla zebrina</i> Montaña, López- Fernández & Taphorn 2008											x	х	ĩ		Villa-Navarro <i>et al.</i> 2021			orn	
Dicrossus filamentosus (Ladiges 1958)						x	х	х	x	x	x	x x	. (	CZUT-IC, IAvHP, ICNMHN, NRM	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Dicrossus gladicauda Schindler & Staeck 2008								x	x			x	1	IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
<i>Geophagus abalios</i> López-Fernández & Taphorn 2004			x	x	x		x		x	x	x	x	Cl I	IACOL, CZUT-IC, AvHP, ICNMHN, MPUJ, NRM	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Geophagus dicrozoster López-Fernández & Taphorn 2004								x	x	x		x	. (	CIACOL, IAvHP, NRM	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Geophagus megasema Heckel 1840			х				х							IAvHP	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017				
Geophagus surinamensis (Bloch 1791)		х	х	x			х						(	CZUT-IC, IAvHP, ICNMHN	Calderón & Hincapié 2001, Correa 2003, Correa 2008, Donascimiento <i>et al.</i> 2017, Ortega <i>et al.</i> 2006			orn	
Geophagus winemilleri López-Fernádez & Taphorn 2004		x	x	x	x		x		x		x	x	: (	CIACOL, IAvHP	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Heroina isonycterina Kullander 1996			х				х							CAS, FMNH	Kullander 1996, Donascimiento et al. 2017				
Heros efasciatus Heckel 1840	x	x			x		x						(	CIACOL, IAvHP, ICNMHN, ROM	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006			orn	
Heros severus Heckel 1840	x	x	x	x	x	x	x	x	x	x	x	k x	CI I	IACOL, CZUT-IC, AvHP, ICNMHN, MLS, NRM	Arbeláez et al. 2004, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Ortega et al. 2006, Santos 2000, Vejarano 2000, Villa-Navarro et al. 2021			orn	
Hoplarchus psittacus (Heckel 1840)		х	х			x	х	x	x	x	x	K X	I	AvHP, ICNMHN, NRM	Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Hypselecara coryphaenoides (Heckel 1840)	x						x	x	x	x	3	K X	CI	ACOL, ICNMHN, NRM	Arbeláez et al. 2004, Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Hypselecara temporalis (Günther 1862)	х	x	x				х							CAS, ICNMHN	Bejarano et al. 2006, Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006			orn	
Laetacara flavilabris (Cope 1870)	x	x	x				x						Ι	AvHP, ICNMHN, NRM, ROM	Donascimiento et al. 2017, Galvis et al. 2007a, Kullander 1986, Lasso et al. 2009, Ortega et al. 2006			orn	
Laetacara fulvipinnis Staeck & Schindler 2007								x	x	x	x	х	. (	CZUT-IC, IAvHP, NRM	Villa-Navarro et al. 2021				

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Taxa	Amazonas	Putumavo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Matavén	Orinoco Basin	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Laetacara thayeri (Steindachner 1875)	x	x					x							CIACOL, ICNMHN, USNM	Donascimiento et al. 2017, Galvis et al. 2007a			orn	
Mesonauta egregius Kullander & Silvergrip									x	x	x	x	x	CIACOL, CZUT-IC, IAvHP, ICNMHN	Lasso et al. 2009			orn	
Mesonauta insignis (Heckel 1840)	x	x		x		x	x	x	x	x	x	x	x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, NRM, ROM	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009, Ortega-Lara 2016, Villa-Navarro <i>et al.</i> 2021			orn	
Mesonauta mirificus Kullander & Silfvergrip	x	x	x			x	x							IAvHP, ICNMHN, NRM	Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Kullander & Silfvergrip 1991, Ortega <i>et al.</i> 2006			orn	
Mikrogeophagus ramirezi (Myers & Harry 1948)									x	x			x	IAvHP, ICNMHN	Lasso et al. 2009			orn	
Pterophyllum altum Pellegrin 1903								x	x		x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MLS, NRM	Lasso et al. 2009, Mojica et al. 2005, Villa-Navarro et al. 2021			orn	VU (A2d)
Pterophyllum scalare (Schultz 1823)	x	x	х	х			x							CIACOL, CZUT-IC, FMNH, IAvHP, ICNMHN, UF	Arbeláez et al. 2004, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000			orn	
Satanoperca acuticeps (Heckel 1840)		x					x							CZUT-IC 14709		x			
Satanoperca daemon (Heckel 1840)		x		x		x	x	x	x	x	x	x	x	CZUT-IC, IAvHP, ICNMHN, NRM	Correa 2003, Donascimiento et al. 2017, Lasso et al. 2009, Villa- Navarro et al. 2021			con, orn	
Satanoperca jurupari (Heckel 1840)	x	x	х	x	x	x	x							CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ, NRM, ROM, UF	Arbeláez et al. 2004, Bejarano et al. 2006, Correa 2003, Correa 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Gutiérrez 2003, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Santos 2000, Vejarano 2000			con, orn	
Satanoperca mapiritensis (Fernández-Yépez 1950)						x	x		x	x	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Symphysodon aequifasciatus Pellegrin 1904	x	x	х	x			x							CIACOL, IAvHP, ICNMHN	Axelrod 1978, Correa 2003, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006	Ļ		orn	
Uaru amphiacanthoides Heckel 1840				x			x							IAvHP, ICNMHN	Correa 2003, Correa 2008, Donascimiento et al. 2017				
Uaru fernandezyepezi Stawikowski 1989								x	x				x	ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021			orn	
Order Cyprinodontiformes																			
Family Rivulidae	x						x							NRM	Donascimiento et al. 2017				
(Garman 1895)										v			v	IAvHD	Lasso at al. 2009				
<i>corpulentus</i> (Thomerson & Taphorn 1993)										л			л	nvin					
Anablepsoides elongatus (Fles & de Rham 1981)	x			х	x		х							CIACOL, ICNMHN	Arbeláez et al. 2004, Correa 2003, Donascimiento et al. 2017				
Anablepsoides ophiomimus (Huber 1992)	x			x			x							ICNMHN	Correa 2003, Donascimiento et al. 2017				
Anablepsoides ornatus (Garman 1895)	x		х	х	x		х							CIACOL, CZUT-IC, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005			orn	
Anablepsoides rubrolineatus (Fels & de Rham 1981)	x	x					x							CZUT-IC, ICNMHN, UF	Donascimiento et al. 2017, Mojica et al. 2005, Ortega et al. 2006				
Anablepsoides taeniatus (Fowler 1945)			x				x							CIACOL, IAvHP	Fowler 1945, Donascimiento et al. 2017				
Anablepsoides tessellatus (Huber 1992)									x	х			х	CIACOL, MPUJ	Donascimiento et al. 2017				
Laimosemion altivelis (Huber 1992)									x	x			x	NRM	Lasso et al. 2009, Vermeulen & Mejia-Vargas 2020				
Laimosemion amanapira (Costa 2004)					x		x							CIACOL 890, 891					

Taxa	Amazonas	Putumayo	Caquetá	Apaporis	Vaupés	Guainía-Negro	Amazon Basin	Atabapo	Inírida	Guaviare	Orinoco	Matavén	<b>Orinoco Basin</b>	Collections	Citations	New record for Colombia	Migratory	Use	Threatened species (Mojica <i>et al.</i> 20012)
Laimosemion carolinae (Vermeulen & Mejia- Vargas 2020)						x	x							IAvHP 13656, 13657					
Laimosemion flammaecauda (Vermeulen & Mejia- Vargas 2020)						x	x							IAvHP 13658, 13659					
Laimosemion foliiscola (Vermeulen & Mejia- Vargas 2020)						x	x							IAvHP 13652, 13653					
Laimosemion leticia Valdesalici 2016	x						x							IAvHP	Donascimiento et al. 2017, Valdesalici 2016, Vermeulen & Mejia-Vargas 2020				
Laimosemion tecminae (Thomerson, Nico & Taphorn 1992)												x	x		Vermeulen & Mejia-Vargas 2020				
Family Fluviphylacidae																			
Fluviphylax obscurus Costa 1996								x	x	x	x		x	CZUT-IC, IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
Fluviphylax pygmaeus (Myers & Carvalho 1955)	x						x	x	x				x	IAvHP, NRM	Donascimiento et al. 2017, Lucinda 2003, Villa-Navarro et al. 2021				
Order Beloniformes																			
Family Belonidae																			
Belonion dibranchodon Collette 1966		x		x			x	x	x	x	x	x	x	CZUT-IC, IAvHP, ICNMHN	Correa 2003, Donascimiento et al. 2017, Lasso et al. 2009, Villa-Navarro et al. 2021				
Potamorrhaphis guianensis (Jardine 1843)	x	x	x	x	x	x	x		x	x	x		x	CAS, CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Arbeláez et al. 2008, Arbeláez et al. 2004, Arroyave 2005, Donascimiento et al. 2017, Galvis et al. 2007a, Lasso et al. 2009, Mojica et al. 2005, Ortega et al. 2006, Prieto 2000, Villa-Navarro et al. 2021			orn	
Potamorrhaphis labiata Sant'Anna, Delapieve & Reis 2012	x	x					x							CIACOL 4478, 4482		х			
Potamorrhaphis petersi Collette 1974					х		х	х	х	х	х		х	CIACOL, IAvHP, ICNMHN	Lasso et al. 2009, Villa-Navarro et al. 2021				
Pseudotylosurus microps (Günther 1866)	x	x	x				х				х		х	CZUT-IC, IAvHP, ICNMHN	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005, Ortega et al. 2006			orn	
Order Perciformes																			
Family Sciaenidae																			
Pachypops fourcroi (Lacepède 1802)		x	x		x	x	x							IAvHP, ICNMHN	Casatti 2002, Donascimiento et al. 2017				
Pachypops trifilis (Müller & Troschel 1849)	-		x				x							IAvHP	Bogotá-Gregory & Maldonado-Ocampo 2005, Donascimiento et al. 2017				
Pachyurus gabrielensis Casatti 2001										x	x		x	CZUT-IC, IAvHP	Lasso et al. 2009, Villa-Navarro et al. 2021				
Pachyurus junki Soares & Casatti 2000			x				x							CIACOL, ICNMHN	Bejarano et al. 2006, Donascimiento et al. 2017				
Pachyurus schomburgkii Günther 1860		x	x		x		x			x	x		x	IAvHP, ICNMHN	Donascimiento <i>et al.</i> 2017, Lasso <i>et al.</i> 2009, Ortega-Lara 2016, Villa-Navarro <i>et al.</i> 2021				
Plagioscion squamosissimus (Heckel 1840)	x	х	x	x	x		x	x	x	х	x		x	CIACOL, CZUT-IC, IAvHP, ICNMHN, MPUJ	Calderón & Hincapié 2001, Contreras 1999, Correa 2003, Correa 2008, Donascimiento <i>et al.</i> 2017, Galvis <i>et al.</i> 2007a, Lasso <i>et al.</i> 2009, Mojica <i>et al.</i> 2005, Ortega <i>et al.</i> 2006, Prieto 2000, Santos 2000, Vejarano 2000, Villa-Navarro <i>et al.</i> 2021		x	con	
Order																			
retraodontiformes																			
Colomesus asellus	x	x	x				x							CIACOL, CZUT-IC.	Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005.			orn	
(Müller & Troschel 1849)		-												IAvHP, ICNMHN, UCO	Ortega et al. 2006				
Order Ceratodontiformes																			
Family Lepidosirenidae																			
Lepidosiren paradoxa Fitzinger 1837	x		x				х							IAvHP, ICNMHN	Arbeláez et al. 2008, Donascimiento et al. 2017, Galvis et al. 2007a, Mojica et al. 2005				(NT)



Figure 4. a) Dendrogram and b) multivariate analysis (NMDS) based on Kulczynski index.

height, reflect co-occurrence of 404 species in the Amazon and Orinoco basins. Nevertheless, the dendrogram denotes a clear grouping of the systems that drain the Amazon basin (except Guainía-Negro), from those that drain the Orinoco basin (Figure 4a) (see Supplementary Appendix 2 for dissimilarity values and heatmap derived from presence/ absence data). Furthermore, within the Amazon basin, there is a node, grouping according to geological origin: systems of Andean origin (i.e. Amazon, Putumayo, and Caquetá rivers) and systems that originate in the lowlands (i.e. Apaporis and Vaupés); where each of the lowland systems present distinct ichthyofaunas, resulting in separate positions in the dendrogram. The overall results of the dendrogram are supported by the predetermined polygons plotted within the NMDS (Figure 4b). Nevertheless, in the multidimensional space of the NMDS, all the systems draining the Amazon are grouped together. On the other hand, if the grouping is done for all river systems of the Amazonia region, regarding the geological origin, the configuration in the multidimensional space is not as clear as from a river basin perspective (see Figure S1). These patterns are supported by the PERMANOVA; species distribution differed significantly between basins (F = 4.3, R = 0.26, P < 0.003) and geological origin (F = 3.6, R = 0.23, P < 0.003).

## Discussion

We provide an extensive compilation of the fishes in the Colombian Amazonia, supported by scientific peer-reviewed publications and, mainly, by reference collections. Our study includes documented distributions of 1104 species at the river systems level. This species richness reflects the megadiversity of the Amazon and the Neotropical region in general (Albert & Reis 201a, Dagosta & de Pinna 2019). There are universal patterns such as latitudinal-altitudinal gradients, the species-area relationship that explains fish diversity, and how it is spatially distributed (Reis et al. 2016, Oberdoff et al. 2019). Other diversity patterns are associated with climatic conditions and sub-basin isolation (Oberdoff et al. 2019). The region known as the Amazon-Orinoco-Guyana nucleus, in addition to being heterogeneous, exhibits the greatest richness of freshwater fish species (Albert & Reis 2011). In the Amazon, the species-area ratio is greater than in the continental periphery, which translates into greater diversification and less extinction (Reis et al. 2016). The west of the Amazon, in addition to being recognized as the center of origin, dispersion, and adaptation of the ichthyofauna (Fontenelle et al. 2021; Salgueiro et al. 2021), exhibits a

decreasing diversity gradient that goes from west to east; the sub-basins are richer in the upstream portion (west) compared to the downstream portion (east) (Oberdoff *et al.* 2019). This is also supported by studies of phylogenetic structure in Amazonian freshwater fishes, where there is a significant west-to-east gradient of phylogenetic diversity; this suggests deep evolutionary divergences between eastern taxa, and more diverse and recent radiations to the west (Salgueiro *et al.* 2021).

Considering that around 5500 and 1616 species are currently recorded for the Neotropical region (Reis *et al.* 2003, Ferraris *et al.* 2017, Fricke *et al.* 2022) and Colombia (DoNascimiento *et al.* 2021), respectively, the number of species reported here is significant. The species list we present here is nearly a fifth of the species recorded for the entire Neotropical region in an about 4% of its area (Albert & Reis 2011a) and, about a third of the species of the entire Amazon basin in about 8% of its area (PRORADAM 1979). Both spatial scales of analysis support the status of Colombia as one of the countries with the greater diversity of freshwater fish species of the planet (DoNascimiento *et al.* 2017). However, a considerable number of aquatic systems within the study area remain unexplored and most likely host undescribed species (Jézéquel *et al.* 2020a). Thus, the real species number in the study area could be way above actual estimates (Lundberg 2001, Junk *et al.* 2007, Leveque *et al.* 2008).

The aquatic ecosystems of the region are characterized by a dense network of *terra firme*, shield-draining streams, and river-floodplains systems (Lundberg *et al.* 1998), that flow under a closed forest canopy (van der Sleen & Albert 2018), where fish faunas are well recognized for their high alpha diversity and many species coexisting together (e.g. Arbelaez *et al.* 2004, Mojica *et al.* 2009, Villa-Navarro *et al.* 2021, Bogotá-Gregory *et al.* 2022). However, a high turnover of species between adjacent systems (e.g. Albert *et al.* 2011, Bogotá-Gregory *et al.* 2020, Villa-Navarro *et al.* 2021) generates a high *gamma* diversity; ultimately reflected in the regional species richness as presented here for the Amazonia region in Colombia.

Our similarity analysis allows recognition of two relatively different distributional patterns of the Amazonia region fishes, defined by species occurrence in the river systems of the Amazon and Orinoco basins. This distributional pattern is congruent with the delimitation proposed by Dagosta & de Pinna (2017) for the Amazonian regions and neighboring areas. Nevertheless, the location of the nodes in the dendrogram that represent the disparities, demonstrates as well, similarity among basins due to shared species. This similarity between basins coupled with analyses within a phylogenetic context might provide support for geological large-scale events that predate the formation of the actual configuration of the Amazon and Orinoco basins in South America. The Amazon-Orinoco species co-occurrence dates back to the late Miocene (10 to 8 Ma) when the ichthyofauna was connected by a proto-Amazon/ Orinoco flowing northward (Hoorn et al. 2010). The Andean orogeny resulted in the uplift of the Vaupés Arch, which in turn interrupted this connection at the end of the Pleistocene, a period in which the fish reconnected again through the Casiquiare River (Winemiller & Willis 2011; Albert et al. 2018). These events have been key in structuring current faunas. For example, using phylogenetic analyses, Fontenelle et al. (2021) were able to reconstruct freshwater stingray dispersals, which occurred between 2 and 1.5 Ma from the Amazon to the Orinoco. Thus, western Amazonia is occupied by older lineages (longer speciationdiversification time) and greater species richness, compared to areas farther from the western Amazonia with lower richness and younger lineages.

Disparities regarding geological origin and water type should be reflected in the fish compositions (Saint-Paul *et al.* 2000, Arbeláez *et al.* 2008, Dagosta & de Pinna 2017). Specifically, the humic-stained 'blackwaters' of lowland forest origin are characterized by a specialized set of species adapted to limiting physicochemical water conditions (Val & de Almeida 1995). The species occurrences within the Amazon basin, support in our analysis ecological distribution of species by biogeochemical water type (Bogotá-Gregory *et al.* 2020); systems of Andean origin (Amazonas, Putumayo, and Caquetá) present higher similarity among them, and the systems of lowland origin (Apaporis and Vaupés) are separated from those of Andean origin.

Differences in species composition ultimately have a basis in evolutionary history. To understand the mechanisms generating these patterns it is important to understand ecology in an evolutionary context (Webb *et al.* 2002). By combining phylogenies with quantitative data on species composition, plant ecologists in the Amazon have made substantial advances toward an understanding of the extent to which mechanisms generate diversity patterns (e.g. Clark *et al.* 1999, Hubbell 2001). However, quantitative studies in Neotropical fishes (Rodríguez & Lewis 1994, Petry *et al.* 2003, Arrington & Winemiller 2006) have yet to combine phylogenies. In part, this is because phylogenies yet are available for only a relatively small fraction of Neotropical fishes. In the near future, complete phylogenies surveys will become available. An analysis like ours will be of immediate utility to those seeking an integrated understanding of how the geographic distribution of Amazonian fishes originated.

There is still a limited understanding of the fish composition of some important areas in the Amazonia region, especially true for systems like the Guainía-Negro that are known to contain high species richness and endemism (see Figure 1-2 in Jézéquel *et al.* 2020a), and are part of the remote areas of the Amazon, where logistics are complicated to explore its fauna. A better understanding of the fish faunas of areas such as the Guainía-Negro and the Andean-Amazonian transition zone might reflect different configurations of the distributional patterns at the basin and regional scales. However, our analysis includes a great number of species, and the addition or deletion of some taxa won't affect considerably patterns obtained herein. Furthermore, exploring remote areas, such as the upper portions of the Rio Negro that remain unexplored (Beltrão *et al.* 2019), might provide new insights to resolve taxonomic conflicts of complex taxa, e.g. Characidae and Loricariidae.

The Amazon is home to the most remarkable diversity of freshwater fish species on earth (Reis et al. 2003, Jézéquel et al. 2020), and increased research projects in poorly studied regions have resulted in a large proportion of new species. Although there are vast areas without data in Amazonia (Dagosta & de Pinna 2017, 2019), the preliminary results presented here are of great importance. By conducting the first quantitative comparison of all of the major river systems of the Amazonia region in Colombia, this study becomes a significant step forward. These results allow for practical grounds for the analysis of the distribution of species, according to hydrographic and biogeographic concepts. This is particularly important when considering areas for conservation purposes, in light of high diversity loss in the Amazon. Deforestation, mining, dam construction, and overfishing threaten the Amazon region (Tedesco et al. 2008), and management and conservation plans still lack basic information (Abell et al. 2008, Castello & Macedo 2016). This kind of basic information is essential to identify priority areas for the conservation of fish assemblages, that represent the main source of income in the region and, in most cases, the only source of animal protein for human consumption.

## **Supplementary Material**

The following online material is available for this article:

**Supplementary Appendix 1:** Biodiversity collections holding fish material from the Amazonia Region from Colombia.

 Table S1: Number of species and percentage of total per taxonomic order and family.

**Supplementary Appendix 2:** Dissimilarity values, Kulczynski based, among river systems.

**Figure S1:** Multivariate analysis (NMDS) of fish composition of the Amazonia Region plus three outgroup systems (i.e., Bita, Tomo, and Ventuari).

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## **Associate Editor**

Juan Schmitter-Soto

### **Author Contributions**

Juan D. Bogotá-Gregory: Substantial contribution in the concept and design of the study.

Carlos DoNascimiento: Substantial contribution in the concept and design of the study.

Flávio C. T. Lima: Contribution to data analysis and interpretation. Astrid Acosta-Santos: Contribution to data collection.

Francisco A. Villa-Navarro: Contribution to data collection.

Alexander Urbano-Bonilla: Contribution to data collection.

José I. Mojica: Contribution to data analysis and interpretation.

Edwin Agudelo: Contribution to manuscript preparation.

## **Conflicts of Interest**

The authors declare that they have no conflict of interest.

## **Data Availability**

Supporting data are available at <a href="https://doi.org/10.5281/">https://doi.org/10.5281/</a> zenodo.6856382>.

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## Ants associated with fronds of the tropical bracken fern *Pteridium esculentum* subsp. *arachnoideum*

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Abstract: Pteridium is a cosmopolitan genus of ferns that possess nectaries on its fronds (fern leaves), thereby attracting ants. Foliar (or extrafloral) nectaries are nectar-producing glands that are not related to pollination, but rather attract ants and other arthropods. Foliar nectaries are found in 101 fern species, belonging to 11 genera and six families. The aim of the study is to characterize the community of ants that visit the fronds of Pteridium esculentum subsp. arachnoideum, as well as daily and seasonal ant abundance in different frond development stages. The study was conducted in the Atlantic Forest of Rio de Janeiro state, Brazil. Bimonthly collections were established, where 30 expanding fronds and 30 fully expanded fronds were randomly marked. In each 1-hour shift starting at 8:30 am and ending at 5:30 pm, the fronds were observed for the presence of ants. Thirty three ant species were recorded on the Pteridium esculentum subsp. arachnoideum fronds, distributed into six subfamilies and 13 genera. The most abundant species were Solenopsis sp.1 and Ectatomma tuberculatum. Eight ant species were observed foraging the nectaries of tropical bracken fern fronds. Ectatomma tuberculatum has been observed feeding on the nectaries and patrolling the fronds. Ant activity peak was on mid-day during the rainy season. The tropical bracken fern Pteridium esculentum subsp. arachnoideum has a rich (the highest recorded until now on Pteridium species) and diverse ant community on its fronds, mainly on the expanding fronds. The presence of generalist predatory ants (Ectatomma tuberculatum and Solenopsis sp.1) during the entire study period suggests a positive interaction between ants and Pteridium esculentum subsp. arachnoideum.

Keywords: ant-plant interactions; Atlantic Forest; behavioral ecology; foliar nectaries; pteridophytes.

## Formigas associadas às frondes da samambaia *Pteridium esculentum* subsp. *arachnoideum*

**Resumo:** Pteridium é um gênero cosmopolita de samambaias que possui nectários em suas frondes (folhas de samambaias), atraindo formigas. Nectários foliares (ou extraflorais) são glândulas produtoras de néctar que não estão relacionadas com a polinização, mas podem atrair formigas e outros artrópodes. Nectários foliares já foram registrados em 101 espécies de samambaias, pertencentes a 11 gêneros e seis famílias. O objetivo do estudo é caracterizar a comunidade de formigas que visitam as frondes de *Pteridium esculentum* subsp. *arachnoideum*, bem como a abundância diária e sazonal das formigas em diferentes estágios foliares. O estudo foi realizado na Mata Atlântica do estado do Rio de Janeiro, Brasil. Foram estabelecidas coletas bimestrais, onde foram marcadas aleatoriamente 30 frondes em expansão e 30 frondes totalmente expandidas. Em cada turno de 1 hora com início às 8h30 e término às 17h30, as frondes marcadas foram observadas quanto à presença de formigas. Trinta e três espécies de formigas foram registradas nas frondes do *Pteridium esculentum* subsp. *arachnoideum*, distribuídas em seis subfamílias e 13 gêneros. As espécies mais abundantes foram *Solenopsis* sp.1 e *Ectatomma tuberculatum*. Foram registradas oito espécies de formigas forrageando os nectários foliares da samambaia. *Ectatomma tuberculatum* 

ao meio-dia e na estação chuvosa. A samambaia tropical *Pteridium esculentum* subsp. *arachnoideum* tem uma elevada riqueza (a maior já registrada até o momento para espécies de *Pteridium*) e diversidade de formigas em suas frondes, com maior frequência nas frondes não totalmente expandidas. A presença de formigas predadoras generalistas (*Ectatomma tuberculatum e Solenopsis* sp.1) durante todo o período de estudo sugere uma interação positiva entre as formigas e *Pteridium esculentum* subsp. *arachnoideum*.

Palavras-chave: interações formiga-planta; Mata Atlântica; ecologia comportamental; nectários foliares; pteridófitas.

## Introduction

*Pteridium* (bracken fern) is a fern genus distributed world-wide. The circumscription of species is widely discussed in the literature, about 20 morphotypes have been recognized, and several infra-specific ranks have been adopted (PPG I 2016, Thomson 2016, Schwartsburd et al. 2018). While some authors recognize only two species: *Pteridium aquilinum* (L.) Kuhn and *P. esculentum* (G. Forst.) Cockayne along their infraspecies (Thomson 2016). All the species of the genus have nectaries on their fronds (fern leaves) (Tryon & Tryon 1982), and the oldest record of nectaries in ferns was reported by Francis Darwin in 1877 for *Pteridium aquilinum* (L.) Kuhn (Lloyd 1901).

Foliar (or extrafloral) nectaries are nectar-producing glands that are not related to pollination, but rather attract ants and other arthropods (Koptur et al. 2013). Fern nectars contain a variety of amino acids and a large amount of sugar, particularly sucrose, fructose and glucose (Koptur 1992, Mehltreter et al. 2022). Foliar nectaries are found in 101 fern species, belonging to 11 genera and six families (Lloyd 1901, Koptur et al. 1982, White & Turner 2012, Mehltreter et al. 2022). Some authors believe that the nectaries promote interactions between ferns and ants (Koptur et al. 1982, 1998, Page 1982).

There are many records of ants and bees associated with the bracken fern nectaries (Page 1982, Tempel 1983, Heads & Lawton 1984, 1985, Olesen 1988; Rashbrook et al. 1992, White & Turner 2012), though some authors reported no ants on the *Pteridium* nectaries for some bracken populations (Rumpf et al. 1994). The function of nectaries remains controversial (Cooper-Driver 1990); some studies reported no benefits from ants that visited the foliar nectaries for *Pteridium* species (Tempel 1983, Heads & Lawton 1984, Rashbrook et al. 1992), while others related benefits for ants and plants (Heads 1986, Jones & Paine 2012). The highest density and frequency rates of ants have been observed on young fronds of *Pteridium* species in the rainy season (Tempel 1983, Rashbrook et al. 1992).

Many studies have characterized arthropod fauna associated with *Pteridium* spp. fronds (Lawton 1976, Balick et al. 1978, Hendrix 1980, Winterbourn 1987), while others have reported ants visiting their nectaries (Lawton 1976, Balick et al. 1978, Page 1982) and assessed the interactions between these two organisms (Page 1982, Tempel 1983, Heads & Lawton 1984, 1985, Rashbrook et al. 1992). However, few of these characterized the entire ant community present on the fronds of this fern (Douglas 1983, Tempel 1983, Heads & Lawton 1984, 1985). These studies evaluated *Pteridium* species of USA, England, Scotland, South Africa, and New Zealand. For the Neotropical Region, Ávila & Otero (2013) recorded five ant species visiting the nectaries of the croziers of *Pteridium* from Venezuela [*Brachymyrmex* sp., *Camponotus rufipes* (Fabricius, 1775), *Linepithema* sp. *Pheidole* sp., and *Solenopsis geminata* (Fabricius, 1804)]. Martins et al. (1995) recorded one species (*Atta sexdens rubropilosa* Forel, 1908) cutting pinnae and rachis of the

bracken fern fronds. Santos and Mayhé-Nunes (2007) reported a single ant species [*Dolichoderus attelaboides* (Fabricius, 1775)] associated with the nectaries of *P. arachnoideum* [*Pteridium esculentum* subsp. *arachnoideum* (Kaulf.) Thomson].

Pteridium esculentum subsp. arachnoideum (Kaulf.) Thomson is a tropical bracken species widely distributed in South and Central America. Despite being a native species in these regions, it has a high invasive potential and can cause several environmental problems in natural and anthropic areas (Schwartsburd et al. 2017, Oliveira et al. 2018). The present study aims to characterize the ant community on fronds of *Pteridium esculentum* subsp. *arachnoideum* (tropical bracken fern), a Neotropical fern species, as well as daily and seasonal ant abundance in different frond development stages.

## **Materials and Methods**

### 1. Study area

The study was conducted in a population of Pteridium esculentum subsp. arachnoideum located in the Restinga (coastal sandy plain) of the Maricá Environmental Protection Area, in the municipality of Maricá, Rio de Janeiro state, Southeastern Brazil (22° 57' 41.05"S, 42° 53' 20.22" W). Restinga is a type of vegetation associated with the Atlantic Forest. Nimer (1972) classified Maricá's climate as hot tropical and super humid, with short dry periods. Studies that characterized Maricá's climate between 1989 and 2000 indicate that the minimum temperature is lower in winter (8.6 °C to 15.2 °C), with July as the coldest month (always below 15 °C), while the highest temperatures are recorded in summer, with means between 29.2 °C and 37.3 °C, and February being the hottest month (temperatures always above 33 °C, reaching 37.7 °C) (Pereira et al. 2001). In the study area there are only two seasons. According to Barbieri (2005), the rainy season in Southeastern Brazil occurs between October and March and the dry season between April and September.

### 2. Collection and laboratory procedures

Tempel (1983) divided the frond development of *Pteridium* into 6 stages. In this study, the fronds in stages 1 to 5 were considered expanding fronds, and those in stage 6 fully expanded fronds (Figure 1). Since *P. arachnoideum* has subterraneous rhizomes, the fronds were used as a sampling unit. Thirty expanding fronds and thirty fully expanded fronds were randomly marked with red ribbon, at least 2m apart to each other. Throughout the day (8:30 am–5:30 pm), the fronds were inspected during each 1-hour shift and all ants on bracken fronds collected with an entomological aspirator, to obtain the abundance of each species. The ants which were feeding on the bracken fern nectaries were recorded. Collections were carried out every two months for one year, one day (without rain) per month, between February 2009 and



Figure 1. Frond stages of *Pteridium esculentum* subsp. *arachnoideum*. A: Fully expanded frond. B-C: Expanding frond. All photos: Marcelo Guerra Santos.

February 2010. The ants were preserved in 70% alcohol, mounted in entomological boxes (Lattke 2003), and identified by Dr. Antônio Mayhé-Nunes and Dr. Rodrigo M. Feitosa. Vouchers were deposited in the herbarium of the Faculdade de Formação de Professores da Universidade do Estado do Rio de Janeiro (RFFP 20.281) and the Padre Jesus Santiago Moure Entomological Collection, Universidade Federal do Paraná, Department of Zoology (DZUP).

### 3. Statistical analyses

To detect differences in ant frequencies (number of observations) between expanding and fully expanded fronds (categorical variables), we performed a Pearson's chi-squared test (Gotelli and Ellison 2011). The expected richness of ants on bracken fronds was calculated using the estimator Chao 2. It provides a minimum estimate of richness in homogeneous samples using presence and absence (incidence) data, in just one or two samples (Magurran 2013). The statistical tests were conducted in PAST (PAleontological STatistics), version 3.10 (Hammer et al. 2001).

Circular statistics were used to estimate the month of highest incidence of the ant species, time of intensity peak on fern fronds. Furthermore, the mean angle, Rayleigh test (p), and length of mean vector (r) were calculated. The program Oriana was used for the calculations of circular statistics (Kovach 2009).

### Results

A total of 599 ants were observed on the fronds of *Pteridium* esculentum subsp. arachnoideum. Of this total, we managed to collect only 529 ants, and all were identified at least to the generic level. We recorded 33 ant species on the tropical bracken fern fronds, distributed among six subfamilies and 13 genera (Table 1). The observed richness was similar to the richness estimated by Chao  $2 = 33.8 \pm 6.0$ . Eight ant species were observed foraging the nectaries of tropical bracken fern fronds, *Brachymyrmex* sp.1 (Figure 2F), *Camponotus crassus* Mayr,



Figure 2. Ants on frond nectaries of *Pteridium esculentum* subsp. *arachnoideum*. A: *Ectatomma tuberculatum* feeding on the nectary. It's possible to see a nectar droplet in their open jaws. B: *Camponotus crassus*. C: *Wasmannia auropunctata*. D: *Ectatomma brunneum*. E: *Pheidole* sp. F: *Brachymyrmex* sp. (arrow). \*Nectaries. Photo A: Isabella Rodrigues Lancellotti. Photos B, C, E, F: Marcelo Guerra Santos. Photo D: Camille Santos Carraco.

1862 (Figure 2B), *Camponotus* sp.1, *Ectatomma tuberculatum* (Olivier, 1792) (Figure 2A), *Ectatomma brunneum* (Fr. Smith, 1858) (Figure 2D), *Pheidole* sp.1 (Figure 2E), *Solenopsis* sp.1, and *Wasmannia auropunctata* (Roger, 1863) (Figure 2C). *Ectatomma tuberculatum* has also been observed patrolling the fronds.

The subfamilies with the highest ant richness were Formicinae and Myrmicinae (both with nine species). The species with the greatest abundance were *Solenopsis* sp.1 (165 individuals) and *Ectatomma tuberculatum* (151 individuals) (Figure 2A), and those with intermediate abundance were *Brachymyrmex* sp.1 (65 individuals), *Camponotus* sp.1 (26 individuals), and *Wasmannia auropunctata* (21 individuals). All other 28 ant species had an abundance of less than 10 individuals (Table 1).

The chi-squared test (X<sup>2</sup>) demonstrated a significant difference for ant abundance between the analyzed months (X<sup>2</sup> = 397.17, DF = 6, P < 0.000001), with the higher abundance in October (100 individuals) and December (226 individuals), both in the beginning of the rainy season (Table 1). October and December are the months most likely to find 25 of the 33 species recorded, among them the species with the highest abundance, *Ectatomma tuberculatum* and *Solenopsis* sp.1 (October and December respectively). April, June, and August (dry season), and February (end of the rainy season) are the months with the lowest probability of finding ant species on *Pteridium esculentum* subsp. *arachnoideum* (Table 1).

There was a significant difference in the frequency of ants (number of observations) visiting the expanding and fully expanded fronds of *Pteridium esculentum* subsp. *arachnoideum* in all the months observed, with ants showing a preference for the former (Table 2). Most ants (19 species) have their highest visitation intensity peak between 10:30 am and 1:30 pm, including the species with the highest abundance, *Solenopsis* sp.1 and *Ectatomma tuberculatum* (Table 3). **Table 1.** Abundance and circular statistical tests (month of highest incidence of the species and Rayleigh test (*p*) of ant species collected on the fronds of *Pteridium esculentum* subsp. *arachnoideum*, between February 2009 and February 2010, in the Restinga of Maricá, Rio de Janeiro state, Brazil. Rainy season (between October and March) and dry season (between April and September) (Barbieri 2005).

Subfamily	Ant species					Month	ı			Relative	Month of	Rayleigh
		Feb 9	Apr 9	Jun 9	Aug 9	Oct 9	Dec 9	Feb 10	Abundance	abundance (%)	highest incidence	test (p)
Dolichoderinae	Dorymyrmex brunneus (Forel, 1908)	1	0	0	0	2	0	1	4	0,76	December	0,137
	Dorymyrmex sp.	2	0	0	0	1	0	0	3	0,57	Janaury	0,137
	Linepithema iniquum (Mayr, 1870)	0	0	0	1	0	0	0	1	0,19	February	<1E-12
	Linepithema sp.	0	0	0	3	0	0	2	5	0,95	August	0,137
	Tapinoma atriceps Emery, 1888	0	0	0	1	1	1	0	3	0,57	October	0,512
	Tapinoma melanocephalum (Fabricius, 1793)	0	1	1	4	4	0	0	10	2,08	October	0,512
	Tapinoma sp.1	0	0	0	1	0	0	0	1	0,19	August	0,512
	Tapinoma sp.2	0	0	0	0	2	1	0	3	0,57	October	0,137
Ectatomminae	Ectatomma brunneum (Fr. Smith, 1858)	0	0	0	0	8	0	0	8	1,51	October	<1E-12
	Ectatomma tuberculatum (Olivier, 1792)	33	9	28	4	40	32	5	151	28,54	December	<1E-12
Formicinae	Brachymyrmex sp.1	0	4	4	14	13	11	19	65	12,29	December	0,895
	Brachymyrmex sp.2	0	0	0	1	1	3	0	5	0,95	October	0,512
	Camponotus crassus Mayr, 1862	1	0	0	1	1	0	1	4	0,76	August	0,512
	Camponotus leydigi Forel, 1886	0	1	0	0	1	0	0	2	0,38	October	0,512
	Camponotus sexguttatus (Fabricius, 1793)	0	0	0	1	0	0	0	1	0,19	August	0,512
	Camponotus sp.1	_	5	_	5	10	4	2	26	4,91	October	0,137
	Camponotus sp.2	0	0	0	0	8	0	0	8	1,51	October	<1E-12
	Camponotus sp.3	0	1	0	0	0	0	0	1	0,19	April	0,512
	Camponotus sp.4	0	0	1	0	2	1	0	4	0.76	November	0.512
Myrmicinae	Cephalotes minutus (Fabricius, 1804)	0	0	0	0	0	1	0	1	0,19	December	0,512
	Cephalotes pusillus (Klug, 1824)	0	0	0	0	1	9	0	10	1,89	December	0,512
	Cephalotes sp.1	0	0	0	0	0	1	0	1	0,19	December	0,512
	Nylanderia sp.	0	0	0	0	0	2	0	2	0,38	October	0,137
	Pheidole sp.1	1	0	2	0	0	2	0	5	0,95	February	0,512
	Pheidole sp.2	0	0	1	0	0	2	0	3	0,57	December	0,512
	Solenopsis sp.1	1	0	0	8	1	154	1	165	31,19	December	<1E-12
	Solenopsis sp.2	1	0	0	0	0	2	0	3	0,57	December	0,137
	Wasmannia auropunctata (Roger, 1863)	0	4	0	15	2	0	0	21	3,97	August	0,137
Ponerinae	Neoponera villosa (Fabricius, 1804)	0	0	2	0	0	0	0	2	0,38	August	0,137
Pseudomyrmecinae	Pseudomyrmex gracilis (Fabricius, 1804)	0	1	0	0	1	0	0	2	0,38	June	0,512
	Pseudomyrmex pallidus (Fr. Smith, 1855)	1	0	0	0	0	0	0	1	0,19	February	0,512
	Pseudomyrmex sp.1	3	0	0	0	0	0	0	3	0,57	February	0,033
	Pseudomyrmex sp.2	3	0	1	0	1	0	0	5	0,95	February	0,512
Abundance		47	26	40	59	100	226	31	529			

 

 Table 2. Ant frequency (number of observations) on *Pteridium esculentum* subsp. *arachnoideum* fronds at different stages of development in the Restinga of Maricá, Rio de Janeiro state, Brazil.

Month/year	Expanding fronds	Fully expanded fronds	Chi-squared test
February 2009	37	20	5,07, <i>P</i> = 0,024
April 2009	53	18	17,25 <i>P</i> = 3,27E-05
June 2009	42	20	7,80 <i>P</i> = 0,005
August 2009	35	18	5,45 <i>P</i> = 0,019
October 2009	82	58	4,11 <i>P</i> = 0,042
December 2009	139	20	89,06 <i>P</i> < 1,0E-06
February 2010	45	12	19,10 <i>P</i> = 1,2E-05
Ν	433	166	

## Discussion

The record of 33 ant species belonging to 13 genera is the highest ant richness recorded on Pteridium fronds until now, of this total, eight were observed foraging the nectaries. Tempel (1983) listed 18 nectar feeding ants, distributed on 12 genera on Pteridium aquilinum, in USA. This author also found Myrmicinae as the richest subfamily (9 spp.). Douglas (1983) reported nine ant species associated with the nectaries of P. aquilinum in USA. Avila and Otero (2013) recorded five ant species visiting the nectaries of the croziers of Pteridium caudatum, in Venezuela. Heads and Lawton (1984, 1985) reported three ant species on nectaries of P. aquilinum in England. In Brazil, Martins et al. (1995) reported a single ant species [Atta sexdens (Linnaeus, 1758)] cutting pinnae and rachis of the Pteridium fronds. Santos and Mayhé-Nunes (2007) recorded *Dolichoderus attelaboides* (Fabricius 1775) as the only ant species associated with the foliar nectaries of P. arachnoideum [Pteridium esculentum subsp. arachnoideum] in the Atlantic Forest of Rio de Janeiro state.

Vargas et al. (2010) recorded 52 ant species in the litter of the Restinga of Maricá (restinga vegetation). So, the richness found on the *P. esculentum* subsp. *arachnoideum* fronds represents 63.5% of the ants registered for this region until now. For angiosperms species with foliar nectaries in Cerrado (Brazilian savanna), 34 ant species were found on *Caryocar brasiliense* Cambess. (Caryocaraceae), 24 on *Ouratea hexasperma* (A.St.-Hil.) Baill. (Ochnaceae), and 12 on *Qualea* grandiflora Mart. (Vochysiaceae) (Oliveira & Pie 1998). In mangrove vegetation, *Talipariti pernambucense* (Arruda) Bovini (Malvaceae) was visited by 19 ant species (Cogni & Freitas, 2002).

The ant visitation on *Pteridium esculentum* subsp. *arachnoideum* fronds was greater in October and December (both in the beginning of the rainy season). Tempel (1983) conducted a study in New Jersey (EUA) and found that nectar secretion by *Pteridium aquilinum* and ant visitation were more frequent from May to August, that is, in summer, with high rates of precipitation. In South Africa, the period in which ants have the greatest impact on *Pteridium* herbivores occurs between November and December, corresponding to the rainy season in this region (Rashbrook et al. 1992). These data indicate that the change in ant visitation of bracken fronds is highly associated with the summer season.

The most abundant ant species (Brachymyrmex sp.1, Camponotus sp.1, Ectatomma tuberculatum, Solenopsis sp.1, and Wasmannia auropunctata) on tropical bracken fern have their highest visitation intensity peak near to mid-day, between 12:00 and 2:00 pm. According to Kaspari (2003), temperature is an important factor that regulates the activities of ant populations. Increased visitation may be attributed to the natural rise in the daily activities of ants as a function of their ectothermy and exudation of foliar nectaries. Ectatomma tuberculatum was one of the ant species with highest abundance, and visited the fronds of Pteridium esculentum during 9:30 am to 4:30 pm with the intensity peak at 1:07 pm. (Table 3). This ant species presents high activity at night, with massive exiting of workers at end of the day (sunset) and massive entry in the nest at beginning of the morning (sunrise), or high foraging activity in the morning and no mass exit at sunset (Wheeler 1986). According to Valenzuela-González et al. (1995), E. tuberculatum foraging was mainly nocturnal during the dry season and diurnal in the rainy season. Page (1982) reported that the foliar nectaries of Pteridium aquilinum were more active in the morning. Mehltreter et al. (2022), analyzing 16 fern species (Aglaomorpha and Campyloneurum genera), observed that nectar secretion occurred mainly during the night and early morning, but could continue until the afternoon, depending on air humidity conditions. In fact, in Restinga of Maricá it was possible to observe a few tropical bracken ferns secreting nectar during the period close to noon (Figure 2A). But we did not measure local climatic data in these days. The nighttime period was not assessed here and probably a different ant community may be visiting the foliar nectaries of Pteridium esculentum subsp. arachnoideum at this period. However, Tempel (1983) evaluated populations of Pteridium aquilinum Kuhn in New Jersey (USA) at night and found no evidence of nocturnal ant activity.

Ectatomma tuberculatum and Solenopsis sp.1, both generalist predator ants (Wheeler 1986, Valenzuela-González et al. 1995, Wojcik et al. 2001, see also comments by Tolofo 2011 on other Ectatomma species), were present during the entire period of observations, and were the most abundant species on the fronds of Pteridium esculentum subsp. arachnoideum. E. tuberculatum has been observed feeding on the nectaries, and patrolling the fronds, whereas Solenopsis sp.1 was only feeding on nectaries. However, other generalist predator ants were also present in lower abundance, as follows: Dorymyrmex brunneus (Forel, 1908), Dorymyrmex sp., Ectatomma brunneum, Neoponera villosa (Fabricius, 1804), Pheidole sp.1, Pheidole sp.2, Pseudomyrmex sp.1 and Pseudomyrmex sp.2 (Table 4). Douglas (1983) observed that Camponotus pennsylvanicus (De Geer, 1773), Formica obscuriventris (Mayr, 1870), and Formica subsericea (Say, 1836) defend the nectaries of the developing croziers, while other smaller species such as Tapinoma sessile (Say, 1836), Temnothorax rugatulus (Emery, 1895), Leptothorax muscorum (Nylander, 1846), and Lasius alienus (Foerster, 1850) (not predatory ant species) only utilize nectar and do not seem to defend the fern croziers. The establishing mutualistic relationship between ants and foliar nectaries seems to depend on the occurrence and abundance of large or aggressive ants visiting the plants (Koptur 1984, Heads 1986).

The frequency of ants (number of observations) was greater on expanding fronds than on fully expanded fronds of *P. esculentum* subsp. *arachnoideum*. Marquis (2012) reports that phenology is vital in determining herbivore attack intensity, since the plant life cycle can allow plants to evade attack or be exposed in its most vulnerable

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Ant species					Ti	me					Time of	Length of mean
	8:30 AM	9:30 AM	10:30 AM	11:30 AM	12:30 PM	1:30 PM	2:30 PM	3:30 PM	4:30 PM	5:30 PM	peak	vector (r)
Brachymyrmex sp.1	2	3	4	11	14	6	7	14	5	0	12:52 (193,095°)	0,859
Brachymyrmex sp.2	0	0	0	0	1	1	1	0	2	0	02:42 (220,525°)	0,914
Camponotus crassus	0	0	0	0	0	0	1	3	0	0	03:15 (228,766°)	0,994
Camponotus leydigi	0	0	0	0	2	0	0	0	0	0	12:30 (187,5°)	0,697
Camponotus sexguttatus	0	0	1	0	0	0	0	0	0	0	10:30 (157,5°)	1
Camponotus sp.1	0	0	3	4	4	6	7	2	0	0	01:37 (204,485°)	0,931
Camponotus sp.2	0	0	3	3	1	0	0	1	0	0	11:40 (175,209°)	0,921
Camponotus sp.3	0	0	0	0	0	0	0	0	1	0	04:30 (247,5°)	1
Camponotus sp.4	0	1	1	0	1	0	1	0	0	0	01:30 (202,5°)	1
Cephalotes pusillus	0	1	1	1	0	0	0	1	6	0	03:30 (232,5°)	0,377
Cephalotes minutus	0	0	0	0	1	0	0	0	0	0	12:30 (187,5°)	1
Cephalotes sp.1	0	0	0	0	0	0	0	0	1	0	01:30 (202,5°)	1
Dorymyrmex brunneus	0	0	0	1	0	1	1	1	0	0	04:30 (247,5°)	0,394
<i>Dorymyrmex</i> sp.	0	0	0	0	0	2	0	0	1	0	04:30 (247,5°)	0,369
Ectatomma brunneum	0	0	2	1	1	0	3	1	0	0	01:00 (195,211°)	0,883
Ectatomma tuberculatum	0	21	21	22	14	15	21	24	13	0	01:07 (196,868°)	0,438
Linepithema iniquum	0	0	0	0	1	0	0	0	0	0	08:30 (127,5°)	0,513
<i>Linepithema</i> sp.	0	0	0	1	2	0	1	1	0	0	02:53 (223,266°)	0,565
Nylanderia sp.	0	0	0	0	0	0	0	2	0	0	02:30 (217,5°)	1
Neoponera villosa	0	0	0	1	0	1	0	0	0	0	02:30 (217,5°)	0,72
Pheidole sp.1	0	1	3	0	0	1	0	0	0	0	09:30 (142,5°)	0,531
Pheidole sp.2	0	1	2	0	0	0	0	0	0	0	10:30 (157,5°)	0,596
Pseudomyrmex gracillis	0	0	1	1	0	0	0	0	0	0	10:30 (157,5°)	0,494

Table 3. Ant species abundance per hour of visitation on *Pteridium esculentum* subsp. *arachnoideum* fronds and circular statistical tests (mean time, mean angle, and length of mean vector), between February 2009 and February 2010 (seven collections), in the Restinga of Maricá, Rio de Janeiro state, Brazil. (n = 529 ants).

Ant species					Tiı	ne					Time of	Length of mean
	8:30 AM	9:30 AM	10:30 AM	11:30 AM	12:30 PM	1:30 PM	2:30 PM	3:30 PM	4:30 PM	5:30 PM	peak	vector (r)
Pseudomyrmex pallidus	0	0	0	1	0	0	0	0	0	0	11:30 (172,5°)	0,398
Pseudomyrmex sp.1	0	0	1	2	0	0	0	0	0	0	11:10 (167,513°)	0,992
Pseudomyrmex sp.2	0	1	0	2	0	0	0	1	0	0	01:02 (195,653°)	0,381
Solenopsis sp.1	0	0	0	0	0	2	1	4	3	0	12:28 (187,177°)	0,374
Solenopsis sp.2	0	1	1	0	0	0	0	1	0	0	10:00 (150°)	0,991
Tapinoma atriceps	0	0	1	0	1	0	0	0	0	0	12:30 (187,5°)	0,476
Tapinoma melanocephalum	0	0	3	2	2	0	0	0	1	0	11:30 (172,5°)	0,707
<i>Tapinoma</i> sp.1	0	0	0	0	0	0	1	0	0	0	02:30 (217,5°)	1
<i>Tapinoma</i> sp.2	0	0	1	0	2	0	0	0	0	0	01:30 (202,5°)	0,319
Wasmannia auropunctata	0	0	4	7	1	4	0	3	2	0	01:30 (202,5°)	0,638

 Table 4. Genera of ants found on Pteridium esculentum subsp. arachnoideum in the Restinga of Maricá, Rio de Janeiro state and their respective feeding habits.

Genus	Feeding habit	Reference
Brachymyrmex	Most species are omnivorous, and some exploit the sugary solutions of extrafloral nectaries or trophobiont insects.	Baccaro et al. (2015); Quirán (2005)
Camponotus	Omnivorous.	Fernández (2003)
Cephalotes	Omnivorous, feed on sugary secretions produced by membracids and extrafloral nectaries, and have a preference for pollen grains.	Baccaro et al. (2015); Moretti & Ribeiro (2006)
Dorymyrmex	Hunt live insects, including alates (flying ants). Some species collect honeydew from sap-sucking insects.	Baccaro et al. (2015)
Ectatomma	Omnivorous. Prey on annelids, gastropods and a number of arthropods, including ants, wasps, bee pupae, lizards and termites. Also frequently seen collecting sugary liquids secreted by hemipterans, extrafloral nectaries and flower and fruit exudates.	Baccaro et al. (2015); Lattke (2003); Tolofo (2011)
Linepithema	Generalists. Feed on sugary solutions from extrafloral nectaries and honeydew from hemipterans, but may be opportunist predators.	Baccaro et al. (2015)
Nylanderia	Generalists, frequently visit extrafloral nectaries.	Baccaro et al. (2015); LaPolla et al. (2011)
Neoponera	Omnivorous, generalist predators or specialists. Occasionally feed on the arillus of fallen seeds on the forest floor.	Baccaro et al. (2015); Lattke (2003)
Pheidole	Omnivorous, predators and necrophagous.	Baccaro et al. (2015); Wilson (2003)
Pseudomyrmex	Omnivorous and very aggressive. Many species are associated with plants that have extrafloral nectaries.	Baccaro et al. (2015); Whitcomb et. al (1972)
Solenopsis	Predators and necrophagous. They may explore extrafloral nectaries.	Baccaro et al. (2015); Wojcik et al. (2001)
Tapinoma	Some species feed on sugary solutions produced by aphids and coccids.	Baccaro et al. (2015)
Wasmannia	Omnivorous.	Baccaro et al. (2015); Fisher & Cover (2007)

phase, when not fully mature. Tempel (1983) found that nectar secretion is significantly higher in the first developmental stages of *Pteridium aquilinum*, and becomes practically inactive in the final stages. As such, the activity pattern of ants is correlated to foliar nectar exudation. Rashbrook et al. (1992) observed a larger number of ants on young fronds, which have more active nectaries (greater nectar exudation). Thus, it can be inferred that in the most vulnerable stage (juvenile), higher nectar production acts as a lure for ants, which sometimes protect individuals that supply nectar. In the Restinga of Maricá we observed very few full expanded fronds of the tropical bracken fern secreting nectar during the day (Figure 2A). However, almost all observed fronds (expanding and full expanded) were not secreting nectar. Even though, the ants still remained scraping the nectaries (Figures 2B–F).

According to Tempel (1993), most of the significant damage to *Pteridium aquilinum* occurs before maturity, demonstrating no need for the additional protection provided by ants in the final stage of development, and in turn, the low nectar production. Furthermore, studies conducted by Santos et al. (2005) found cyanogenesis in all young *Pteridium arachnoideum* fronds but in only 9.1% of the mature fronds. Cyanogenesis is a defensive process in which the plant releases hydrocyanic acid when injured by herbivores (Vetter 2000). The levels of phenolic substances, which may also act defensively, increase significantly during the maturation of *P. esculentum* subsp. *arachnoideum* fronds (unpublished data). Furthermore, the fronds exhibit a norsesquiterpene denominated ptaquiloside, which is responsible for toxic, mutagenic and cancerigenous action in *Pteridium* species (Yamada et al. 2007).

The tropical bracken fern *Pteridium esculentum* subsp. *arachnoideum* has a remarkedly rich (the highest recorded until now on *Pteridium* species) and diverse ant community on its fronds, mainly on the expanding fronds, which peaks at the mid of the day in the rainy season. The presence of generalist predatory ants (*Ectatomma tuberculatum* and *Solenopsis* sp.1) during the entire study period suggests that there may be a positive interaction between ants and *Pteridium esculentum* subsp. *arachnoideum*. Future studies are needed to understand the relationship between these ants and the tropical bracken fern, especially those that interact with leaf nectaries.

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## **Associate Editor**

José Mermudes

## **Author Contributions**

Isabella Rodrigues Lancellotti: Substantial contribution in the concept and design of the study; data collection; data analysis and interpretation; manuscript preparation; critical revision, adding intellectual content.

Marcelo Guerra Santos: Substantial contribution in the concept and design of the study; data collection; data analysis and interpretation; manuscript preparation; critical revision, adding intellectual content.

Anderson dos Santos Portugal: Data analysis and interpretation; critical revision, adding intellectual content.

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Rodrigo Machado Feitosa: Species identification, data analysis and interpretation; manuscript preparation critical revision, adding intellectual content.

## **Conflicts of Interest**

The authors declare that they have no conflict of interest related to the publication of this manuscript.

## **Data Availability**

Supporting data are available at <a href="https://doi.org/10.48331/scielodata">https://doi.org/10.48331/scielodata</a>. XB751P> and <a href="https://data.scielo.org/dataset.xhtml?persistentId">https://data.scielo.org/dataset.xhtml?persistentId</a> = doi:10.48331/scielodata.XB751P>.

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# Reproductive biology of the emerald frog *Hylorina sylvatica* (Anura: Batrachylidae) in northwest Patagonia, Argentina

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*Abstract: Hylorina sylvatica* (Anura: Batrachyidae), or the emerald frog, is a pond-breeding anuran endemic to the austral temperate forests of Chile and Argentina. It is considered a vulnerable species in Argentina, where it has a narrow distribution; records and biological information relating to the frog in this area are scarce. In this study, conducted in 2016, the reproductive parameters of the emerald frog were investigated in detail in a semitemporary wetland of Northwestern Patagonia, Argentina. During the spring, the wetland was visited weekly in search of calling males, adults and individuals in amplexus. When amplexus was observed, eggs and larvae were collected from among the aquatic vegetation using dip-nets. Egg size and larval stage at hatching were registered. Calling males were registered during the second week of October, and the first couples were observed on 26 October. Three pairs of emerald frogs were captured and placed in enclosures within the wetlands in the afternoon. The males and females were released. The eggs were kept in each enclosure until hatching. Hatching occurred after 10–14 days in the enclosures. This information contributes to our knowledge of the biology of the emerald frog in Patagonia, Argentina, and is the only information currently available on this species in Nahuel Huapi National Park, where the species breeds in various aquatic environments, from semi-temporary wet meadows to large permanent ponds.

Keywords: Patagonian anurans; wetlands; amplexus; eggs; embryonic development.

# Biología reproductiva de la rana esmeralda *Hylorina sylvatica* (Anura: Batrachylidae) en el noroeste de la Patagonia Argentina

Resumen: Hylorina sylvatica (Anura: Batrachyidae) o rana esmeralda, es un anuro que se reproduce en estanques, endémico de los bosques templados australes de Chile y Argentina. Actualmente es considerada una especie vulnerable en Argentina. La distribución es estrecha en Argentina con pocos registros de la especie y muy limitada información sobre la biología de esta especie en la región. En este estudio realizado durante 2016, investigué en detalle los parámetros reproductivos de la rana esmeralda en un humedal semitemporal del Noroeste de la Patagonia Argentina. Durante la primavera de 2016, visité el humedal semanalmente en busca de coros, adultos y amplexos. También después de que se observaron amplexos, recolecté huevos y larvas entre la vegetación acuática utilizando un muestreo con redes de mano. Se registró el tamaño del huevo y el estado larvario al eclosionar. Los coros de machos se registraron durante la tercera semana de octubre y los primeros amplexos se observaron el 26 de octubre. Tres parejas de rana esmeralda fueron capturadas y colocadas en clausuras dentro de los humedales durante la tarde. Los machos eran más pequeños que las hembras. Después de 24 h conté el número de huevos puestos en cada recinto y luego se liberaron machos y hembras. Los huevos se mantuvieron en cada clausura hasta que eclosionaron. La eclosión se produjo entre 10-14 días en las clausuras. Esta información contribuye al conocimiento de la biología de la rana esmeralda que habita la Patagonia Argentina y es la única información disponible al momento de esta especie en el Parque Nacional Nahuel Huapi, donde la especie se reproduce en diferentes ambientes acuáticos, desde humedales semitemporales hasta lagos y lagunas permanentes.

Palabras claves: anuros patagónicos; humedales; amplexo; huevos; desarrollo embrionario.

### Introduction

The austral temperate forest of Chile and Argentina harbors around 62 anuran species, of which approximately 80% are endemic (Formas 1979). These species breed during spring or summer, and some species can extend the reproductive season until autumn (Formas 1979, Úbeda 1998). The endemic Batrachylidae family has a wide diversity of reproductive modes and life history traits (Jara et al. 2021, Grosso et al. 2022). Batrachylidae present a total of 12 species, belonging to four genera: Chaltenobatrachus and Hylorina with one species each and Atelognathus and Batrachyla with five species each (Formas 1997, Barrasso & Basso 2019). Hylorina, Atelognathus and Chaltenobatrachus are typical pond-breeding amphibians that breed during spring and summer in lakes, lagoons, ponds or small streams (Barrio 1967, Úbeda et al. 1999, Cisternas et al. 2013, Barrasso et al. 2020). In contrast, Batrachyla species have developed the strategy of laying their eggs in humid soils with embryonic development outside water (Cei 1980, Úbeda 1998, Lobos et al. 2013; Jara et al. 2019, 2021). The breeding phenology of this family is unknown, as well as other aspects of their biology and ecology. Since these aspects provide valuable information for conservation programs (Paton & Crouch 2002), more field studies on this batrachofauna should be carried out. For example, Paton & Crouch (2002) determined that the timing of wetland inundation and duration of the wetland can explain the success of several amphibian species in Rhode Island (USA); they recommend that biologists gather data on amphibian movement phenology in other regions to help regulators and managers develop legislation to protect the habitat of pond-breeding amphibians. The relationship between local variations in breeding phenology and climate conditions can also provide clues to various aspects of species conservation (Loman 2016).

One of the most interesting species of Batrachylidae is the emerald frog or golden frog, *Hylorina sylvatica* Bell 1843; its striking coloration is similar to that of tropical species. It also has arboreal habits, slender limbs with long, slender fingers, and opposable thumbs associated with its ability to climb (Cei 1962, Formas 1979, Rabanal & Ñuñez 2008, Charrier 2019). Endemic to the southern temperate forests of Chile and Argentina, this species is found in Chile from Ramadillas (Biobío Region) to Bernardo O'Higgins National Park on Wellington Island (Magallanes and Chilean Antarctic Region) (Donoso-Barros 1976, González et al. 2015), while in Argentina it has a more limited latitudinal distribution and is restricted to a narrow strip of forest on the eastern slope of the Andes: from Yuco, on the north shore of Lake Lácar, Lanín National Park, to the Middle Lake in Los Alerces National Park (Vellido & Úbeda 2001, Mut Coll et al. 2002).

In Argentina *H. sylvatica* has been found in some locations in Nahuel Huapi National Park (southern Neuquén Province and northwestern Río Negro Province) and in Los Alerces National Park (northern Chubut Province) (Úbeda 1998). Adults are diurnal, have arboreal habits and are found in dark areas under fallen trunks, hidden in leaf litter. During the breeding season males concentrate in open areas and call from the shoreline of the water bodies (Úbeda 1998). Larval development is prolonged (about 13 months according to Moncada 2011), hence adults breed in permanent and semi-permanent water bodies, including shallow lakes and large wet meadows (Figure 1). According to Vaira et al. (2012), this species is considered vulnerable because the number



Figure 1. Aquatic environments inhabited by *H. sylvatica*: A) Llao Llao, the wet meadow where the study was conducted, B) Lake Escondido, showing the littoral zone where males call during November, and C) Mallin Goye, a large semi-temporary wetland where males call during December.

of sites they inhabit is relatively lower than in Chile, and information on the biology and ecology of Argentinian *H. sylvatica* populations is scarce in comparison with that of Chilean populations. Our aim in this work is to gather data on the reproduction and egg development of *H. sylvatica* in a population located in a protected area of Northwest Patagonia, Argentina, and then compare the life history traits of *H. sylvatica* with other syntopic species in the area.

### **Materials and Methods**

### 1. Study area

This research was conducted in Llao Llao Nature Reserve (-41.0500 latitude and -71.500 longitude, 821 m elevation) in Northwestern Patagonia, Argentina. The area includes 1226 ha of a well preserved Andean Patagonian forest that receives approximately 1800 mm rainfall each year, primarily during fall and winter (May-August) (Jara 2016). Another four species of anuran amphibians have been recorded in the area: Batrachyla taeniata, B. leptopus, (Batrachylidae), P. thaul (Leptodactylidae), and Rhinella spinulosa (Bofonidae) (Moncada 2011, Jara et al. 2021). The calling activity of Hylorina sylvatica males goes from October to December (Moncada 2011). Data on their reproductive phenology was collected from the Llao Llao wetland, a wet meadow of around 0.16 ha with 0.38 m maximum water depth (Figure 1A). This wetland may undergo several years with permanent waters, then have years with a dry phase in summer, depending on annual precipitation. The bottom of the pond is completely covered by dense mats of Schoenoplectus californicus, Carex niderdenliana (Cyperaceae) and Agrostis leptotricha (Poaceae), with patches of rushes such as Juncus balticus and J. invulucratus in the center of the pond (Jara 2016).

### 2. Collected field data

The wetland was visited once a week from September 2016 to December 2016. Throughout the study, daily precipitation (mm) and air temperature (maximum and minimum temperature) were obtained from AIC (Autoridad Interjurisdiccional de las Cuencas de los ríos Limay, Neuquén y Negro) meteorological station in Bahía López (41° 4' 27.88" S latitude; 71° 34' 6.85" O longitude), which is located 2.75 km from the wetland.

The presence of calling males and mating pairs were considered indicators of breeding activity. The number of male calls was recorded on each sampling day (male calls were registered on 8 days). Using the Pearson product-moment correlation coefficient, this variable was then tested to determine whether it was associated with air temperature. Active searches were conducted during daylight hours (12:00-17:00 pm), and water depth, water temperature, pH and conductivity were recorded at each visit. Water temperature was measured using i-Button temperature loggers (one logger per enclosure, temperature range -40/+80 °C, precision 0.5 °C). Once the pairs were observed, sampling was carried out with a hand net in search of eggs and tadpoles. The shoreline and the deepest area of the wetland were each swept 10 times.

To study egg oviposition and the number of eggs laid by each female, three pairs were captured. Each pair was kept in an enclosure of  $41 \times 29 \times 18$  cm, consisting of a plastic basket covered with a mesh (1 mm) that allowed water flow. Enclosures were placed 1 m apart. To prevent frogs from escaping or being predated by birds, the top of the enclosure was covered with a cotton mesh. After 24 h (spontaneous separation of the breeding pairs), individuals were measured (snout-vent length) with a caliper to the nearest 0.1 mm, then released at the capture sites. All the eggs were counted in situ, and a subsample of eggs (10 per enclosure) was taken to the laboratory where their diameter, with and without jelly, was measured (to the nearest 0.01 mm) using a stereoscopic microscope with an ocular micrometer. The eggs were then returned to the field (to each enclosure) and kept there until they had all hatched. The newly hatched larvae were released into the pond.

## **Results**

There were two distinct rainfall peaks during September and November (Figure 2). Reproductive activity started in the second week of October, with calling males registered after precipitation on sunny days. The males were observed calling from the shoreline of the wetland at noon, when the air temperature was relatively high (Figure 3A). The number of male calls increased with air temperature (Pearson correlation = 0.891, p = 0.003, n = 8); no calling was recorded on cold days (air temperature below  $10 \,^{\circ}$ C). The first breeding pairs were observed on October 26, and five more the following week. The *H. sylvatica* pairs (in axillary amplexus, Figure 3D) were detected easily due to their conspicuous coloration, whether partially concealed in the



**Figure 2.** Breeding phenology of *H. sylvatica* in relation to climatic conditions and water temperature of the wetland. A) shows the duration of each phenological event with horizontal bars, and water temperature in spring 2016, and B) shows accumulated precipitation per day and air temperature during the study period.



**Figure 3.** *Hylorina sylvatica*: A) adult calling from the littoral zone of the wetland, B) captured female, C) axillary amplexus (note differences in size between male and female) and D) breeding pair captured and placed in enclosure in the field.

vegetation or moving actively in deep areas. One pair was observed over a period of one hour (14:00 pm–15:00 pm, air temperature 22 °C ± 1) on October 26. I followed the pair with the camera zoom lens and recorded the time. The female swam actively while the male only clung to the female throughout the entire observation time. The female made wavy paths in the center of the pond as she swam. She stopped swimming frequently and submerged for a few minutes (3 minutes ± 2), then she surfaced again, apparently to breathe, before continuing to swim.

The *H. sylvatica* males observed were smaller than the females (Figure 3A, B) (male size 53.32 mm  $\pm$  3 mm (n = 5) and female 60.6 mm  $\pm$  0.9 mm (n = 4); t = -4.5, p = 0.003). From the fourth week of October and the second week of November I collected 118 eggs and captured 41 tadpoles. The eggs collected were adhered to submerged vegetation at depths of between 18 and 22 cm, whereas the tadpoles were captured in densely vegetated patches at depths of between 20 and 35 cm.

Three breeding pairs of H. sylvatica were captured and kept in the enclosures (Figure 3C), one on the 5th of November and two on the 18th. The average number of eggs per enclosure was  $74 \pm 11$ , and they were attached to vegetation stems or lying in the bottom of the enclosure. The diameter of the eggs without jelly was  $2.35 \pm$ 0.45 mm (n = 30) and the diameter with jelly was  $3.92 \pm 0.36$  mm (n = 30). The eggs inside the enclosure developed in neutral pH (mean =  $6.88 \pm 0.37$ , range 6–7.5), low conductivity (mean =  $69.2 \pm$ 14.8 SD  $\mu$ s.cm<sup>-1</sup>) and well oxygenated water (mean = 6.8 range 5–8 mg/l). The water temperature during egg development was  $13.1 \pm$ 9.1 °C; the minimum temperature was recorded during the mornings (5 °C) and the maximum in the afternoons (28 °C). Time to hatching was 10-14 days inside the enclosure and approximately 16 days in the pond. In the enclosures, approximately 76 % of the eggs hatched. Neither eggs parasitism by fungus nor predation by invertebrate was observed in the enclosures.

### Discussion

The results shown here indicate that some aspects of the life history of the frog H. sylvatica reflect local variations in reproductive phenology and egg oviposition. Indeed, breeding activity has been observed during December and January in Chilean populations (Barrio 1967, Formas 1979); however, in this study males were observed calling in the Llao Llao wetland from the middle of October until December. The beginning of the breeding season varies from year to year in the area, and this variation is probably related to temperature and the amount of precipitation. The number of eggs laid was registered from late October until the end of November, when the wetland was drying more quickly. The eggs in the enclosures were found on the bottom or adhered to the stems of plants (Carex spp.), either individually or in groups of two or four eggs. The behavior observed in the H. sylvatica pairs indicates that during mating the eggs are dispersed throughout the pond, into both shallow and deep areas. This observation was also supported by the location of the eggs collected; they were observed individually at the bottom or attached to the vegetation, as in the enclosures. These results differ from those obtained by Barrio (1967), who describes the eggs of H. sylvatica as a gelatinous mass. Barrio (1967) observed H. sylvatica eggs laid in the water near the shore of a wetland in Chile, reported that the eggs were initially placed independently, but he noticed that after the first few days they tended to stick together. The number of eggs laid by each female (70-90) was lower than the number reported by other authors (400-600 eggs; Formas 1979, Charrier 2019) It is possible that the number of eggs was underestimated in this study. The enclosures were small and amplexant pairs observed in the study wetland swam long distance (around 9 meters in one hour) to disperse the eggs into the pond; this may have affected their behavior and consequently the number of eggs laid. The number of reproductive pairs analyzed was also low. Some aspects of reproduction in H. sylvatica require further investigation, to determine the real number of eggs that one female can produce.

During incubation of the eggs in the enclosures, no fungus infection was observed. Although two leech species (Helobdella fantasmae n. sp. and H. nahuelhuapensis) and a high density of aquatic beetles (Rhantus antacticus nahuelis, R. signatus, Lancetes flavipes) were observed during the sampling period, none of these predators were seen to feed on H. sylvatica eggs. However, recent investigation has shown that H. sylvatica tadpoles are predated by some aquatic insects, such as diving beetle larvae, dragonfly naiads and water bugs (Úbeda et al. 2021), and this is supported here by the tail damage shown by several captured tadpoles. Dispersion of the eggs in the pond by amplexant pairs during could be interpreted as a strategy to avoid predation by invertebrates and to prevent eggs from being colonized by fungus. Because the eggs are placed individually and are relatively small, they are difficult for predators to detect, which also reduces the impact of fungus contamination. In the years 2005-2006 and 2009-2010, H. sylvatica was able to complete its life cycle in this pond: as a result of heavy rains the pond did not dry out for two consecutive years (Moncada 2011, Jara et al. 2021). This meant that in 15 years only two breeding seasons were successful for this species in this wetland (Moncada 2011, Jara & Úbeda pers. obs.). It is important to know how species like *H. sylvatica* respond to an altered hydroperiod so as to predict how this species and other amphibians that breed in diverse

 Table 1. Summary of life history traits of sympatric and syntopic anuran species found in the study area (from Moncada 2011, Moncada & Úbeda 2020, Jara et al. 2018 and 2021 and Jara unpublished data\*).

Life history traits									
Anuran species	Egg diameter (mm)	Clutch size	Type of egg	Parental care	Breeding season	Overwintering tadpoles	Larval period (months)	Metamorphosis weight (gr)	
Hylorina sylvatica	$2.35 \pm 0.45*$	74 ± 11*	aquatic eggs laid individually*	no	Spring*	yes	12–13	no data available	
Batrachyla taeniata	$2.75\pm0.32$	$108\pm 64$	terrestrial eggs laid together in humid soil	yes	Summer– Fall	yes	8–9*	$0.46\pm0.05\texttt{*}$	
Batrachyla leptopus	no data available	$70\pm56*$	terrestrial eggs laid together in humid soil	yes	Summer– Fall	yes	8–9*	$0.49\pm0.1*$	
Pleurodema thaul	$1.58 \pm 0.12$	$452\pm172$	aquatic eggs in a gelatinous mass attached to submerged vegetation	no	Spring	no	3-4*	$0.62 \pm 0.10*$	

aquatic habitats may respond to the influence of climate change on aquatic ecosystems.

*Hylorina sylvatica* sometimes shares the habitat with other species of the Batrachylidae family, such as *Batrachyla leptopus* and *B. taeniata*, and also with the most abundant lepdodactylid frog in the region, *Pleurodema thaul*. In Chilean populations, tadpoles of *H. sylvatica* have been seen to coexist with *Bufo variegatus* (*Nannophryne variegata*), *Batrachyla taeniata*, *Batrachyla leptopus*, and *Batrachyla antartandica* (Formas & Pugin 1978). Also in Chile, *H. sylvatica* was observed in lotic water bodies and temporary ponds (Formas & Pugin 1978, Veloso & Nuñez 2003). This shows that the species can use a great variety of habitats for breeding, and can therefore be considered a versatile species. Tadpole habitat can vary greatly in environmental conditions; for example, Formas & Pugin (1978) reported that in Chile, tadpoles of this species were found in acidic waters (pH 5.2).

The breeding phenology and reproductive strategy of H. sylvatica differ considerably from those of other species of the same family (Table 1). For example, the breeding cycle of Batrachyla taeniata and B. leptopus lasts from mid-January to April; the eggs are terrestrial and larger than those of H. sylvatica (Table 1). Moreover, clutches are cared for by the males in Batrachyla. Clutch size in H. sylvatica (around 500 eggs, Formas (1979) is larger than that of Batrachyla species (between 70 to 108 eggs per clutch, Table 1), which is not surprising considering that H. sylvatica do not take care of their eggs. However, both genera have overwintering tadpoles and long larval development (Table 1), (Moncada 2011). Batrachyla do not present overlapping of tadpole cohorts, whereas in H. sylvatica large premetamorphic tadpoles from one season frequently coexist with early-hatching tadpoles of the following season (Moncada 2011). Although P. thaul is a pond-breeding anuran like H. sylvatica, P. thaul eggs are smaller (Table 1) and are oviposited in a gelatinous string that can curl up in the aquatic vegetation, secondarily adopting a globular shape (Moncada & Ubeda 2020). For a short period of time tadpoles of four species coexist in the same wetland, therefore determining the diet of each species is essential to evaluate whether the species compete for resources. In addition, the differences in phenology between these species generates body-size asymmetries in the tadpole community (i.e., tadpoles of different sizes and stages coexist), which probably leads to interference between tadpoles of different sizes or predation of large tadpoles on smaller ones, as occurs in other amphibian communities (Heyer et al. 1975, Griffiths et al. 1991, Faragher & Jaeger 1998).

Finally, *H. sylvatica* was also observed in other aquatic habitats in the study area. For example, a high abundance of calling males was detected in the littoral zone of lake Escondido and in a semipermanent wet meadow (Mallin Goye); both these water bodies are larger and deeper than Llao Llao wetland. The breeding phenology and dynamics of these larval populations may differ from those of the Llao Llao populations, since lake Escondido has fish predators (the native *Percichthys trucha* and exotic salmonid species *Oncorhynchus mykiss*, both voracious predators, Macchi et al. 2007) and large odonate naiad predators in littoral areas (Jara unpublished data), while Mallin Goye has many predatory invertebrates (Jara unpublished data). Predation therefore appears to be the main constraint regulating the survival rate of *H. sylvatica* in these habitats. More studies are necessary to analyze how hydroperiod and predation drive the larval population of this frog in local populations.

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## **Associate Editor**

Denise de Cerqueira Rossa-Feres

## **Conflicts of Interest**

I have no conflict of interest related to the publication of this manuscript.

## Ethics

All applicable institutional and/or national guidelines for the care and use of animals were followed.

## **Data Availability**

Supporting data are available at <http://rdi.uncoma.edu.ar/handle/ uncomaid/16689>

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## Ichthyofauna of Santa Helena Relevant Ecological Interest Area (REIA), Paraná, Brazil

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*Abstract:* The Relevant Ecological Interest Area (REIA), popularly known as "Refúgio Biológico de Santa Helena", is part of the Atlantic Forest Biome and one of the 78 ecoregions mapped by IBAMA as basic unit for planning priorities focused on national biodiversity conservation. Quarterly collections were carried out from November 2017 to November 2019 to inventory the ichthyofauna of this Conservation Unit. Specimens were captured with the aid of gillnets, fishing sieve and seine. In total, 3,919 specimens belonging to two class, eight orders, 27 families and 74 species were sampled. Characiformes and Siluriformes presented the highest species richness; they accounted for 40 (54%) and 17 (23%) species, respectively. *Geophagus sveni* (181 individuals = 17%), *Trachelyopterus galeatus* (109 individuals = 10%) and *Schizodon borellii* (105 individuals = 10%) were the most abundant fish species captured with gillnet. *Moenkhausia* was the most abundant genus captured with seine and fishing sieve, with emphasis on species *Moenkhausia bonita* (930 individuals = 33%) and *Moenkhausia gracilima* (845 individuals = 30%). Moreover, two "endangered" species (*Brycon orbignyanus* and *Pseudoplatystoma corruscans*) were registered. Therefore, we present an updated inventory of species belonging to the ichthyofauna of REIA, and it may contribute to future management plans focused on this Conservation Unit. *Keywords: Ichthyofaunistic Inventory; Conservation Unit; Endangered Species*.

## Ictiofauna da Área de Relevante Interesse Ecológico (ARIE) de Santa Helena, Paraná, Brasil

**Resumo:** A Área de Relevante Interesse Ecológico (ARIE), popularmente conhecida como "Refúgio Biológico de Santa Helena", faz parte do Bioma Mata Atlântica, uma das 78 ecorregiões mapeadas pelo IBAMA como unidade básica de planejamento e prioridades para a conservação da biodiversidade nacional. Foram realizadas coletas trimestrais de novembro de 2017 a novembro de 2019 para inventariar a ictiofauna desta Unidade de Conservação. Os espécimes foram capturados com o auxílio de redes de emalhar, peneira e rede de arrasto. No total, foram amostrados 3.919 exemplares pertencentes a duas classes, oito ordens, 27 famílias e 74 espécies. Characiformes e Siluriformes apresentaram a maior riqueza de espécies; somando um total de 40 (54%) e 17 (23%) espécies, respectivamente. *Geophagus sveni* (181 indivíduos = 17%), *Trachelyopterus galeatus* (109 indivíduos = 10%) e *Schizodon borellii* (105 indivíduos = 10%) foram as espécies de peixes mais abundantes capturadas com rede de espera. *Moenkhausia bonita* (930 indivíduos = 33%) e *Moenkhausia gracilima* (845 indivíduos = 30%). Além disso, duas espécies "ameaçadas" (*Brycon orbignyanus* e *Pseudoplatystoma corruscans*) foram registradas. Assim, apresentamos um inventário atualizado das espécies pertencentes à ictiofauna da ARIE, podendo contribuir para futuros planos de manejo voltados para esta Unidade de Conservação.

Palavras-chave: Inventário Ictiofaunístico; Unidade de Conservação; Espécies ameaçadas.

## Introduction

The Atlantic Forest biome is one of the main biodiversity hotspots worldwide (Rezende et al. 2018). This biome comprises 17 Brazilian states and originally covered approximately 1.3 million km<sup>2</sup> (Hirota & Ponzoni 2019). However, most of its native forest remnants were subjected to anthropic actions that have severely fragmented and degraded it; consequently, nowadays, it only covers 12% of its original area (Pires et al. 2018, Kasecker et al. 2018). Nevertheless, it is considered a biodiversity *hotspot* that plays prominent role in conservation biology; thus, protecting this biome can help stopping the endangerment of several species (Norman 2003).

The Atlantic Forest provides essential ecosystem services such as water supply, climate regulation, agriculture, fishing, electric power, and tourism (Varjabedian 2010, SOS Mata Atlântica 2022). However, it is under severe threat due to anthropic actions that lead to its degradation and continuous shrinking (SOS Mata Atlântica 2020) as well as affect fish biodiversity at different ecological levels (Bezerra et al. 2019); thus, it is urgent and necessary adopting conservation measures. Conservation Units are one of the ways to protect this biome and its biota since they help protecting the remaining fauna and flora in Brazil and abroad. However, the effective protection provided by these areas, mainly for both freshwater ecosystems and their biodiversity, remains insufficient (Azevedo-Santos et al. 2019).

Conserving aquatic habitats – and, most specifically, South American fish – is a growing challenge due to the fast anthropogenic changes taking place in the 21<sup>st</sup> century; thus, conservationists and public policy-makers (Reis et al. 2016) should pay greater attention to this topic, since the conservation of South American Freshwater fish in the so-called "Anthropocene" faces increasing challenges due to the significant number of human activities leading to large-scale environmental degradation (Pelicice et al. 2021).

The South American freshwater fish fauna is one of the most diverse on the planet; it accounts for approximately 5,160 species, although estimates point towards final diversity ranging from 8,000 to 9,000 species for continental fresh waters and nearshore marine waters combined (Reis et al. 2016). Unfortunately, all fish species in this geographic region are exposed to some endangerment level, mainly due to habitat loss and degradation processes. This context justifies the importance of taking priority actions based on scientific information to promote freshwater ecosystems' preservation and restoration, as well as to preserve natural flow regimes, connectivity, river and riparian environments and critical habitats (Pelicice et al. 2021).

Public protection policies developed for Conservation Units (CUs), with emphasis on protecting aquatic environments, are strongly recommended; ichthyofaunistic inventories are one of the ways to help developing these policies and management plans focused on freshwater fauna conservation (Azevedo-Santos et al. 2021). Species inventories help identifying watershed regions that need to be better inventoried (Jarduli et al. 2020); they are considered useful ecological indicators, since they help improving the knowledge about taxonomic groupings, featuring species' functional diversity, understanding the social value of different regions and the composition of migratory species, as well as identifying endangered species (Poff et al. 2010).

Environments presenting endangered species – which are classified as "Critically Endangered – CR", "Endangered – EN" or "Vulnerable – VU", based on the International Union for the Conservation of Nature and Natural Resources (IUCN) – should be prioritized in conservation and preservation programs (IUCN 2021), and subjected to permanent monitoring and inspections (Cavalli et al. 2018). Paraná State has 110 municipal protected areas, 14 Environmental Protection Areas (EPAs), 78 Municipal Parks, eight Municipal Forests, two Ecological Stations, two Forest Gardens, one Protected Forest, one Natural Monument, one Botanical Garden, two Ecological Reserves, and one Relevant Ecological Interest Area (REIA), which is known as "Refúgio Biológico de Santa Helena" (IAT 2020). These protected areas cover 2,878.76 km<sup>2</sup>, which only correspond to 0.001% of total Paraná State's area (IBGE 2020).

REIA, also known as "Refúgio Biológico de Santa Helena" (RBSH) is a peninsula located within Itaipu Reservoir, in Santa Helena County, Paraná State, Brazil. It is located approximately 100 km away from Foz do Iguaçu County, in Paraná Hydrographic Basin 3, where Itaipu Binacional dam is located in (25°24'19.51"S 54°35'7.05"W). It is a private conservation unit belonging to Itaipu Binacional. RBSH area accounts for 1,482 ha of reforested native and non-native vegetation and it shelters fauna rescued during the reservoir filling season (Kliver 2010).

According to these data, CUs are scarce; therefore, it is necessary encouraging the implementation of new conservation areas and rigorous inspection procedures to ensure the preservation and conservation of natural resources, as recommended by the Sustainable Development Goals of the 2030 Agenda (ONU 2021). In addition, urgent fieldwork and collaborative collections must be carried out, while there is still time, due to imminent risk of species endangerment (Bailly et al. 2021, Engel et al. 2021), a fact that turns fish fauna inventories into important tools to help better understanding and preserving the aquatic fauna (Frota et al. 2021, Pereira et al. 2021).

We carried out an updated inventory of the ichthyofauna belonging to Santa Helena Relevant Ecological Interest Area to aid the sustainable management of this conservation unit based on knowledge about the diversity of fish species distributed.

### **Materials and Methods**

### 1. Study area

The Conservation Unit (CU), known as "Refúgio Biológico de Santa Helena" (RBSH), was launched in 1984 to help sheltering and protecting animals that had lost their habitats due to Itaipu Binacional Reservoir formation, in October 1982. It presents strategic location, since it is part of the biodiversity corridor area covered by Paraná Biodiversity Program. In addition, it is connected to Itaipu Reservoir protection strip (Kliver 2010), a fact that further justifies the importance of maintaining and conserving this environment. This Conservation Unit is located right to the South of the former mouth of São Francisco Falso River, in Paraná River basin, which covers approximately 4,695 km and is formed by the confluence between Grande and Paranaíba rivers (Carolsfeld et al. 2003).

### 2. Collection data

Ichthyofauna sampling was carried out quarterly from November 2017 to November 2019. Fish were collected at six different sites: RB1 (24°51'15.12" S 54°21'21.12" W); RB2 (24°48'30.50" S 54°21'5.33" W); RB3 (24°49'39.97" S 54°21'27.63" W) with the aid of gill nets,

### Ichthyofauna of Santa Helena (REIA), Brazil



Figure 1. Brazilian map highlighting "Refúgio Biológico de Santa Helena", Itaipu Reservoir, Upper Paraná River, Brazil (arrow), and the location of the six sampling points (QGIS Geographic Information System. Open-Source Geospatial Foundation Project. http://qgis.org"; Google Earth website. http://earth.google.com/, 2020).

fishing sieve and seine; and RB4 (24°48'35.5" S 54°22'01.5" W); RB5 (24°50'39.8" S 54°20'27.6" W) and RB6 (24°49'57.8" S 54°20'42.4" W) with the aid of fishing sieve and seine (Figures 1 and 2). Sampling areas were selected to assure the highest environmental heterogeneity level to increase the likelihood of sampling the maximum number of species that occur in the ichthygeographic complex, which was defined in the current scientific research (Table 1).

The area of the gill nets used in the current study, was equal to  $482 \text{ m}^2$  installed around the conservation unit. These gillnets were set in the water at dusk and removed at dawn (12-h exposure). A sieve  $(1.0 \times 0.6 \text{ m})$  was used to sample fish from the coastal zone; whereas a seine (10 m, in length; and 2.4 mm mesh opening) was used whenever the environment presented ideal conditions for it. After the sampling points were selected, the effort was standardized in 10 minutes. The current research has the following authorizations: ICMBIO via SISBIO: n. 57181; Animal Use Ethics Committee (CEUA) 2016-031. It was registered at the National System for the Management of Genetic Heritage and Associated Traditional Knowledge (SisGen) under the following code: A3242E0.

Information about the conservation status of fish species was provided based on criteria set by the Red List of Threatened Species and by the International Union for Conservation of Nature (IUCN 2021). Meristic and morphometric data used in the species identification process were based on Graça & Pavanelli, (2007). Species identification was mainly performed based on Ota et al. (2018) and confirmed through specialized literature about the respective taxon. The taxonomic status classification was based on Fricke, R., Eschmeyer, W. N. & R. Van der Laan (eds) (2021), whereas endemism classification was based on Langeani et al. (2007) and Ota et al. (2018).

Fish Orders and Families were named and classified based on Betancur-R. et al. (2017), Oliveira et al. (2011), Thomaz et al. (2015) and Mirande (2019). Migratory species were classified following Agostinho et al. (2007) and Carolsfeld et al. (2003).

Specimens were deposited in the Ichthyological Collection of Federal Technological University of Paraná UTFPR, Santa Helena *Campus* (CISH), as well as in the Ichthyological Collection of Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura, NUPÉLIA (NUP) (vouchers numbers Table 2).

For the percentage calculations, absolute numbers were used, considering the effort separately (gill nets and sieve/trawlers).

Species accumulation curve based on sampling effort (Figure S1), in association with the bootstrap method (Smith & Van Belle 1984), was used to evaluate sampling efficiency. Standard error was calculated by using the function 'specaccum' in the 'vegan' package (Oksanen et al. 2014) of R 4.0 software (R Development Core Team 2019).

## Results

The freshwater ichthyofauna of RBSH comprises 74 species distributed in two classes, eight orders and 27 families (Table 2, Figure 3 and Figure 4). Characiformes was the most representative order (40 species), it was followed by Siluriformes (15 species) and Cichliformes (9 species). Characidae recorded the largest number of



Figure 2. Sampling sites at "Refúgio Biológico de Santa Helena", Itaipu Reservoir, Upper Paraná River, Brazil. RB1 has the tip of the peninsula on one side and Itaipu protection strip on the other side; they form a bay whose environment is covered by *Brachiaria* grass and floating macrophytes (A); RB2 has access to the mouth of São Francisco Falso River, which is the main tributary of Itaipu Lake (B); RB3 has direct connection to Paraná River and forms a bay with calm waters, whose main feature lies on its extensive aquatic macrophyte banks (C); RB4 presents the formation of sand and gravel banks on Paraná River banks (D); RB5 bank is covered by Poaceae and floating macrophytes (E); and the RB6 environment is located 1.2 km from Santa Helena balneary's front side, PR (F).

Table 1. Features of sampling points around "Refúgio Biológico de Santa Helena", Itaipu Reservoir, Upper Paraná River, Brazil.

Sites	Floating macrophytes	<b>Coastal vegetation</b>	Forest fragment	Environment
RB1	Presence of <i>Eichhornia</i> sp., and <i>Elodea</i> sp.	Grass formation extending into the water	Itaipu protection strip	Semi lentic
RB2	Presence of <i>Eichhornia</i> sp., and <i>Elodea</i> sp.	Formation of grasses that extend into the water	Riparian vegetation	Semi lentic
RB3	High amounts of <i>Eichhornia</i> sp., <i>Salvinia</i> sp., <i>Pistia</i> sp., and <i>Elodea</i> sp.	Grass formation extending into the water	Riparian vegetation	Lentic
RB4	Absent	Absent	Riparian vegetation	Lotic
RB5	High amounts of <i>Eichhornia</i> sp., <i>Salvinia</i> sp., and <i>Elodea</i> sp.	Grass formation extending into the water	Itaipu protection strip	Lentic
RB6	Presence of <i>Eichhornia</i> sp., and <i>Elodea</i> sp.	Grass formation extending into the water	Itaipu protection strip	Semi lentic

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**Table 2.** List of fish species' incidence and total abundance of sampled fish around "Refúgio Biológico de Santa Helena", Itaipu Reservoir, Upper Paraná River, Brazil RB = Refúgio Biológico [Biological Refuge]; \*Fish captured only based on using sieve; (\*\*) Fish captured by using both sieve and gill nets; <sup>LDM</sup> = long-distance migration; <sup>(+)</sup> conservation *status*: Endangered (EN) A2cd (ICMBio, 2018); <sup>(-)</sup> conservation *status*: <sup>VU</sup> = Vulnerable and <sup>CR</sup> = Critically Endangered MMA Ordinance N°. 148, of June 7, 2022 and IUCN red list categories and criteria: <sup>(DD)</sup> = Data Deficient and <sup>(LC)</sup> = Least Concern.

Таха	RB1	RB2	RB3	RB4	RB5	RB6	Abundance	Voucher	Ota et al. 2018
CHONDRICHTHYES									
MYLIOBATIFORMES									
Potamotrygonidae									
Potamotrygon sp.	Х						2	NUP 23069	Non-native
Potamotrygon amandae Loboda & Carvalho, 2013 <sup>DD</sup>			Х				4	NUP 23072	Non-native
ACTINOPTERYGII									
CHARACIFORMES									
Acestrorhynchidae									
Acestrorhynchus lacustris (Lütken, 1875)**	Х		Х		Х		5	NUP 23100	Native
Cynodontidae									
<i>Rhaphiodon vulpinus</i> Spix & Agassiz, 1829 <sup>LDM</sup>		Х	Х				25	NUP 23105	Native
Characidae									
Stethaprioninae									
Astyanax lacustris (Lütken, 1875)*	Х	Х	Х		Х	Х	14	NUP 23085	Native
Psalidodon aff. fasciatus (Cuvier, 1819)*		Х					7	NUP 23043	Native
Hemigrammus ora Zarske, Le Bail & Géry, 2006*	Х	Х	Х	Х	Х	Х	133	NUP 23029	Non-native
Hyphessobrycon eques (Steindachner, 1882)*	Х	Х	Х		Х		128	NUP 23094	Possibly non-native
<i>Hyphessobrycon moniliger</i> Moreira, Lima & Costa 2002*					Х		1	NUP 23063	Non-native
Moenkhausia gracilima Eigenmann, 1908*	Х	Х	Х	Х	Х	Х	845	NUP 23080	Native
Moenkhausia bonita Benine, Castro & Sabino, 2004*	Х	Х	Х	Х	Х		930	NUP 23083	Native
Moenkhausia forestii Benine, Mariguela & Oliveira, 2009*	Х		Х		Х		12	NUP 23076	Non-native
Psellogrammus kennedyi (Eigenmann, 1903)*	Х	Х	Х		Х		18	NUP 23074	Non-native
Characinae									
Galeocharax gulo (Cope, 1870)		Х	Х				2	NUP 23056	Native
Roeboides descalvadensis Fowler, 1932*	Х	Х	Х	Х	Х		82	NUP 23075	Non-native
Stevardiinae									
Piabarchus stramineus (Eigenmann, 1908)*		Х		Х			54	NUP 23087	Native
Knodus moenkhausii (Eigenmann & Kennedy, 1903)*	Х						1	NUP 23040	Possibly non-native
Diapoma guarani (Mahnert & Géry, 1987)*		Х	Х		Х		65	NUP 23093	Native
Aphyocharacinae									
Aphyocharax anisitsi Eigenmann & Kennedy, 1903*	Х	Х	Х		Х		18	NUP 23117	Native
Aphyocharax sp.*	Х	Х	Х	Х	Х		33	NUP 23070	Native
Cheirodontinae									
Serrapinnus kriegi (Schindler, 1937)*					Х		8	NUP 23064	First record
Serrapinnus notomelas (Eigenmann, 1915)*	Х	Х	Х	Х	Х		81	NUP 23084	Native

Таха	RB1	RB2	RB3	RB4	RB5	RB6	Abundance	Voucher	Ota et al. 2018
Bryconidae									
<i>Brycon orbignyanus</i> (Valenciennes, 1850) <sup>LDM (+) (-)CR</sup>			Х				1	CISH 191/O	Native
Crenuchidae									
Characidium aff. zebra Eigenmann, 1909*	Х			Х			2	NUP 23101	Native
Erythrinidae									
Hoplias aff. malabaricus (Bloch, 1794)	Х	Х	Х	Х	Х	Х	64	NUP 23044	unvalued
Hoplias intermedius (Günther, 1864)*					Х		3	NUP 23026	Native
Hoplerythrinus unitaeniatus (Agassiz, 1829)*	Х						1	NUP 23047	Non-native
Hemiodontidae									
Hemiodus orthonops Eigenmann & Kennedy, 1903 <sup>LDM</sup>	Х	Х	Х				58	NUP 23027	Non-native
Parodontidae									
Apareiodon affinis (Steindachner, 1879)*		Х	Х	Х	Х	Х	103	NUP 23097	Native
Prochilodontidae									
Prochilodus lineatus (Valenciennes, 1836) <sup>LDM</sup>		Х	Х				4	NUP 23045	Native
Anostomidae									
Leporinus friderici (Bloch, 1794) <sup>LDM **</sup>	Х	Х	Х				43	NUP 23033	Native
Leporinus lacustris Campos, 1945	Х		Х				14	NUP 23034	Native
Leporinus cf. tigrinus Borodin, 1929*	Х						5	NUP 23102	Non-native
<i>Megaleporinus macrocephalus</i> (Garavello & Britski, 1988) <sup>LDM</sup>	Х	Х	Х				20	NUP 23109	Non-native
Megaleporinus obtusidens (Valenciennes, 1836) <sup>LDM-LC</sup>	Х	Х	Х				4	NUP 23036	Native
Schizodon borellii (Boulenger, 1900) <sup>LDM</sup>	Х	Х	Х				105	NUP 23037	Non-native
Schizodon nasutus Kner, 1858 <sup>LDM</sup>	Х						1	NUP 23038	Native
Serrasalminae									
Metynnis lippincottianus (Cuvier, 1818)**	Х	Х	Х		Х		120	NUP 23022	Non-native
Piaractus mesopotamicus (Holmberg, 1887) <sup>LDM</sup>	1		1				2	NUP 23106	Native
Serrasalmus marginatus Valenciennes, 1837**	Х	Х	Х		Х		106	NUP 23028	Non-native
Serrasalmus maculatus Kner, 1858**	Х	Х	Х				43	NUP 23030	Native
Lebiasinidae									
Pyrrhulina australis Eigenmann & Kennedy, 1903*					Х		4	CISH 159/O	Native
SILURIFORMES									
Auchenipteridae									
Ageneiosus inermis (Linnaeus, 1766) <sup>LDM</sup>		Х	Х				2	NUP 23025	Non-native
Ageneiosus ucayalensis Castelnau, 1855	Х	Х					3	NUP 23032	Non-native
Auchenipterus osteomystax (Miranda Ribeiro, 1918)	Х		Х				8	NUP 23115	Non-native
Trachelyopterus galeatus (Linnaeus, 1766)**	Х	Х	Х				110	NUP 23107	Native
Callichthyidae									
Hoplosternum littorale (Hancock, 1828)		Х	Х				3	NUP 23031	Native
...Continuation

Taxa	RB1	RB2	RB3	RB4	RB5	RB6	Abundance	Voucher	Ota et al. 2018
Doradidae									
Pterodoras granulosus (Valenciennes, 1821)	Х	Х	Х				22	NUP 23057	Non-native
Loricariidae									
Hypostominae									
Hypostomus strigaticeps (Regan, 1908)	Х						1	NUP 23048	Native
Pterygoplichthys ambrosettii (Holmberg, 1893)**	Х	Х	Х		Х		46	NUP 23061	Non-native
Loricariinae									
Loricariichthys platymetopon Isbrücker & Nijssen, 1979		Х	Х				3	NUP 23055	Non-native
Loricariichthys rostratus Reis & Pereira, 2000	Х	Х	Х				6	NUP 23060	Non-native
Pimelodidae									
Pimelodus mysteriosus Azpelicueta, 1998	Х	Х	Х				3	NUP 23059	Non-native
Sorubim lima (Bloch & Schneider, 1801) <sup>LDM</sup>	Х						1	NUP 23088	Non-native
Iheringichthys labrosus (Lütken, 1874)			Х				1	NUP 23071	Non-native
Pinirampus pirinampus (Agassiz, 1829) <sup>LDM</sup>	Х		Х				6	NUP 23058	Native
Pseudoplatystoma corruscans (Spix & Agassiz, 1829) <sup>LDM (-)VU</sup>			Х				2	CISH 42TB	Native
GYMNOTIFORMES									
Gymnotidae									
<i>Gymnotus sylvius</i> Albert & Fernando-Matioli, 1999*			Х		Х		5	NUP 23081	Native
Hypopomidae									
<i>Brachyhypopomus gauderio</i> Giora & Malabarba, 2009*			Х		Х		4	NUP 23023	Non-native
Sternopygidae									
<i>Eigenmannia trilineata</i> López & Castello, 1966*			Х				5	NUP 23095	Native
Rhamphichthyidae									
Rhamphichthys hahni (Meinken, 1937)**			Х				2	CISH 118TB	Non-native
CICHLIFORMES									
Cichlidae									
Astronotus crassipinnis (Heckel, 1840)**	Х	Х	Х				21	NUP 23096	Non-native
Cichlasoma paranaense Kullander, 1983*	Х	Х					4	NUP 23077	Native
Apistogramma commbrae (Regan, 1906)*			Х		Х		7	NUP 23103	Non-native
Geophagus sveni Lucinda, Lucena & Assis, 2010**	Х	Х	Х			Х	183	NUP 23116	Non-native
Geophagus iporangensis Haseman 1911		Х					1	NUP 23039	Possibly Native
<i>Satanoperca setepele</i> Ota, Deprá, Kullander, Graça & Pavanelli, 2021**	Х	Х	Х	Х			69	NUP 23092	Non-native
Crenicichla britskii Kullander, 1982*	Х	Х	Х		Х		11	NUP 23078	Native
Cichla kelberi Kullander & Fereira, 2006**	Х	Х	Х		Х	Х	34	NUP 23108	Non-native
Laetacara araguaiae Ottoni & Costa, 2009*	Х		Х		Х		29	NUP 23079	Non-native
INCERTAE SEDIS									
Sciaenidae									
Plagioscion squamosissimus (Heckel, 1840) <sup>LC</sup>	Х	Х	Х				88	CISH 148TB	Non-native

Continue...

Таха	RB1	RB2	RB3	RB4	RB5	RB6	Abundance	Voucher	Ota et al. 2018
SYNBRANCHIFORMES									
Synbranchidae									
Synbranchus marmoratus Bloch, 1785*LC			Х		Х		6	CISH 178/A	Native
PLEURONECTIFORMES									
Achiridae									
Catathyridium jenynsii (Günther, 1862)		Х	Х				8	NUP-23024	Non-native
CYPRINODONTIFORMES									
Poeciliidae									
Pamphorichthys hollandi (Henn, 1916)*	Х		Х	Х	Х	Х	54	NUP-23082	Native
Total species = 74							3,919		

#### ...Continuation

species (18), it was followed by Cichlidae (9) Anostomidae (7) and Pimelodidae (5). In total, 3,919 individuals were collected (Figure 5).

With respect to the abundance of individuals sampled with gill nets, *Geophagus sveni* Lucinda, Lucena & Assis, 2010 was the most abundant species (181 specimens); it accounted for 16.7% of all collected specimens. Among specimens collected with fishing sieve, *Moenkhausia bonita* Benine, Castro, Sabino, 2004 was the most representative species with 930 collected individuals (32.8% of the total sample).

Total species richness varied among sampled sites; RB3 recorded the largest number of species (57); it was followed by RB1 and RB2 (51 and 44 species, respectively). Sampling sites exclusively using fishing sieve presented the following species richness: RB5 (30 species), RB4 (13 species) and RB6 (9 species), as shown in Table 2.

RB3 recorded the highest species richness (35 species) in sampling sites where fish collection was only based on gill nets; *G. sveni* was the most abundant species (76 individuals) in these sites, and it was followed by *Schizodon borellii* (Boulenger, 1900), which accounted for 66 individuals. RB1 recorded 31 species; *G. sveni* and *Trachelyopterus galeatus* (Linnaeus, 1766) were the most abundant species found in it – they accounted for 62 and 40 individuals, respectively. RB2 recorded 28 species; *G. sveni* and *T. galeatus* were the most representative ones (43 and 37 individuals, respectively).

RB5 recorded the highest species richness (30 species) in sampling sites where fish collection was based on fishing sieve; *M. bonita* (127 individuals) and *Hemigrammus ora* Zarske, Le Bail, Géry, 2006 (39 individuals) were the most abundant species found in it. RB1 presented 26 species; *Moenkhausia gracilima* Eigenmann, 1908 (190 individuals) and *M. bonita* (185 individuals) were the most abundant species in it. RB2 recorded 22 species; *M. gracilima* (431 individuals) and *M. bonita* (420 individuals) were the most representative ones. RB3 presented 31 species; *M. gracilima* was the most representative one (207 individuals) and it was followed by *M. bonita* (87 individuals). RB4 has shown 11 species; *M. bonita* and *Piabarchus stramineus* (Eigenmann, 1908) were the most representative species collected in this site (111 and 34 individuals, respectively). RB6 was the site presenting the smallest number of species (7); *Apareiodon affinis* (Steindachner, 1879) was the most representative species (66 individuals).

We have registered at least 14 migratory species in the surroundings of this Conservation Unit. RB3 was the sampling site showing the highest migratory species richness (12); it also presented two endangered species, *Brycon orbignyanus* (Valenciennes, 1850) and *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829). Eleven (11) migratory species were recorded at RB1. RB2 recorded the lowest migratory species richness; it presented eight migratory species; among them, one finds, *Megaleporinus obtusidens* (Valenciennes 1836), *Prochilodus lineatus* (Valenciennes 1836) and *Rhaphiodon vulpinus* Spix & Agassiz, 1829.

It is worth emphasizing that we recorded three different reproduction patterns in habitats located around the Conservation Unit, namely: (i) internal fertilization and internal development – represented by species *Pamphorichthys hollandi* (Henn, 1916), which was recorded at RB1, and by family Potamotrygonidae, which was recorded at RB1 and RB3; (ii) fertilization and external development, although with internal gametic association (insemination – see: Fukakusa et al. (2020) – represented by family Auchenipteridae, which was recorded at RB1, RB2 and RB3; and (iii) fertilization and external development (without insemination) with other species.

We registered the presence of 33 non-native species in the upper Paraná River basin (Ota et al. 2018). We emphasize that the four most abundant species collected with gillnets are non-native, which indicates their ability to adjust in this ecosystem. Among the recorded species, *Brycon orbignyanus* (Valenciennes, 1850), was considered Endangered (EN) by the Akama et al. (2018) and Critically Endangered (CR) by the Official List of Extinct Brazilian Fauna Species (MMA Ordinance No. June 7, 2022) and *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829) Vulnerable (VU) also by the MMA Ordinance No. June 7, 2022.

#### Discussion

Results have shown that the Relevant Ecological Interest Area (REIA) – "Refúgio Biológico de Santa Helena" – provides habitat for at least 74 fish species, including on long-distance migrant and endangered species. Species accumulation curve did not reach the asymptote; this outcome suggested the incidence of an even richer fish fauna composition in this environment.

Agostinho et al. (2007), recorded species such as *Steindachnerina insculpta* (Fernández-Yépez, 1948), *Crenicichla nierdeleinii* (Holmberg, 1891), *Leporellus vittatus* (Valenciennes, 1850), *Hypophthalmus* 



**Figure 3.** Sample representation of the main fish species collected in the surroundings of "Refúgio Biológico de Santa Helena" – images out of scale. 1) *Potamotrygon* sp. 210 mm; 2) *Potamotrygon amandae* 195 mm; 3) *Acestrorhynchus lacustris* 153.42 mm; 4) *Rhaphiodon vulpinus* 360 mm; 5) *Astyanax lacustris* 45 mm 6) *Psalidodon* aff. *fasciatus* 35 mm; 7) *Hemigrammus ora* 26 mm; 8) *Hyphessobrycon eques* 18 mm; 9) *Hyphessobrycon moniliger* 27.2 mm; 10) *Moenkhausia* gracilima 17.77 mm; 11) *Moenkhausia bonita* 18.55 mm; 12) *Moenkhausia forestii* 23.48 mm; 13) *Psellogrammus kennedyi* 25.38 mm; 14) *Galeocharax gulo* 141.2 mm; 15) *Roeboides descalvadensis* 27.97 mm; 16) *Piabarchus stramineus* 18.59 mm; 17) *Knodus moenkhausii* 28.4 mm; 18) *Diapoma guarani* 24.37 mm; 19) *Aphyocharax anisitsi* 30.59 mm; 20) *Aphyocharax* sp. 28.76 mm; 21) *Serrapinnus kriegi* 25.35 mm; 22) *Serrapinnus notomelas* 17.58 mm; 23) *Brycon orbignyanus* (damaged in the gill net – approximate value 188 mm); 24) *Characidium* aff. *zebra* 28.78 mm; 25) *Hoplias* aff. *malabaricus* 240 mm; 26) *Hoplias intermedius* 32.69 mm; 27) *Hoplerythrinus unitaeniatus* 166 mm; 28) *Hemiodus orthonops* 152.24 mm; 29) *Apareiodon affinis* 31.15 mm; 30) *Prochilodus lineatus* 458 mm; 31) *Leporinus friderici* 197.24 mm; 32) *Leporinus lacustris* 155 mm; 33) *Leporinus* cf. *tigrinus* 15.38 mm; 34) *Megaleporinus macrocephalus* 175 mm; 35) *Megaleporinus obtusidens* 235 mm; 36) *Schizodon borellii* 180 mm; 37) *Schizodon nasutus* 215 mm.



**Figure 4.** Sample representation of the main fish species collected in the surroundings of "Refúgio Biológico de Santa Helena" – images out of scale. 38) *Metynnis lippincottianus* 18.24 mm; 39) *Piaractus mesopotamicus* 295 mm; 40) *Serrasalmus marginatus* 150 mm; 41) *Serrasalmus maculatus* 160 mm; 42) *Pyrrhulina australis* 47.12 mm; 43) *Ageneiosus inermis* 360 mm; 44) *Ageneiosus ucayalensis* 220 mm; 45) *Auchenipterus osteomystax* 210 mm; 46) *Trachelyopterus galeatus* 99.98 mm; 47) *Hoplosternum littorale* 156 mm; 48) *Pterodoras granulosus* 248 mm; 49) *Hypostomus strigaticeps* 139 mm; 50) *Pterygoplichthys ambrosettii* 293 mm; 51) *Loricariichthys platymetopon* 254 mm; 52) *Loricariichthys rostratus* 235 mm; 53) *Sorubim lima* 286 mm; 54) *Pimelodus mysteriosus* 220 mm; 55) *Iheringichthys labrosus* 138.72 mm; 56) *Pinirampus pirinampus* 379 mm; 57) *Pseudoplatystoma corruscans* 570 mm; 68) *Gymnotus sylvius* 168.5 mm; 65) *Geophagus sveni* 135 mm; 66) *Geophagus iporangensis* 148.51 mm; 67) *Satanoperca setepele* 129.07 mm; 68) *Crenicichla britskii* 33.72 mm; 69) *Cichla kelberi* 272 mm; 70) *Laetacara araguaiae* 35.9 mm; 71) *Plagioscion squamosissimus* 430 mm; 72) *Synbranchus marmoratus* 595 mm; 73) *Catathyridium jenynsii* 194 mm; 74) *Pamphorichthys hollandi* 19.79 mm.



Figure 5. Species richness recorded for each family and order found in "Refúgio Biológico de Santa Helena", Itaipu Reservoir, Upper Paraná River, Brazil. Families within each order are represented by the same color. (purple = Characiformes; pink = incertae sedis to Sciaenidae; yellow = Siluriformes; light gray = Cichliformes; green = Gymnotiformes; orange = Myliobatiformes; brown = Synbranchiformes; lialac = Cyprinodontiformes; dark pink = Pleuronectiformes).

*edentatus* Spix & Agassiz, 1829 and *Salminus brasiliensis* (Cuvier, 1816) in Santa Helena Balneary, Itaipu Reservoir, in 1987. The RBSH Management Plan carried out in 2010 presented the record of *H. edentatus* Spix & Agassiz, 1829. The non-registration of the six species listed above does not mean that they disappeared from the study site, since differences among capture methods and the effects of fishing equipment selectivity can influence sampling results.

*Geophagus sveni* was the most abundant species recorded with the passive collection effort (gill nets); this outcome has shown the important role played by Cichliformes in the investigated ichthyogeographic region. Specie *G. sveni* is native to the middle portion of the Tocantins Rivers drainage and its incidence in Paraná River basin can be associated with aquaculture or with its trade as ornamental fish (Langeani et al. 2007, Lucinda et al. 2010, Soares et al. 2017).

*Moenkausia bonita*, *M. gracilima* and *H. ora* were the most abundant species collected through the active capture (sieve) method. The numerical representation of these species can indicate that they close their life cycles in RBSH coastal zone habitats that function play an important role in filtering the functional characteristics of fish (Quirino et al. 2021). Small species often present high food plasticity and the ability to colonize different waterbodies, mainly lentic environments, although they essentially occupy coastal zones (Casatti et al. 2003, Vidotto & Carvalho 2007). The record of 32 species captured in shallow areas based on the sieve technique reinforces the importance of preserving these coastal areas, which have important environmental maintenance functions, such as the structural protection of habitats, food resources and reproduction (Cassatti et al. 2003).

The diversity of neotropical freshwater fish species mainly comprises three ostariophysan (Characiformes, Siluriformes and Gymnotiformes) and two Acanthomorpha (Cichliformes, Cyprinodontiformes) fish orders (Tagliacollo et al. 2021) – all the orders were recorded in the current study. Characiformes and Siluriformes presented the highest species richness. Characidae was the most representative family, a fact that may be linked to the wide geographic distribution of its species in continental waters covering Southwestern Texas, Mexico, and Central and South America (Nelson et al. 2016). RB3 was the sampling point presenting the highest species richness (57 species, in total). This richness may be associated with the physical features of this environment, which is formed by a calm-water bay with extensive underwater macrophyte banks that can provide places for the reproduction, refuge and feeding.

The Upper Paraná River floodplain (about 230 km) above the Itaipu reservoir, represents the last free-flowing section of the upper Paraná River and serves as a nursery habitat for many migratory species, which are very important for artisanal fisheries in tropical river systems, in terms of economic value and ecological sustainability (Hoeinghus et al. 2009). Long-distance migratory species, captured in low numbers in this study, as *B. orbignyanus*, *P. lineatus*, *Leporinus friderici* (Bloch, 1794), *Megaleporinus obtusidens*, *Piaractus mesopotamicus* (Holmberg, 1887), *Pinirampus pirinampus* (Agassiz, 1829) and *P. corruscans*, often show low abundance in dammed, as reported by

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Agostinho et al. (2007), who evaluated 77 reservoirs in South America and observed that more than 50% of the analyzed environments did not have migratory species as components of their dominant fauna, as well as that few reservoirs presented more than two migratory species among the prevalent ones. One of the main impacts on this group of species lies on the interruption of their natural migration routes resulting from the construction of artificial dams (Carolsfeld et al. 2003, Agostinho et al. 2016, Azevedo-Santos et al. 2019), a fact that significantly changes ecosystem function, sediment balance flood pulse and thermal regime (Reis et al. 2016), and that can even decrease migratory species' body size (Lopes et al. 2020).

Therefore, protecting species showing reduced natural stocks and/or endangered species, such as *B. orbignyanus* (EN/CR) and *P. corruscans* (Spix & Agassiz, 1829) (VU) is an important service provided by Conservation Units (Akama et al. 2018). Maintaining tributaries without artificial dams, where fish can complete their life cycle, is the most viable and effective alternative for species conservation (Marques et al. 2018, Lopes et al. 2021). São Francisco Falso River, which is the main tributary near "Refúgio Biológico de Santa Helena", is an example of free-dam river it that can help protect the fish fauna of the region.

According to Bailly et al. (2021), the Paraná-Paraguay basin hosts approximately 23 long-distance migratory fish species; "Refúgio Biológico de Santa Helena" a recorded 10 of these species, which corresponded to 43.5% of species recorded in their research. Among the herein recorded fish species, one finds the natives *B. orbignyanus*, *M. obtusidens*, *P. mesopotamicus*, *P. pirinampu*, *P. lineatus*, *P. corruscans*, *R. vulpinus* and the non-natives *Megaleporinus macrocephalus* (Garavello, Britski, 1988), *Pterodoras granulosus* (Valenciennes, 1821), and *Sorubim lima* (Bloch & Schneider, 1801). In addition, the current study has also recorded the following migratory species: the native *L. friderici* (Bloch, 1794) and non-natives *Ageneiosus inermis* (Linnaeus, 1766), *Hemiodus orthonops* Eigenmann & Kennedy, 1903, and *S. borellii* (Agostinho et al. 2007).

The record of migratory species in the present study may be associated with habitats forming the Conservation Unit. In addition to *B. orbignyanus*, it is worth emphasizing the incidence of the *P. corruscans*, which directly depend on upstream migration to complete their reproductive cycle (Carolsfeld et al. 2003). It is noteworthy that most of these species have economic importance, to a higher or lesser degree of acceptance (Bailly et al. 2021). Thus, the current research strongly encourages restoring and maintaining environments to help maintaining long-distance migratory and endangered species populations.

Migratory species play key role in aquatic ecosystem conservation processes. *Piaractus mesopotamicus*, for example, plays important role in seeds' (Muniz et al. 2014) cout spread due to its feeding behavior as herbivore; catfish species *P. pirinampu* and *P. corruscans* have high commercial value, whereas all other registered species also play fundamental role in ecosystem maintenance through ecological processes, besides having commercial value (Carolsfeld et al. 2003).

Fish communities are subjected to increasing global-scale anthropogenic pressures capable of changing their biodiversity and threatening ecosystem services (Villéger et al. 2017). If on take into consideration that practically all environments in the Paraná River watershed have suffered one, or more, environmental impacts, the conservation of native migratory species can be a promising alternative for ecosystem protection purposes. The fact that they require dam-free river stretches free and coastlines preserved for reproduction purposes, gives them in the status of key species for the conservation and preservation of these ecosystems. Thus, such a protection can help conserving several habitats and identifying areas with endemic or endangered species, as well as areas with high biological diversity (Agostinho 2007a, Azevedo-Santos et al. 2019). Thus, results in the current research may represent a step towards identifying and protecting fish species that occur in the vicinity of Conservation Units, by encouraging the implementation of conservation actions in continental water environments.

Among the anthropic impacts, one finds species introduction, as well as artificial impoundments, which have significant negative impacts on freshwater ecosystems (Muniz et al. 2021). The submersion of the geographic barrier "Sete Quedas" [Guairá Falls], in association with other anthropic actions such as fishkeeping and fish farms, are the likely explanation for the incidence of non-native species in the investigated area. Plagioscion squamosissimus (Heckel, 1840) stood out among these species. It was introduced in the environment before the damming process took place (Cecilio et al. 1997) and recorded high abundance level in Itaipu reservoir in 2000, based on Benedito-Cecilio & Agostinho (2000). This Amazon-native species (Casatti 2005) was introduced by São Paulo Energy Company (CESP) in dams located in Northeastern Brazil in the 1950s; it reached Paraná River in the 1970s (Braga 1997). Its introduction may also be associated with its trading potential (Ota et al. 2018). This species is one of the most frequent non-native species in Brazil, together with species Poecilia reticulata Peters, 1859 and with species belonging to genera Cichla Bloch & Schneider 1801 and Astronotus Swainson 1839 (Latini et al. 2016).

Species Kullander & Ferreira, 2006 and *Astronotus crassipinnis* (Heckel, 1840) were recorded around RBSH; they were the first to evidence declining species richness, as well as biomass and ecosystem functions associated with them (Leal et al. 2021). However, among the Cichlids, *G. Sveni* was the most representative in the study area of this research and its occurrence can be associated with the aquarium trade (Ota et al. 2018).

Species *Potamotrygon amandae* is widely distributed in Paraná-Paraguay basin (Loboda & Carvalho, 2013); this species can also be mentioned as example of occupation in upper Paraná River basin, due to the submergence of "Sete Quedas". *Potamotrygon* Garman, 1877 has significant medical importance since its sting is dangerous to human health (Haddad Júnior 2003, Moreira & Vidal 2022). We emphasize that it was not possible to identify an individual of *Potamotrygon* at the species level, due to an atypical color pattern and overlapping characteristics between the species recognized by Ota et al. (2018) for the study area. For this reason, we maintain the identification as *Potamotrygon* sp. and further efforts and comparative material are needed to elucidate the taxonomic identity of this individual.

The species popularly known in the region as "piranhas" are another example of non-native species establishment. Although *Serrasalmus marginatus* Valenciennes, 1837 and its congener, *Serrasalmus maculatus* Kner, 1858, compete to each other, *Serrasalmus marginatus* Valenciennes, 1837 recorded higher abundance in the investigated site, likely because it is more aggressive than its congener (Agostinho et al. 2007, Agostinho & Júlio Jr. 2002). Rodrigues et al. (2018) argue that *S. maculatus* behaves as a competitor, deviating from its preferences for food and reproductive resources of non-native species, which allows its population to persist in the upper Paraná floodplain. Thus, *S. marginatus* remained more abundant (71.1%) than *S. maculatus* after 12 years, at least in the region sampled in the current study.

This pattern of decreasing a native species to the detriment of a nonnative species was also suggested by Ganassin et al. (2021) between the non-native migratory *S. borellii* and its congeneric *Schizodon altoparanae* Garavello & Britski, 1990.

Our record of *Serrapinnus kriegi* (Schindler, 1937) demonstrates that even a well sampled area can open new records and should be monitored. This record represents the first record for the Itaipu reservoir, and the second record in the Upper Paraná Basin (Vicentin et al. 2019). This species was described for the Paraguay River basin, but are currently also recognized for the basins of Lower Paraná and Uruguay Rivers (Miquelarena et al. 2008, Mantinian 2011, Carvajal-Vallejos et al. 2014, Bertaco et al. 2016, Serra et al. 2018). Its origin in the Upper Paraná River basin is still uncertain.

Although the Upper Paraná fish fauna is well-documented (Langeani et al. 2007, Ota et al. 2018), studies focusing on Conservation Units remain scarce. Most studies conducted in Brazilian protected areas address terrestrial ecosystems, a fact that limits freshwater biodiversity protection since, overall, they only cover small stretches of river systems (Azevedo-Santos et al. 2019).

One of the actions capable of helping to preserve sensitive areas lies on strengthening inspections conducted in buffer zones, based on Law n. 9,985, from July 18<sup>th</sup>, 2000, and on the general objective of Decree n. 4,339/2002, which highlights the importance of promoting the conservation, *in situ* and *ex situ*, of biodiversity components, such as genetic, species and ecosystem variability, as well as ecosystem services maintained by biodiversity. Furthermore, the current study can be used as reference to help updating the ichthyofauna in the management plan developed for "Refúgio Biológico de Santa Helena", Brazil.

#### **Supplementary Material**

The following online material is available for this article:

Figure S1 – Species accumulation curve, based on the methodologies adopted to collect fish on the banks of "Refúgio Biológico de Santa Helena", Itaipu Reservoir, Upper Paraná River Basin, Brazil.

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#### **Author Contributions**

Heleno Brandão: provided substantial contribution to all research stages.

Daniel Rodrigues Blanco: provided substantial contribution to all research stages.

Lucas Emilio Perin Kamfert: provided substantial contribution to all research stages.

Denise Lange: have contributed to data analysis and interpretation; to critical revision; as well as added intellectual content to the current study.

Igor Paiva Ramos: have contributed to data analysis and interpretation; to critical revision; as well as added intellectual content to the current study.

#### **Conflicts of Interest**

The author(s) declare that they have no conflict of interest related to the publication of this manuscript.

#### **Ethics**

Animal Use Ethics Committee (CEUA), Universidade Tecnológica Federal do Paraná, Dois Vizinhos campus- protocolo nº 2016-031.

#### **Data Availability**

The data that supporting in the current this study is openly available in Dataverse (https://data.scielo.org/dataverse/brbn) at (https://doi. org/10.48331/scielodata.WG8LBJ).

Observation to Dataverse: Submitted for Review – The draft version of this dataset is currently under review prior to publication.

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# Wood-inhabiting corticioid and poroid fungi (Basidiomycota) from Reserva Ecológica da Universidade Estadual de Goiás, a remnant of the Brazilian Cerrado

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Abstract: Corticioid and poroid fungi are traditional morphological groups composed of ligninolytic species. Due to their efficiency in wood decomposition process, many species have great ecological importance, especially in nutrient cycling, as well as for their biotechnological properties. Nevertheless, knowledge about these fungi is scarce in many phytogeographic regions of Brazil, as is the case of the Cerrado, since mycodiversity studies in this biome are mainly focused on areas of the São Paulo state. Here we present the taxonomic inventory of corticioid and poroid fungi from the Reserva Ecológica da Universidade Estadual de Goiás (REC-UEG), a Cerrado remnant in Anápolis, Goiás, Brazil. The area is covered by three typical Cerrado landscapes (cerrado stricto sensu, mesophilic forest, and gallery forest), widely explored for scientific and educational purposes by the academic and regional community which seeks to learn about and preserve its biodiversity. Exsiccates deposited in the fungarium of the Universidade Estadual de Goiás (HUEG-Fungi) were analyzed. They are the result of collections made over 20 years, in approximately 103 ha of the reserve. Samples were characterized macro and microscopically and identified based on specialized literature. 51 species were recognized, which are distributed in 33 genera, 15 families, and five orders. Species were most frequent in forested areas and among them, six are new occurrence records for the Cerrado, nine for the Midwest region, and nine for the Goiás state. These results contribute to increase the knowledge of these fungi in the Cerrado, as well as geographic distribution, and show the relevance of preserving the reserve for the regional Funga representativity.

Keywords: Hymenochaetaceae; inventory; macrofungi; Polyporaceae; wood decayers.

## Fungos corticioides e poroides (Basidiomycota) que habitam madeira da Reserva Ecológica da Universidade Estadual de Goiás, um remanescente do Cerrado Brasileiro

**Resumo:** Fungos corticioides e poroides são assim agrupados com base em aspectos morfológicos e compostos por espécies essencialmente lignícolas. Por sua eficiência no processo de decomposição da madeira, muitas espécies desses grupos apresentam grande importância ecológica, especialmente na ciclagem de nutrientes, além de propriedades para aplicações biotecnológicas. Entretanto, o conhecimento sobre esses fungos é escasso em algumas regiões fitogeográficas do Brasil, como é o caso do Cerrado, uma vez que os estudos da micodiversidade no bioma estão focados principalmente em áreas do estado de São Paulo. Portanto, aqui apresentamos o inventário taxonômico de fungos corticioides e poroides da Reserva Ecológica da Universidade Estadual de Goiás (REC-UEG), um remanescente de Cerrado no município de Anápolis, Goiás, Brasil. A área é formada por três fitofisionomias típicas do Cerrado (cerrado *stricto sensu*, mata mesófila e mata de galeria) e é amplamente explorada para fins científicos e educacionais pela comunidade acadêmica regional, que buscam conhecer e preservar sua biodiversidade. Foram analisadas exsicatas depositadas no fungário da Universidade Estadual de Goiás (HUEG-Fungos), cujo acervo é fruto de coletas realizadas ao longo de 20 anos nos cerca de 103 hectares da reserva. As amostras foram caracterizadas macro e microscopicamente e identificadas com base na literatura especializada. Foram reconhecidas 51 espécies, distribuídas em 33 gêneros, 15 famílias e cinco ordens. As espécies são mais frequentes em áreas de mata na reserva e entre elas seis configuram novos registros de ocorrência

para o Cerrado, nove para região Centro-Oeste e nove para o estado de Goiás. Desse modo, esses resultados contribuem para ampliar o conhecimento desses fungos no Cerrado, assim como da distribuição geográfica das espécies, além de mostrar a importância da preservação da reserva para a representatividade da Funga regional. *Palavras-chave: Hymenochaetaceae; inventário; macrofungos; Polyporaceae; decompositores de madeira.* 

#### Introduction

Brazil is a forest country, with approximately 58% of its territory covered by natural and planted forests (SNIF 2016). It is known that the large availability of woody resources in tropical forests promotes the presence of several species of macrofungi, as they are predominantly lignocellulolytic organisms (Zmitrovich et al. 2015, Medeiros et al. 2015).

Fungi that are associated with this substrate at some stage in their life cycle are named "wood-inhabiting fungi". The main diversity of wood-inhabiting fungi is represented by some groups of Basidiomycota (Zmitrovich et al. 2015). The decomposition of woody substrates by these fungi is possible due to enzyme production that degrades the constituents of wood (Lundell et al. 2010). For this reason, some species have been used in biotechnological processes to obtain new sources of bioproducts and in bioremediation activity (Salvachúa et al. 2013, Olicón-Hernández et al. 2017, Grassi et al. 2018, Wehaidy et al. 2018).

Within the phylum Basidiomycota, several groups are traditionally defined according to morphological criteria and life habits (Ghobad-Nejhad 2011). Among these are the corticioid and poroid fungi, which are characterized by annual or perennial, resupinate to stipitate basidiomata and exposed hymenium. The resupinated habit (usually) is characteristic of corticioid fungi, while the presence of pores (and variants) on the hymenium is found in poroid fungi (Ryvarden 2004, Larsson 2007). They have worldwide distribution (He et al. 2019) and in Brazil, they occur in all six biomes (Maia et al. 2015). Most of these occurrence records come from long-term surveys, inventories, research made in important remnants of these biomes, or environmental protection areas (conservation units) (Bononi 1984, Bononi et al. 2008, Drechsler-Santos et al. 2013, Motato-Vásquez et al. 2015, Bononi et al. 2017, Xavier et al. 2018).

In the Cerrado (Brazilian savanna), one of the richest and most threatened biomes in the world (Myers et al. 2000, Lahsen et al. 2016, Colli et al. 2020), inventories of corticioid and poroid fungi started in the 1960s, mainly focused on areas in the state of São Paulo (Fidalgo et al. 1965). Since that, research was conducted in other regions of the biome within the states of Goiás (Leonardo-Silva et al. 2020) and Mato Grosso do Sul (Bononi et al. 2017). However, the lack of species inventories in large areas leads to a significant gap in knowledge about the presence and distribution of the taxa.

Over two decades, collections have been made frequently in the Reserva Ecológica da Universidade Estadual de Goiás (REC-UEG), a remnant of Cerrado, located in Central Brazil. These samples are the result of academic-scientific activities carried out by both undergraduate and graduate students, also educational and recreational activities focused on environmental education for elementary school students. The collected species are presented in this study and compose the inventory of corticioid and poroid fungi from the REC-UEG, contributing to increase the knowledge about these fungi groups around the Cerrado and Midwest regions of Brazil.

#### **Material and Methods**

#### 1. Study area

The REC-UEG is located in the Campus Central-Sede da Universidade Estadual de Goiás, Anápolis, Goiás, Brazil (Figure 1). It comprises 134 ha while 103 ha is covered by the reserve. The REC-UEG is limited by the University Campus (north), the agro-industrial district of Anápolis (south), rural properties and cargo airport (east), and clothing industries (west).

The region's weather is classified as tropical Cwb type according to Köppen-Geiger climate classification, with a dry cold season (April to September) and a rainy warm season (October to March). The average annual temperature is 25 °C, altitude between 1000 and 1200 m (Cardoso et al. 2014). The area is composed almost entirely of savanna native vegetation (cerrado stricto sensu) and forest type (mesophilic forest or semideciduous dry forest and gallery forest) (Figure 2), which Myrtaceae, Rubiaceae, Leguminosae, and Asteraceae are the most dominant families. The cerrado stricto sensu has a shrub-arboreal vegetation characteristic of the phytophysiognomy. The mesophilic forest is observed as denser vegetation, where plant species are predominant with various levels of deciduousness in the dry season and is not associated with watercourses. The gallery forest is also composed of dense vegetation and evergreen following small rivers and stream courses (Ribeiro & Walter 2008). Lastly, a vegetation corridor is formed over the Barreiro stream inside the reserve.

Due to the strong environmental impact and reduction of native biodiversity caused by anthropic actions, in 2016 an area management plan was proposed by UEG. Thus, the reserve represents a means to preserve and conserve local biodiversity, native vegetation, springs, and waterways in the area encouraging academic-scientific activities; restoration of degraded areas, recompose native vegetation, and promote environmental education activities including both university community and the regional population.

#### 2. Data collection and analysis

Collections were carried out randomly between 2001 and 2021, in and around REC-UEG. All basidiomata found in wood and leaf litter were photographed and we took information, such as substrate type (living or dead wood) and environment (phytophysiognomy). Preservation and herborization of collected material followed the standard techniques for fungi (Gadelha-Neto et al. 2013) and were deposited at the fungarium of the Universidade Estadual de Goiás (HUEG-Fungi) (Thiers 2021 [continuously updated]).

The dried material was identified taxonomically by macro and microscopic analysis using relevant taxonomic identification keys (Ryvarden 2001, Núñez & Ryvarden 2001, Ryvarden 2004, 2015, 2016, Țura et al. 2008, Abrahão et al. 2009, Gomes-Silva et al. 2010, Nogueira-Melo et al. 2012, Zmitrovich et al. 2012, Gorjón 2020). For macroscopic characters, we considered the shape, consistency, texture, color, dimension, hymenophore morphology, and the number

#### Corticioid and poroid fungi in Central Brazil



Figure 1. Location of the study area showing typical Cerrado vegetation where the samples were collected in the Reserva Ecológica da Universidade Estadual de Goiás (REC-UEG), Goiás, Brazil.



Figure 2. Phytophysiognomies of the collection area in the rainy season of the Reserva Ecológica da Universidade Estadual de Goiás (REC-UEG), Goiás, Brazil. A-C: Cerrado *stricto sensu*. D-F: Mesophilic Forest. G-I: Gallery Forest.

of pores per mm (in poroid species) of basidiomata. For observations and measurements of microscopic characters, freehand sections were made from dried basidiomata and mounted in 2% potassium hydroxide (KOH) and 1% phloxine (Teixeira 1995). The hyphal system, basidia, basidiospores, and cystidia were observed in Olympus CX31 optical microscope while measurements were performed using the Piximètre software version 5.10 R 1541 (Henriot & Cheype 2017). Melzer's reagent and cotton blue were used to test the amyloid or dextrinoid and cyanophilic reactions of the microscopic structures, respectively. The color classification was based on Kornerup & Wansher (1978). Nomenclature and classification system followed Index Fungorum (http://www.indexfungorum.org) and Mycobank (https://www. mycobank.org/) databases. Global Geographical distribution was based on recent literature, and, in Brazil, we used the List of Brazilian Algae, fungi, and plants (http://floradobrasil.jbrj.gov.br).

We performed the interpolation and extrapolation curve for the data for the area. The curve was based on specimen's abundance (Hill number q = 0; 95% confidence interval), and the extrapolation estimated for double sample size (Chao et al. 2014). The analysis was performed using the iNEXT package (Hsieh et al. 2016) in R software version 3.6.1 (R Core Team 2017) and RStudio environment version 1.2.1335 (RStudio Team, 2019).

### Results

We found 253 specimens, 51 species, distributed in 33 genera, 15 families, and five orders (Figure 3). Polyporales (39 species) and Hymenochaetales (6 species) were the most representative orders, comprising 88% of the total. Polyporaceae was the most frequent family (47% of occurrences; 24 species), followed by Hymenochaetaceae (10%; 5 species), Ganodermataceae (8%; 4



Figure 3. Distribution of corticoid and poroid fungi specimens recorded in the Reserva Ecológica da Universidade Estadual de Goiás (REC-UEG), Goiás, Brazil, according to order (A), family (B), genus (C) and occurrence (D).



Figure 4. Accumulation curve and extrapolation with 95% confidence interval (shaded area) of corticoid and poroid fungi in the Reserva Ecológica da Universidade Estadual de Goiás (REC-UEG), Goiás, Brazil.

species), and Panaceae (6%; 3 species). *Trametes* was the bestrepresented genus (12%; 6 species) and the most common species with 10 or more occurrences are *Funalia caperata*, *Lentinus berteroi* (both with 9.5%; 24 specimens), *Pycnoporus sanguineus* (8%; 20 specimens), *Coriolopsis floccosa*, *Favolus brasiliensis* (both with 6%; 15 specimens), *Hymenochaete rheicolor*, *Polyporus tricholoma* (both with 4.7%; 12 specimens), and *Hexagonia variegata* (4.3%; 11 specimens) (Figure 3). Six of the sampled species are new occurrences for the Cerrado, nine for the Midwest region, and nine for the state of Goiás. We observed that 98% of the species occurred in forest formations, and the rarefaction and extrapolation curve suggest that sampling in the area was satisfactory, although new collections indicate an increase in diversity (Figure 4).

The list of corticioid and poroid fungi species occurring in the REC-UEG is described below. Following we provide data on substrates, occurring phytophysiognomy, and fungarium voucher of each species, as well as taxonomic remarks of those cited for the first time for the

Cerrado or with nomenclatural conflicts. An asterisk (\*) before the name of the species indicates that the taxon is reported for the first time for the Cerrado, two asterisks (\*\*) Midwestern region, or three asterisks (\*\*\*) Goiás state.

Agaricales Schizophyllaceae

#### Schizophyllum commune Fr.

Description: Cooke (1961). Substrate: dead wood. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 3989, 4721, 8126, 8133, 8606, 9615, 10646.

#### \*\*Schizophyllum umbrinum Berk.

Description: Cooke (1961). Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: 8613.

#### Gloeophyllales Gloeophyllaceae

#### Gloeophyllum striatum (Fr.) Murrill

Basionym: *Daedalea striata* Fr. Description: Núñez & Ryvarden (2001). Substrate: dead wood. Phytophysiognomy: gallery forest. Material examined HUEG: 159, 10799, 15108.

Hymenochaetales Hymenochaetaceae

*Fuscoporia callimorpha* (Lév.) Groposo, Log.-Leite & Góes-Neto Basionym: *Polyporus callimorphus* Lév. Description: Groposo et al. (2007). Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: 8531, 8533, 8567, 10775.

Fuscoporia gilva (Schwein.) T. Wagner & M. Fisch. Basionym: Boletus gilvus Schwein.
Description: Ryvarden (2004) as Phellinus gilvus (Schwein.) Pat. Substrate: dead wood.
Phytophysiognomy: gallery forest.
Material examined HUEG: 4720, 8552.

 \*\*Hymenochaete damicornis (Link) Lév. Basionym: Stereum damicorne Link. Description: Parmasto (2001).
 Substrate: leaf litter. Phytophysiognomy: mesophilic forest. Material examined HUEG: 1573, 15109.

\*\*\*Hymenochaete iodina (Mont.) Baltazar & Gibertoni Basionym: Polyporus iodinus Mont.
Description: Ryvarden (2004) as Cyclomyces iodinus (Mont.) Pat. Substrate: dead wood.
Phytophysiognomy: gallery forest.
Material examined HUEG: 4020, 10708.

Hymenochaete rheicolor (Mont.) Lév. Basionym: Stereum rheicolor Mont. Description: Parmasto (2001).
Substrate: living and dead wood. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 4030, 9305, 10639, 14098, 14602, 14626, 14628, 14639, 14646, 14647, 15110, 15111.

#### Incertae sedis

Trichaptum perrottetii (Lév.) Ryvarden Basionym: Trametes perrottetii Lév. Description: Ryvarden (2016).
Substrate: dead wood.
Phytophysiognomy: mesophilic forest.
Material examined HUEG: 10765.

Polyporales Fomitopsidaceae

Daedalea ryvardeniana Drechsler-Santos & Robledo Description: Drechsler-Santos et al. (2012).
Substrate: dead wood.
Phytophysiognomy: gallery forest and mesophilic forest.
Material examined HUEG: 4022, 4432, 4477, 4772, 4982, 10732.

Ganodermataceae

 Amauroderma aurantiacum (Torrend) Gibertoni & Bernicchia Basionym: Ganoderma aurantiacum Torrend.
 Description: Ryvarden (2004).
 Substrate: leaf litter.
 Phytophysiognomy: mesophilic forest.
 Material examined HUEG: 15126, 15127, 15128, 15129.

*Amauroderma calcigenum* (Berk.) Torrend Basionym: *Polyporus calcigenus* Berk. Description: Ryvarden (2004). Substrate: leaf litter. Phytophysiognomy: mesophilic forest. Material examined HUEG: 10640, 15123, 15124, 15125.

#### Ganoderma multiplicatum (Mont.) Pat.

Basionym: *Polyporus multiplicatus* Mont. Description: Ryvarden (2004). Substrate: dead wood. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 11881, 15134.

#### Ganoderma testaceum (Lév.) Pat.

Basionym: *Polyporus testaceus* Lév. Description: Bhosle et al. (2010). Substrate: dead wood. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 4367, 10659, 10685, 10781.

#### Incertae sedis

\**Rickiopora latemarginata* (Rick) Westph., Tomšovský & Rajchenb. (Figure 5A).

Basionym: *Daedalea latemarginata* Rick. Description: Westphalen et al. (2016). Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: 10643.

Remarks: The genus *Rickiopora* Westph., Tomšovský & Rajchenb. was described by Westphalen et al. (2016) to accommodate the species *Daedalea latemarginata* and *Antrodiella angulatopora* Ryvarden, previously considered synonymous (Rajchenberg 1987), in *R. latemarginata*. The species is characterized by pileate to effused-reflex basidiomata, rigid and curled when dried, poroid hymenophore with larger angular to irregular pores (2–4 per mm), sometimes forming daedaloid to hydnoid areas in old, dried specimens; monomitic to pseudo-dimitic hyphal system, and subglobose, hyaline, smooth, thin-walled basidiospores.

Our specimen was found only once in the collection area, even after years of sampling, growing on dead wood from an unidentified angiosperm. Currently, *R. latemarginata* is recorded in Argentina, Brazil, Costa Rica, and Venezuela (Rajchenberg 1987, Ryvarden 2015, Westphalen et al. 2016). Previously cited for Brazil in the Amazonia and Atlantic Forest biomes (Maia et al. 2015, Motato-Vásquez et al. 2015), the occurrence in the present study is the first for the Cerrado.

#### Irpicaceae

\*\*\* Gloeoporus thelephoroides (Hook.) G. Cunn. Basionym: Boletus thelephoroides Hook. Description: Ryvarden (2015). Substrate: dead wood. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 4010, 4717, 8524, 8525, 8560, 10730, 14631.

## \*\*\* Vitreoporus dichrous (Fr.) Zmitr.

Basionym: *Polyporus dichrous* Fr. Description: Ryvarden (2015) as *Gloeoporus dichrous* (Fr.) Bres. Substrate: dead wood. Phytophysiognomy: gallery forest. Material examined HUEG: 4773, 10736.



Figure 5. Species cited for the first time in the Cerrado. *Rickiopora latemarginata* (A). *Auriscalpium villipes* (B) with velutine pilear surface near the union with the stipe (C) and hydnoid hymenial surface (D). *Climacodon pulcherrimus* (E) and hydnoid hymenial surface (F). *Perenniporiella micropora* (G) and poroid hymenial surface (H). *Trametes psila* (J) and poroid hymenial surface (I). *Trametes marianna* (K) and poroid hymenial surface (L). Bar = 1 cm (A, B, E, G, J, K); 1 mm (C, D, F, H, I, L).

#### Meripilaceae

 \*\*Rigidoporus microporus (Sw.) Overeem Basionym: Boletus microporus Sw. Description: Ryvarden (2016).
 Substrate: dead wood.
 Phytophysiognomy: mesophilic forest.
 Material examined HUEG: 10798.

#### Meruliaceae

 \*Climacodon pulcherrimus (Berk. & M.A. Curtis) Nikol. (Figure 5E, F). Basionym: Hydnum pulcherrimum Berk. & M.A. Curtis. Description: Moreno et al. (2007). Substrate: dead wood. Phytophysiognomy: gallery forest. Material examined HUEG: 10626.

Remarks: *Climacodon pulcherrimus* is characterized by the dimidate and flattened basidioma; pilear surface light orange (5A4), finely tomentose; hymenial surface light orange (5A4) becoming

reddish orange (7A8) in some parts, hydnoid, spines up to 4 mm long, 2–5 per mm; basidiospores ellipsoid, hyaline, smooth, thin-walled (4)  $4.6 - 5.6 (6.7) \times (1.8) 2 - 3 (3.1) \mu m$ . We found our species strongly attached to decaying wood near the stream. Interestingly, after a long herborization period, some regions of the hymenial surface show darker regions (caramelized appearance). *Climacodon pulcherrimus* has a cosmopolitan distribution (Bononi 1979, Moreno et al. 2007) and, in Brazil, occurs in the Amazonia and Atlantic Forest biomes (Maia et al. 2015), and is now cited for the first time for the Cerrado.

#### Panaceae

Cymatoderma caperatum (Berk. & Mont.) D.A. Reid Basionym: Thelephora caperata Berk. & Mont. Description: Welden (1960).
Substrate: dead wood and leaf litter. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 4003, 4099, 8582, 9307, 10619, 10766, 10767.  \*\*\*Cymatoderma dendriticum (Pers.) D.A. Reid Basionym: Thelephora dendritica Pers. Description: Welden (1960).
 Substrate: dead wood.
 Phytophysiognomy: mesophilic forest.
 Material examined HUEG: 8568, 8576, 14634.

#### Panus strigellus (Berk.) Overh.

Basionym: *Lentinus strigellus* Berk. Description: Ryvarden (2015). Substrate: dead wood. Phytophysiognomy: gallery forest. Material examined HUEG: 2245, 8614.

#### Phanerochaetaceae

\*\*\**Phlebiopsis amethystea* (Hjortstam & Ryvarden) Chikowski & C.R.S. Lira

Basionym: *Porostereum amethysteum* Hjortstam & Ryvarden. Description: Hjortstam & Ryvarden (1990). Substrate: dead wood. Material examined HUEG: 8138.

#### Polyporaceae

Coriolopsis floccosa (Jungh.) Ryvarden Basionym: Polyporus floccosus Jungh. Description: Ryvarden & Johansen (1980). Substrate: dead wood. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 4034, 8129, 8130, 8523, 8538, 8547, 8550, 8556, 10707, 10718, 14567, 14576, 14580, 14582, 14601.

 \*\*Earliella scabrosa (Pers.) Gilb. & Ryvarden Basionym: Polyporus scabrosus Pers. Description: Ryvarden (2015). Substrate: dead wood.
 Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 1698, 3990, 3996.

#### \*\*Echinochaete brachypora (Mont.) Ryvarden Basionym: Polyporus brachyporus Mont. Description: Ryvarden (2015). Substrate: dead wood. Phytophysiognomy: gallery forest. Material examined HUEG: 10688.

#### Favolus brasiliensis (Fr.) Fr.

Basionym: *Daedalea brasiliensis* Fr.
Description: Palacio et al. (2021).
Substrate: living and dead wood.
Phytophysiognomy: cerrado *stricto sensu*, gallery forest, and mesophilic forest.
Material examined HUEG: 2230, 4775, 4974, 8124, 8520, 8534, 8569, 8580, 10630, 10652, 10743, 10768, 14094, 14622, 15112.

## Fomes fasciatus (Sw.) Cooke

Basionym: *Boletus fasciatus* Sw. Description: Ryvarden (2015). Substrate: dead wood. Phytophysiognomy: gallery forest. Material examined HUEG: 8546, 11435. Funalia caperata (Berk.) Zmitr. & Malysheva Basionym: Polyporus caperatus Berk.
Description: Ryvarden & Johansen (1980) as Coriolopsis caperata (Berk.) Murrill.
Substrate: dead wood.
Phytophysiognomy: gallery forest and mesophilic forest.
Material examined HUEG: 3994, 4031, 8526, 8528, 8548, 8551, 8558, 8559, 8563, 8573, 10616, 10723, 14569, 14572, 14574, 14575, 14588, 14591, 15115, 15116, 15117, 15118, 15119. 15120.

#### Hexagonia hydnoides (Sw.) M. Fidalgo

Basionym: *Boletus hydnoides* Sw. Description: Ryvarden (2015). Substrate: dead wood. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 8147, 8154, 8156, 8157, 8541, 8555, 10627, 10722, 14624.

#### Hexagonia variegata Berk.

Description: Ryvarden (2015) as *H. papyracea* Berk. Substrate: living and dead wood. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 4774, 8127, 8536, 8544, 8564, 10699, 10734, 14155, 14640, 15113, 15114.

#### Lentinus berteroi (Fr.) Fr.

Basionym: *Agaricus berteroi* Fr. Description: Ryvarden (2015). Substrate: dead wood. Phytophysiognomy: cerrado *stricto sensu*, gallery forest, and mesophilic forest. Material examined HUEG: 4018, 4465, 4760, 4968, 8132, 8137, 8150, 8506, 8516, 8591, 8602, 10609, 10629, 10755, 10770, 10789, 11433, 14607, 14609, 14610, 14613, 14615, 14617, 14618.

#### Lentinus velutinus Fr.

Description: Ryvarden (2015). Substrate: dead wood. Material examined HUEG: 8530.

#### \*\*Microporellus obovatus (Jungh.) Ryvarden

Basionym: *Polyporus obovatus* Jungh. Description: Ryvarden (2015) as *Flabellophora obovata* (Jungh.) Corner. Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: 14632.

Neodictyopus dictyopus (Mont.) Palacio, Robledo & Drechsler-Santos Basionym: Polyporus dictyopus Mont.
Description: Ryvarden (2016) as Po. dictyopus.
Substrate: living and dead wood.
Phytophysiognomy: gallery forest and mesophilic forest.
Material examined HUEG: 4724, 4747, 8532, 8578, 14092, 14592, 15122.

Remarks: *Polyporus dictyopus* was placed in *Neodictyopus* Palacio, Robledo, Reck & Drechsler-Santos based on morphological and phylogenetic analyses (Palacio et al. 2017), and recently transferred to *Picipes* Zmitr. & Kovalenko by Ji et al. (2022). Despite that, we will use *N. dictyopus* as the current name since Ji et al. (2022) did not include South American specimens of the specie in their analyses. \*\*\* Perenniporia martia (Berk.) Ryvarden Basionym: Polyporus martius Berk. Description: Ryvarden (2016).
Substrate: dead wood.
Phytophysiognomy: gallery forest.
Material examined HUEG: 8549, 10645.

\**Perenniporiella micropora* (Ryvarden) Decock & Ryvarden (Figure 5G, H).

Basionym: *Perenniporia micropora* Ryvarden. Description: Decock & Ryvarden (2003). Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: 10641.

Remarks: The genus *Perenniporiella* was proposed in 2003 by Decock and Ryvarden segregated from *Perenniporia* Murrill (Decock & Ryvarden 2003). Currently, the genus has six species and *P. micropora* differs from the others by the thin, flexible, effused reflexed basidioma, smaller pores, circular to irregular, 8–10 per mm, and basidiospores globose, thick-walled (4.4)  $4.5 - 5.6 (5.8) \times (3) 3.1 - 4.4 (4.5) \mu m$ . The species has been recorded in Belize, Brazil, Costa Rica, Cuba, and Peru (Decock & Ryvarden 2003, Drechsler-Santos et al. 2015). In Brazil, it is cited for the Amazonia and Atlantic Forest biomes (Drechsler-Santos et al. 2015, Maia et al. 2015) and the occurrence reported here is the first for the Cerrado.

#### Polyporus guianensis Mont.

Description: Ryvarden (2016). Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: 8575, 8581, 9308, 14088, 14093, 15121.

#### \*\*Polyporus leprieurii Mont.

Description: Ryvarden (2016). Substrate: dead wood. Phytophysiognomy: mesophilic forest and gallery forest. Material examined HUEG: 2255, 4014.

#### Polyporus tricholoma Mont.

Description: Ryvarden (2016). Substrate: dead wood. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 8565, 8566, 8570, 8579, 10642, 10667, 10716, 10759, 10795, 14099, 14598, 14599.

#### Pycnoporus sanguineus (L.) Murrill.

Basionym: *Boletus sanguineus* L. Description: Ryvarden (2016). Substrate: living and dead wood. Phytophysiognomy: gallery forest and mesophilic forest. Material examined HUEG: 8135, 8155, 8158, 8159, 8504, 8505, 8507, 8508, 8535, 8537, 8554, 10621, 10647, 10729, 10731, 10733, 10751, 10782, 10784, 14585.

\*\*\* Trametes elegans (Spreng.) Fr. Basionym: Daedalea elegans Spreng. Description: Ryvarden (2016). Substrate: dead wood. Phytophysiognomy: gallery forest. Material examined HUEG: 8134, 8140, 8542, 10636, 14649. \*Trametes marianna (Pers.) Ryvarden (Figure 5K, L). Basionym: Polyporus mariannus Pers. Description: Ryvarden (2016). Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: HUEG 10769.

Remarks: *Trametes marianna* is characterized by the pileate, flattened, semicircular to flabeliform basidioma; pilear surface light orange (5B4) to light brown (5D4), concentrically zoned with sulcate zones; hymenial surface greyish orange (5B3) to brownish orange (5C3), pores circular to irregular, 6–7 per mm; basidiospores cylindrical to ellipsoid, hyaline, smooth, thinwalled (6.5)  $7.4 - 9.4 (10.2) \times 4 - 5.1 (5.8) \mu m$ . A tropical species (Ryvarden 2016) and, in Brazil, occurs in Amazonia and Atlantic Forest biomes (Maia et al. 2015) and is now cited for the first time for the Cerrado.

Trametes pavonia (Hook.) Ryvarden Basionym: Boletus pavonius Hook.
Description: Ryvarden (2016).
Substrate: dead wood.
Phytophysiognomy: gallery forest and mesophilic forest.
Material examined HUEG: 10735, 10739, 10791.

Remarks: *Trametes pavonia* (Hook.) Ryvarden is an illegitimate name because this binomial was already used since 1851: *T. pavonia* (Berk.) Fr [= *T. elegans* (Spreng.) Fr.]. Despite that, we have chosen to use the name since some authors have frequently used it as current. Although the focus of our paper is to explore the fungal diversity in the study area, and not to solve nomenclatural problems of specific taxa, we point out that a new name should be proposed for the species after a review of the type material.

\*\*\* Trametes polyzona (Pers.) Justo

Basionym: *Polyporus polyzonus* Pers. Description: Núñez & Ryvarden (2001) as *Coriolopsis polyzona* (Pers.) Ryvarden. Substrate: dead wood. Material examined HUEG: 8128.

\*Trametes psila (Lloyd) Ryvarden (Figure 5I, J). Basionym: Fomes psila Lloyd. Description: Nogueira-Melo et al. (2012) as Coriolopsis psila (Lloyd) Ryvarden. Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: 4035, 10676.

Remarks: A dense layer of thick, matted, light orange (6A5) to reddish brown (8D4) tomentum covering the pileus and small pores (6–7 per mm) invisible to the naked eye on the hymenial surface are characteristic of the species. *Trametes psila* was described in 1915 by Lloyd as *Fomes psila* Lloyd from material collected in Brazil and, currently, it is also recorded in Mexico. In Brazil, its occurrence was known for the Amazon and Atlantic Forest biomes (Nogueira-Melo et al. 2012), and the record of the present study is the first for the Cerrado. \*\*\*Trametes versicolor (L.) Lloyd Basionym: Boletus versicolor L. Description: Ryvarden (2016). Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: 8131.

#### Steccherinaceae

Antrodiella versicutis (Berk. & M.A. Curtis) Gilb. & Ryvarden Basionym: Polyporus versicutis Berk. & M.A. Curtis. Description: Ryvarden (2015).
Substrate: living wood.
Phytophysiognomy: gallery forest.
Material examined HUEG: 10625.

#### Russulales

Auriscalpiaceae

 \*Auriscalpium villipes (Lloyd) Snell & E.A. Dick (Figure 5B-D). Basionym: Hydnum villipes Lloyd. Description: Ryvarden (2001). Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: 14876.

Remarks: *Auriscalpium* is a genus described by Gray in 1821 based on *Hydnum auriscalpium* L. Currently, the genus comprises 10 widely distributed species, some of which are known to grow on pinecones (Ryvarden 2001, Wang & Yang 2019). Of these, *A. villipes* is characterized by the central or laterally stipitate basidioma, flabelliform to reniform pileus; pilear surface greyish orange (5B4) to light bown (5D5), velutine near the union with the stipe, becoming glabrous towards the margin; hymenial surface concolor to pilear surface, hydnoid, spines up to 80 mm long, stipe cylindrical, velutine to tomentose; dimitic hyphal system and basidiospores ellipsoid, hyaline and finely ornamented  $(3.8) 4.1 - 4.9 (5.1) \times (3) 3.3 - 3.9$ (4.3) µm. It is a species of neotropical distribution (Ryvarden 2001, Wang & Yang 2019) and the only one of the genus that occurs in Brazil. The records in the country come from studies carried out in the Atlantic Forest (Gibertoni et al. 2004), which is the first record for the Cerrado biome.

#### Stereaceae

\*\*Stereum hirsutum (Willd.) Pers. Basionym: Thelephora hirsuta Willd. Description: Tura et al. (2008). Substrate: dead wood. Phytophysiognomy: mesophilic forest. Material examined HUEG: 8522, 8561.

\*\*Stereum ostrea (Blume & T. Nees) Fr. Basionym: Thelephora ostrea Blume & T. Nees. Description: Chamuris (1988). Substrate: dead wood. Material examined HUEG: 4098.

#### Discussion

The corticioid and poroid Funga of the Cerrado is historically recognized as one of the less studied in the country, a result of poor sampling efforts and few trained taxonomists in the region. According to our recent studies 223 species are known in the biome and the present inventory has about 19% of these species. Furthermore, these records add 24 new species known in Goiás and rank the state as the second richest in corticioid and poroid fungi in the Cerrado, just behind the state of São Paulo.

The diversity of these fungal groups in the REC-UEG is higher in the number of families, genera, and species than those recorded by other inventories of Cerrado macrofungi that included the same taxa (Quevedo et al. 2012, Bononi et al. 2017, Leonardo-Silva et al. 2020). Although the area is formed by a fragment of the biome and part of it has been deforested by anthropic actions, its species richness may be influenced by the varied vegetation found in the Cerrado physiognomic forms, especially the forest formations, and the sampling period, showing the importance of long-term studies to evidence the regional diversity.

Although there is a wide variety of wood-inhabiting corticioid and poroid fungi species, most belong to the orders Hymenochaetales and Polyporales (Kirk et al. 2008). Both orders have species widely distributed worldwide and are known for their wood degrading ability (Lundell et al. 2010, He et al. 2019). These fungi obtain their energy demands by metabolizing the constituents of wood, living or dead, such as cellulose and lignin. This process is only possible due to the broad enzymatic profile of these species, evidencing the potential for biotechnological applications (Zmitrovich et al. 2015, El-Gendi et al. 2022). Currently, some genera and species found in the corticioid and poroid Funga of the REC-UEG are already considered as having potential for biotechnological processes. Trametes and Polyporus are largely used (or studied) for obtaining enzymes and degrading potential environmental pollutants (Cruz-Morató et al. 2013, Olicón-Hernández et al. 2017, Wehaidy et al. 2018). In addition, previous studies focusing on biotechnological aspects of some species from the reserve have shown potential results (Leonardo-Silva et al. 2018, Naves et al. 2019).

Species widely distributed in Brazil (Maia et al. 2015) also dominated the data recorded at the REC-UEG. On the other hand, 32% of the low-occurrence species in the area, including all the new records reported here, may be related to substrate specificity; production of inconspicuous basidiomata, especially the corticioid fungi; physiological and nutritional aspects of each species for basidioma development, which reduce their sampling on the field. The higher richness found in forest formations was expected since this vegetation presents ideal environmental conditions and varied substrate availability for fungi growth. Differently, the herbaceous vegetation of cerrado *stricto sensu* exposes the community to high temperatures, low humidity levels, and the entrance of winds, reducing the growth and colonization of species that are more sensitive to these climatic variations.

Although the REC-UEG suffers a strong environmental impact due to its location, it is still possible to observe expressive biodiversity that resists. Besides the richness of corticioid and poroid fungi that we reported, previous studies in the area also presented new occurrences for the Cerrado (Alvarenga & Xavier-Santos 2017, Camilo-Cotrim et al. 2020, Ferreira-Sá et al. 2023). Thus, the number of specimens collected over the years, as well as the species richness shows the importance of preservation for regional Funga representativeness. Ditto, it is necessary to establish measures to protect the area, which is also used as a didactic resource by graduate, undergraduate and elementary school students who carry out research activities and educational excursions. In addition, some species collected in the area have been identified, conserved *ex situ*, and represent part of the genetic and biotechnological heritage of the Cerrado.

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## **Author Contributions**

Lucas Leonardo-Silva: Substantial contribution in the concept and design of the study, to data collection, analysis, and interpretation; to manuscript preparation.

Geovane Pereira-Silva: Contribution to data collection, analysis, and interpretation.

Izabel Cristina Moreira: Contribution to data collection and manuscript preparation.

Robson Bernardo Silveira-Silva: Contribution to data collection and manuscript preparation.

Solange Xavier-Santos: Substantial contribution in the concept and design of the study; Contribution to data collection and critical revision, adding intellectual content.

## **Conflicts of Interest**

The authors declare that they have no conflict of interest related to the publication of this manuscript.

## **Data Availability**

The data resulting from this research has been archived in the public data repository Biota Neotropica Dataverse: https://doi.org/10.48331/scielodata.ELHOOR.

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## Fish defaunation in reservoirs of the Lower Paranapanema River basin, Brazil

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*Abstract:* Until now no study has used a defaunation index to quantify the decline of Neotropical freshwater fishes in environments fragmented by dams and reservoirs. So, we applied this index to 143 native fish in five reservoirs in the Lower Paranapanema River, that is situated in one of the Brazilian aquatic environments most impacted by anthropic degradation. Fish species were classified according to their functional groups, which were selected according to the biological characteristics that may reflect in defaunation events. The biggest reservoir in area with more tributaries and forest cover showed lowest defaunation index. The functional groups of fishes more affected by defaunation included species characterized by periphytivores, invertivores and algivores, non-migratory habit, with external fertilization, and parental care. Although reservoirs have different characteristics, this method can be tested in any other hydrographic basin. The results suggested continued conservation efforts to preserve the integrity of tributaries and the native fishes in reservoirs and pointed out the importance of maintaining native vegetation cover and fish restocking programs in the reservoirs with the highest defaunation values. Our finding can be use as the first data source for future studies using this defaunation index.

Keywords: anthropogenic impact; functional group; fish fauna loss; impoundment; land use.

#### Defaunação de peixes em reservatórios do baixo rio Paranapanema, Brasil

**Resumo:** Até o momento nenhum estudo utilizou um índice de defaunação para quantificar o declínio de peixes neotropicais de água doce em ambientes fragmentados por barragens e reservatórios. Dessa forma, testamos esse índice em 143 espécies nativas em cinco reservatórios do baixo rio Paranapanema, que está localizado em um dos ambientes aquáticos brasileiros mais impactados pela degradação antrópica. As espécies de peixes foram classificadas de acordo com seus grupos funcionais selecionados de acordo com as características biológicas que podem influenciar nos eventos de defaunação. O maior reservatório em área, com mais tributários e maior cobertura florestal apresentou menor índice de defaunação. Os grupos funcionais mais afetados pela defaunação incluíram espécies caracterizadas por hábito alimentar perifitívoro, invertívoro e algívoro, hábito não migratório, com fertilização externa e cuidado parental. Embora os reservatórios tenham características diferentes, esse método pode ser testado em qualquer outra bacia hidrográfica. Os resultados sugerem esforços contínuos para preservar a integridade dos tributários e dos peixes nativos nos reservatórios com maiores valores de defaunação. Nossos dados podem ser utilização como a primeira base de dados para futuros estudos que utilizem o índice de defaunação. **Palavras-chave:** *impacto antropogênico; grupo funcional; perda de ictiofauna; represamento; uso da terra.* 

#### Introduction

The conversion of natural landscapes by fragmentation, habitat loss, direct exploitation, the wide spread of invasive species, hunting and water pollution are the principal anthropogenic drivers of defaunation (Young et al. 2016, Galetti et al. 2021). The main predictors of defaunation at the local scale include quantity of landscape-scale native vegetation cover and rate of habitat conversion (e.g., into agricultural and urban areas). The diversity and composition of the fish assemblages may be changed by interference with hydrography, limnology and land use (Fausch et al. 1990, Orsi & Britton 2014, Ganassin et al. 2021), and these changes are intensified in succession of cascading reservoirs (Agostinho et al. 2007a). The replacement of native vegetation with agriculture increases sediment input (Ryan & Emmett 2002, Wantzen & Mol 2013) and nutrients, which interferes with fish fauna reproduction, feeding, and recruitment (Roy et al. 2003). Among the main services offered by fish is the interaction in the dynamics of the food chain and the cycling of nutrients, which enable the resilience of the ecosystem (Holmlund & Hammer 1999) and trophic effects (Bauer & Hoye 2014), also affected in the defaunation process. The simplification of habitats promoted by reservoirs removes or changes native species environments, creates others favorable to non-native species and to native sedentary species with low economic value and no fishing relevance (Agostinho et al. 2007a), reduces fish access to nursery and feeding grounds (Winemiller et al. 2016) and affecting the composition of the native fish fauna, which is directly related to the conservation of environments free of dams and reservoirs (Marques et al. 2018). Reservoirs also act as an environmental filter for specific functional traits, such as those related to reproduction, feeding and habitat use (Muniz et al. 2021).

The combined result of human actions leads to the impoverishment of the local source of vertebrate fauna, i.e., defaunation (Terborgh 2008). The defaunation index is meant to estimate the loss of species and populations or functional extinction of ecological communities and the decline in the abundance of individuals on a global or local scale (Dirzo & Miranda 1990, Dirzo et al. 2014). This index has been extensively used for mammals such as to compare ecological communities over large zoogeographical regions (Giacomini & Galetti 2013), examine the integrity of site-specific faunas and demonstrate how defaunation is changing the historical configuration of assemblages (Bogoni et al. 2018) and the influence of land use on defaunation (Pereira et al. 2021).

Beside extensive studies have assessed the threat of degraded environments and their impacts on species populations of Neotropical freshwater fish fauna (Meffe & Sheldon 1990, Casatti et al. 2009, Casatti et al. 2012, Cohen et al. 2016, Kopf et al. 2016) a quantitative value such as an index has not been used to estimate the decline, even though it is known that populations of freshwater species are more affected than terrestrial ecosystems (McLellan et al. 2014, Turak et al. 2017, Albert et al. 2021). We aimed to evaluate the fish fauna loss in the habitats fragmented by cascading reservoirs, what allows to compare isolated environments resulting from the blockage of fish movements (Agostinho et al. 2007a, Pelicice et al. 2018), thereby assigning a defaunation value for each reservoir. For this study, we chose the Lower Paranapanema River basin as the model. We also investigated comprehending patterns of defaunation for different functional groups of fishes enables us to understand the extent to which an ecosystem is modified (i.e., dams and land use change), and how its components are threatened is also critical to determine conservation strategies.

## **Material and Methods**

#### 1. Study area

The Paranapanema River is an important, extensively exploited tributary of the Upper Paraná River basin (Maack 2017, Jarduli et al. 2020), which is characterized by high human occupation and intense anthropogenic activities, making this basin the most exploited and fragmented in the Southeast and South regions of Brazil (Agostinho et al. 2007b, Agostinho et al. 2016, ANA 2016). The Paranapanema River basin has an area of 106.500 km<sup>2</sup> and covers 247 municipalities, with around 2.3% of the Brazilian population concentrated in this river basin (five million inhabitants) (ANA 2016). There are currently 11 hydroelectric plants (HEPs) in operation on the main river channel. The Paranapanema River basin is divided into three regions: Upper Paranapanema, Middle Paranapanema and Lower Paranapanema River basins, and they are quite different from each other because they have distinct geomorphological characteristics (Sampaio 1944).

In the Lower Paranapanema River basin, anthropic actions have extensively modified the habitat in this basin as well. The construction of cascade reservoirs changed the hydrographic and limnological characteristics of the basin (Nogueira et al. 2006, Poff et al. 2007, Pelicice et al. 2014), and urban and agricultural/livestock expansion changed land use by the removal of native vegetation (ANA 2016), altering natural habitats (Young et al. 2016). For this study, the sections disconnected by hydroelectric plants were delimited in the drainage area of the five HEPs installed in the Lower Paranapanema River (Figure 1): HEP Rosana (year of completion: 1987), HEP Escola Politécnica - Taquaruçu (1994), HEP Escola Engenharia Mackenzie -Capivara (1977), HEP Canoas I (1999) and HEP Canoas II (1999) (CTG Brasil 2020), the main characteristics of each reservoir area described in Table 1.

#### 2. Data collection and functional groups

A list of native fish fauna in the Lower Paranapanema River basin was confirmed by an extensive search of the available scientific literature. Searches were done in online databases, like Google Scholar, Scielo, Web of Science, Scopus and Eschmeyer's Catalog of Fishes, private libraries and cross-references searches using the keyword 'Paranapanema', combined with the keywords 'fish', 'survey', 'ichthyofauna', 'fish fauna', and 'diversity', and included species descriptions, inventories and ecological studies between 1995 to 2018, presented in the supplementary material (Table S1). The species surveyed in this study were assumed to exist in the Lower Paranapanema River basin, and the list of the presence/absence of species present in each reservoir is presented in the supplementary material, Table S2.

Functional groups were selected according to the biological characteristics of the fish that may reflect defaunation events, and for which information was available in the literature (Table S3), FishBase data (www.fishbase.org) and from specialists. For some species, there is a lack of basic information on their biology and ecology, which supports the choice of these functional groups. The species were categorized according to trophic guild (algivores, periphytivores, insectivores, invertivores, detritivores, herbivores, omnivores or piscivores),



Figure 1. Land use in the Lower Paranapanema River basin, southern Brazil, SP - state of São Paulo, PR - state of Paraná, MS - state of Mato Grosso do Sul.

Table 1. Main features of reservoir of Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River basin, states of São Paulo and Paraná, southern Brazil.

Hydroelectric plant	Perimeter (km)	Drainage area (km <sup>2</sup> )	Main tributaries	Туре
Rosana	433	99,000	Pirapó and Pirapozinho	Run-of-the-river
Taquaruçu	301	88,000	Anhumas, Centenário, Tenente, Capim and Santo Inácio	Run-of-the-river
Capivara	1550	84,500	Tibagi, Capivara, Cinzas and Vermelho	Accumulation
Canoas I	120,3	40,920	Pari and Queixada	Run-of-the-river
Canoas II	98,8	39,556	Alambari	Run-of-the-river

Adapted: Duke Energy (2008); CTG Brasil (2020).

migratory behavior (migratory or non-migratory), fertilization (external or internal) and parental care or not (Table S3).

#### 3. Hydrographic variables and land use

The hydrographic basins were delimited in the drainage area of the Rosana, Taquaruçu, Capivara, Canoas I, and Canoas II reservoirs. Four Shuttle Radar Topographic Mission (SRTM) images were used, which are radar images with spatial resolution of 90 m  $\times$  90 m from EMBRAPA (Brazilian Agricultural Research Corporation) (Miranda 2005) to obtain altimetric data. The images were imported to the QGIS 3.4 software and the delimitation was performed automatically using the TauDEM extension. For the drainage network, secondary data were used in shapefile format provided by ANA (Water and Sanitation National Agency).

For the determination of land use in the study area, we used images from the OLI/Landsat-8 sensor acquired on the United States Geological Survey (USGS) website and processed in the ESRI ArcGIS 10.5 software (ArcGIS trial license). The method used was traditional pixel-based classification. The classes of classification were interpreted and associated with land use and land cover classes: agriculture/pasture, forest cover, reforestation, ground vegetation, non-vegetated areas, water, wetlands and urban infrastructure (Figure 1 and Table S4).

#### 4. Defaunation index and variables

The method we used was previously applied to mammalian defaunation (Bogoni et al. 2018, Benítez-López et al. 2019, Wen et al. 2020), but modifications were made for the freshwater environment scenario. The defaunation index (or  $D_i$ ) (Giacomini & Galetti 2013) was estimated for the entire fish assemblage (i.e., total defaunation per site) and each functional guild/group using the matrix of presence and absence compiled (Table S2). The defaunation index is a weighted measure of dissimilarity between a focal assemblage and a reference assemblage (for example, historical baseline). Our reference assemblage was all the species mentioned in Table S2 and the focal assemblage was the species present in each reservoir, based on the method Giacomini & Galetti (2013) described.

This index ranges from 0 (completely intact) to 1 (completely defaunated), being based on the Bray-Curtis dissimilarity index with a value of importance for the species. In the analysis, we examined levels of defaunation in terms of the species importance value ( $\omega$ ), defined as an intrinsic feature, the body size, and the data for each of the 143 species were from FishBase (Froese & Pauly 2021) (Table S5). In representing  $\omega$ , we assigned adult body sizes (Vazzoler 1996) elevated to the power of <sup>3</sup>/<sub>4</sub> to account for the metabolic allometry of different species as a function of body size (Brown et al. 2004; Giacomini & Galetti 2013).

Body size is a proxy of vulnerability to extinction and conservation concern (Giacomini & Galetti, 2013), with implications on life history, ecological interactions (Brown et al. 2004) and conservation (Hansen & Galetti 2009). Defaunation is calculated using the following formula:  $\sum_{k=1}^{S} \omega k (N_{k,r} - N_{k,f}) / \sum_{k=1}^{S} \omega k (N_{k,r} + N_{k,f})$ . Where *r* is the reference fish assemblage, *f* is the focal assemblage, *S* is the total number of species,  $\omega k$  is the importance of species k in terms of its functional influence on defaunation, and N is the occurrence (presence = 1, absence = 0) of species k in the reference and focal assemblage.

#### 5. Statistical analysis

The beta diversity is the change in species composition along a spatial or environmental gradient (Magurran 2011). This analysis was used to understand the structure of the fish communities in the reservoirs, which species are replaced or more easily lost than others, and if environments with a higher defaunation index share these species with reservoirs with a lower defaunation index. We used the analysis of beta diversity components as implemented in the "Betapart package" v.1.5.4 – "R-project" (Baselga et al. 2021). The total dissimilarity for all reservoirs, the turnover (Simpson's index,  $\beta$ sim), and nestedness (the difference between the Sorensen and Simpson indices,  $\beta$ sne) components were determined by the package computations. The input data table consists of the presence and absence of fish species for each reservoir (Table S2). Cluster and dissimilarity matrices of turnover and nestedness were also performed using the "Betapart package".

#### Results

Considering all fish faunas from the Lower Paranapanema River basin, the average defaunation value found was  $D_i = 0.24$ . Canoas I  $(D_i = 0.50)$  and Canoas II  $(D_i = 0.47)$  reservoirs had the highest defaunation values. On the other hand, Capivara Reservoir had the lowest defaunation index  $D_i = 0.02$ , while Rosana Reservoir had  $D_i = 0.24$  and Taquaruçu  $D_i = 0.30$  (Figure 2).



Figure 2. Defaunation index of Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River, states of São Paulo (SP) and Paraná (PR), southern Brazil, MS – state of Mato Grosso do Sul.

In evaluating feeding habit, the periphytivores were most related to defaunation  $(D_i = 0.63)$ , followed by invertivores  $(D_i = 0.48)$ , while the least affected groups were piscivores  $(D_i = 0.19)$  and herbivores  $(D_i = 0.08)$  (Figure 3). For the Rosana Reservoir, the highest defaunation value was found in the algivore functional group  $(D_i =$ 0.44), and the least affected group was that of herbivores  $(D_i = 0.12)$ (Figure 3). In the Taquaruçu Reservoir, the highest defaunation values were in the functional groups periphytivores  $(D_i = 0.76)$  and invertivores  $(D_i = 0.55)$ . In this reservoir, herbivores had the lowest defaunation values in all the scenarios analyzed (Figure 2; Figure 3). In this reservoir, algivores, periphytivores, herbivores, omnivores and piscivores showed no defaunation ( $D_i = 0.00$ ), and invertivores had the highest value ( $D_i = 0.10$ ) (Figure 3). Canoas I Reservoir showed maximum defaunation values ( $D_i = 1.00$ ) for the functional groups algivores and periphytivores and lower defaunation values for the herbivore and piscivore groups ( $D_i = 0.18$ ) (Figure 3). In the Canoas II Reservoir, the periphytivores showed the highest defaunation value ( $D_i = 1.00$ ), and the lowest value was found in the herbivores ( $D_i = 0.05$ ) (Figure 3).

In relation to reproductive strategies, those most related to defaunation had a non-migratory habit ( $D_i = 0.31$ ), practiced external fertilization ( $D_i = 0.26$ ) and showed parental care behavior ( $D_i = 0.30$ ) (Figure 3). Capivara Reservoir had the lowest defaunation values in all



Figure 3. Defaunation index of functional groups; total defaunation, feeding habit (algivores, periphytivores, insectivores, invertivores, detritivores, herbivores, omnivores, piscivores), reproductive strategies (migratory, non-migratory, external fertilization, internal fertilization, parental care, no parental care). Reservoirs: Ros: Rosana; Taq: Taquaruçu; Cap: Capivara; Ca I: Canoas I; Ca II: Canoas II in the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil. The red line represents the mean values.

functional groups, where migratory and internal fertilization behaviors did not show defaunation  $(D_i = 0.00)$ . The highest defaunation values were found in Taquaruçu Reservoir for internal fertilization  $(D_i = 0.51)$ , Canoas I Reservoir for migratory habit  $(D_i = 0.30)$ , external fertilization  $(D_i = 0.38)$  and no parental care  $(D_i = 0.33)$ , and Canoas II Reservoir for non-migratory habit  $(D_i = 0.50)$  and parental care  $(D_i = 0.52)$ .

Capivara Reservoir had the lowest defaunation index, largest reservoir area and more area with forest cover for land use (31.57%) and Canoas II Reservoir had the highest defaunation values, smaller reservoir area and smallest area occupied by forest (5.73%) (Table S4).

The mean dissimilarity ( $\beta$ sØr) between reservoirs was 0.51, with a mean nestedness ( $\beta$ sne) of 0.33 and turnover ( $\beta$ sim) of 0.17 (Figure 4). Cluster analysis indicated that the reservoirs had high nesting, where Capivara Reservoir and Canoas I Reservoir showed 48% nestedness with Capivara Reservoir and where Canoas II Reservoir showed 45% nestedness with Capivara Reservoir; high turnover indicated in the cluster analysis was Canoas II Reservoir with Rosana Reservoir, namely 20% (Table 2).



Figure 4. Cluster of turnover (βsim) (a) and nestedness (βsne) (b) of fish species in Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil. These clusters result from Beta diversity analysis (Betapart/R-project), and the index was calculated from a matrix of presence and absence of fish species in each reservoir. (c) Graphic representations of total turnover (βsim), nestedness (βsne) and total beta diversity (βsØr).

**Table 2.** Pairwise index matrix of turnover (βsim) and nestedness (βsne) components of fish species in Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil.

	Reservoirs					
_	Rosana	Taquaruçu	Capivara	Canoas I		
Turnover (βsim)						
Taquaruçu	0.15000000					
Capivara	0.06593407	0.02500000				
Canoas I	0.18367347	0.12244898	0			
Canoas II	0.20754717	0.13207547	0	0.08163265		
Nestedness (ßsne)						
Taquaruçu	0.05467836					
Capivara	0.20130731	0.26911765				
Canoas I	0.24489796	0.21088435	0.48421053			
Canoas II	0.20911950	0.17619520	0.45360825	0.03601441		
Beta diversity (βsØr)						
Taquaruçu	0.2046784					
Capivara	0.2672414	0.2941176				
Canoas I	0.4285714	0.3333333	0.4842105			
Canoas II	0.4166667	0.3082707	0.4536082	0.1176471		

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## Discussion

This is the first study to calculate the defaunation index for Neotropical freshwater fish assemblages based on information of occurrence in reference and focal assemblage, total number of species and the importance of species; and how functional groups are affected by defaunation.

Canoas I and Canoas II reservoirs, the two smallest reservoirs in the drainage area of the lower region of the Paranapanema River and the ones with the absence of representative tributaries (Pelicice & Agostinho 2008, Orsi et al. 2016), were the most affected by the defaunation. Before establishing the Canoas system in 1998, the free lotic stretch between Capivara Reservoir and the Salto Grande Dam comprised the richest in this region (Britto et al. 1997). According to our beta-diversity results, the communities of Canoas I and Canoas II reservoirs are nested in the least defaunated reservoirs (Capivara), where all species present in the most defaunated reservoirs also occurred in the least defaunated. Therefore, the species occurring in the smallest reservoirs were more easily lost than others, which was intensified in a reservoir cascades.

Capivara Reservoir showed lower defaunation indices, it is the largest reservoir with more number of tributaries in the Lower Paranapanema River basin and it is the most preserved. This result corroborates the fact that the largest and most representative tributary of the Paranapanema River, the Tibagi River, shelters much of the fish fauna of the Paranapanema River basin (Hoffmann et al. 2005, Jarduli et al. 2020). Therefore, the conservation of environments free of dams and reservoirs is directly related to fish diversity conservation. Marques et al. (2018) recorded 79 species in Porto Primavera Reservoir, a large reservoir with a length of 270 km in the Paraná River mainstem. They reported the importance of riverside stretches upstream of the reservoir, and Garcia et al. (2019) recorded 63 species in a stretch of 110 km in the Congonhas River, which has lotic features and directly flows into reservoirs. In the Neotropical region, the fragmentation and the simplification of habitats promoted by reservoirs is the main human interference in natural hydrological regimes (Agostinho et al. 2007a). Small species that depend on small-order lotic environments, such as algivores, periphytivores, insectivores, and invertivores, suffer more decline due to environmental changes (Agostinho et al. 2008), and the quality of lotic environments is associated with the degree of urbanization of its surroundings (Helms et al. 2005).

Environmental changes affect groups that are more sensitive to large-scale changes, such as small ones, and dependent on small-order lotic environments, such as periphytivores and algivores (Agostinho et al. 2008). In our study, these functional groups were most affected by the defaunation in the basin, probably because of the extensive loss of integrity of lotic environments, including that caused by urbanization (Peressin & Cetra 2014). Alga and periphyton colonize substrate-submerged rocks and logs and represents a vital resource dependent on organic matter from riparian vegetation (Angermeier & Karr 1983). These functional groups were represented by six species of small loricariids and one small lebiasinid that inhabit small-order streams, necessary to maintain short food chains of Neotropical rivers (Casatti et al. 2005, Zuanon & Ferreira 2008). Several species present in dammed environments can indirectly use this food resource associated with the macrophytes that colonize reservoir margins (Hahn et al. 2008, Algarte et al. 2017). Insectivores and invertivores were also affected, and invertivores displayed the second highest defaunation index. The predominance of insectivorous species may have been associated with the great taxonomic and functional diversity of this group and the spatial heterogeneity that favors colonization by invertebrates (Araújo-Lima et al. 1995). Environmental changes, such as marginal vegetation loss, can influence the abundance and richness of invertebrates and reduce this trophic group (Luiz et al. 1998). Although there is extensive colonization by insects and aquatic invertebrates in reservoirs (Jorcin & Nogueira 2008), animals that support the food chain of various small fish species that occur along the banks of reservoirs (Casatti 2002, Gido et al. 2002, Ferrareze et al. 2015), damming can cause spatial-temporal changes in these communities, associated with the discontinuity of the aquatic system (dos Santos et al. 2016). The piscivore group's defaunation values were low but were above the average in two reservoirs (Rosana and Taquaruçu). This group is the top predator species in the food chain and usually occurs as a small number of species. The elimination of one or a few of them will spread throughout the food chain, interfering with the control of organisms of lower trophic levels and consequently affecting the top-down mechanism (Pelicice et al. 2005, Ticiani & Delariva 2020).

The migratory species did not show defaunation in the largest reservoir (Capivara), in agreement with the fact that the largest and most representative tributaries of the Paranapanema River, the Tibagi, Congonhas rivers and others, harbor a large part of the fish fauna in this basin (Jarduli et al. 2020), as they preserve lotic conditions that favor migratory species (Shibatta et al. 2007). Another factor to be considered, which is directly related to the availability of suitable areas, is the good biotopes for reproduction and recruitment, with spawning areas and nursery grounds (Orsi et al. 2016), which do not occur in smaller systems (Agostinho et al. 2004). These environments, which are still favorable for migratory species, may be affected as new dams are built in tributaries, increasing the defaunation of fish. It is important to emphasize that the decrease in populations of migratory species due to the interruption of their routes by dams has been widely recorded throughout the Upper Paraná River basin (Agostinho et al. 2002, Pelicice et al. 2014, Marques et al. 2018), although our results did not detect high levels of defaunation for the migratory functional group. Nonmigrators had higher defaunation rates than did migrators, the negative pressure exerted on migratory populations is higher in a succession of cascading reservoirs, and it is in tributaries without dams that they seek favorable environmental conditions for reproduction (Agostinho et al. 2004, Pelicice et al. 2014, Garcia et al. 2019).

Species with external fertilization and parental care were more affected by defaunation, mainly in the small reservoirs (Canoas I and Canoas II). The lack of representative tributaries and the considerable variation in the water level caused by the dam's operation exposes the nests built on the banks and the eggs adhered to some bank substrate, reducing the recruitment success (Agostinho et al. 2004). Internal fecundation seems to be a successful strategy in the first years after the formation of a reservoir, but in older reservoirs species with more elaborate reproductive strategies have greater occupation success, like cichlids with complex mating choice, nest-building and parental care and small-sized opportunistic characids that colonize shallow shores (Agostinho et al. 2016). Among the reservoirs analyzed, Canoas I and Canoas II reservoirs are the newest, which may be related to the fact that species with parental care have not yet established themselves, which occurs in older reservoirs (Agostinho et al. 2007a).

The area with the highest percentage of land use for agriculture/ pasture showed the highest defaunation levels (Canoas II), while the reservoir with the highest percentage of forest cover (Capivara) had the lowest defaunation index. Therefore, environments with less anthropic disturbance uphold the integrity of the fish fauna, either by preserving areas of development and initial growth of fish larvae, maintaining the routes of migratory species (Antonio et al. 2007), or making it difficult to establish non-native species (Nordheimer & Jeschke 2018). Pristine forest fragments can be a constant source of species to impact streams for maintaining the local, regional and functional structure of fish assemblages (Zeni et al. 2019). Freshwater fish were also affected by the removal of native vegetation, which promotes the siltation that most affects the assemblages (Rabeni & Smale 1995). Sensitive and specialized species decrease to the detriment of tolerant and opportunistic fishes (Casatti et al. 2012) and there is an increase in non-native and sediment-tolerant species introduced by humans (Sutherland et al. 2002).

It is worth mentioning that our matrices were built on the basis of presence/absence data and not abundance or biomass. The authors of the method, Giacomini & Galetti (2013), proposed primarily quantitative density data, because they are able to detect many levels of depletion in species density, but it can be used with occurrence, depending on practical limitations and data availability. Therefore, perhaps some groups may not appear to be depleted at first, but they may fall into two situations: 1) data of presence and absence come from old surveys; 2) the species is currently present, but the population is small and declining. In this way, we highlight that the index has limitations in terms of a complete understanding of the general overview of fish defaunation in the basin, with the central focus being to portray the current scenario and to determine whether defaunation has occurred in local or chronic events in view of the factors analyzed. Another limiting factor was the lack of basic information about the biology of several species, which prevented some newly described ones from entering the analysis, and the lack of data before establishing the reservoirs. Even though the information obtained through the review analysis there are no replicas and there is no control area (no affected by the events studies), did not allow us to perform a deeper statistical analysis, go thru a hypothesis test and performed an analysis examining the effect of landscape characteristics (i.e., land use, reservoir size and tributary number) and the trends of each predictive variable in explaining the defaunation levels recorded in the reservoirs. Even with these limitations, the index was useful to indicate impoverishment and for the future analysis this study can be use as the first defaunation index data source from Lower Paranapanema River. It also highlights the importance of analyzing other variables contributing to defaunation or the synergistic combination of them, such as invasive species, water pollution, physical modification, direct exploitation, climate change (Young et al. 2016), conservation status, economic or social value and number of tributaries, and their support capacity before establishment of the hydroelectric plants, since these areas can be used to mitigate the impact on the fish fauna and support the recruitment development of species.

Mitigation measures must be adapted to the characteristics of the reservoirs, in the reservoirs with the highest defaunation values, we suggest maintaining native vegetation cover in land use and fish restocking programs. In reservoirs with satisfactory environmental conditions, we suggest further conservation efforts to maintain integrity in tributaries and the native fishes. Regarding species permanence, non-migratory and migratory species persist in the reservoirs as long as they have sufficient tributaries to be used as migratory routes. In reservoirs without or with few habitats for reproduction and early stages of development, populations tend to decrease or disappear if measures are not taken for their recovery. It is noteworthy that these measures must have technical-scientific monitoring to obtain valid results. Although the reservoirs analyzed have different characteristics, this method can be tested in any other hydrographic basin in South America. The context and scenario in which the Paranapanema River basin is located are not exclusive to the Upper Paraná River or other Brazilian river basins.

#### **Supplementary Material**

The following online material is available for this article:

**Table S1.** Studies between 1995 to 2018 that investigated fish diversity in the Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River basin, states of São Paulo and Paraná, southern Brazil.

**Table S2.** Native fish fauna present in the Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil. Taxonomic classification followed Fricke, Eschmeyer and Fong 2022.

**Table S3.** References consulted for classification of functional groups: feeding habit, reproductive strategies, fertilization and parental care, of the species from the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil.

**Table S4.** Percentage of land use in watersheds that flow into the Rosana, Taquaruçu, Capivara, Canoas I and Canoas II reservoirs in the Lower Paranapanema River, states of São Paulo and Paraná, southern Brazil.

 Table S5. References consulted for maximum length of species

 from the Lower Paranapanema River, states of São Paulo and Paraná,

 southern Brazil.

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Ana Carolina Vizintim Fernandes Barros: conceived the ideas; designed the methodology and prepared figures and tables; wrote the paper, prepared the manuscript for submission.

Alan Deivid Pereira: conceived the ideas; designed the methodology and prepared figures and tables, analyzed and interpreted the data; wrote the paper.

Diego Azevedo Zoccal Garcia: conceived the ideas, wrote the paper; reviewed and revised drafts of the paper.

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Mário Luís Orsi: reviewed and revised drafts of the paper; gave final approval and secured the funding to support the work.

#### **Conflicts of Interest**

The authors declare that they have no conflict of interest related to the publication of this manuscript.

## Ethics

We declare that the procedures used in this study have no conflict with the Brazilian Laws regarding the use of vertebrates in scientific research.

#### **Data Availability**

Our data was compiled from published literature. https://doi. org/10.48331/scielodata.2BM7QW

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## Phylogeography of the white-crowned parrot (Pionus senilis)

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*Abstract:* The white-crowned parrot *Pionus senilis* (von Spix, 1824) is distributed throughout Middle America, inhabiting the Gulf of Mexico coastal area from Tamaulipas (Mexico) to northern Panama. We used mitochondrial data (COI, ND2 and ND4) from 55 specimens to infer phylogenetic relationships, and analyzed the phylogeographic structure, genetic diversity, divergence periods, and historical demography to explore phylogeographic patterns. We found three divergent lineages: two geographically separated by the Isthmus of Tehuantepec, and the third, in Costa Rica by the Nicaragua Depression. The analysis of molecular variance and statistical analyses were consistent with genetically distinct populations. The Central American lineage diverged 1.33 million years ago, whereas the other two lines branched off 1.19 million years ago. This phylogenetic pattern has been reported in other species of Middle American birds.

Keywords: Psittacidae; genetic structure; conservation genetics.

### Filogeografia do maitaca-de-testa-branca (Pionus senilis)

**Resumo:** A curica-de-testa-branca *Pionus senilis* (von Spix, 1824) está distribuída por toda a América Central, habitando a área costeira do Golfo do México de Tamaulipas (México) ao norte do Panamá. Usamos dados mitocondriais (COI, ND2 e ND4) de 55 espécimes para inferir relações filogenéticas e analisamos a estrutura filogeográfica, diversidade genética, períodos de divergência e demografia histórica para explorar padrões filogeográficos. Encontramos três linhagens divergentes: duas geograficamente separadas pelo Istmo de Tehuantepec, e a terceira, na Costa Rica pela Depressão da Nicarágua. A análise de variância molecular e as análises estatísticas foram consistentes com populações geneticamente distintas. A linhagem da América Central divergiu há 1.33 milhão de anos, enquanto as outras duas linhas se ramificaram há 1.19 milhão de anos. Este padrão filogenético foi relatado em outras espécies de aves da América Central.

Palavras-chave: Psittacidae; estrutura genética; genética da conservação.

## Introduction

A comprehensive study of biodiversity must not only include ecological variability, but genetic variability as well, since it is essential for the persistence and evolutionary continuum of a species or lineage (Frankham et al. 2002). The International Union for Conservation of Nature places genetic diversity as one of the three global priorities for conservation (IUCN 1980). The order Psittaciformes has the highest number of endangered species among groups of birds, with 111 (28%) of the 360 species listed as in danger of extinction and shrinking population sizes in 56% of its species (Berkunsky et al. 2017). Given the current extinction processes, the genetic studies needed to support conservation programs are of utmost importance (Avise 2002, Frankham et al. 2002, Olah et al. 2022). Phylogeography can be considered a theoretical bridge between population genetics and phylogenetic biology. Ever since phylogeography was conceived and has been applied, it has made valuable contributions to the comprehension and protection of biodiversity (Avise et al. 2016). Information thus obtained may be useful to determine possible evolutionarily significant units (ESUs), which are needed to apply conservation plans. Phylogeographic studies have been applied to solve the existence of several cryptic Psittacidae taxa (Russello and Amato 2004; Joseph et al. 2011; Murphy et al. 2011). They have made it possible to observe the effect of fragmentation and bottlenecks on population structure (Ringler et al. 2012; Miller et al. 2013; Bergner et al. 2016), as well as elucidate how evolutionary history has woven the current diversity patterns in the species (Murphy et al. 2007; Caparroz et al. 2009; Murphy et al. 2011). These studies have fostered awareness of how important the preservation of a species' evolutionary potential is for it to persist, thus improving our understanding of factors associated with habitat fragmentation, the effect of endogamy, and loss of populations. Since species lacking robust information are in particular need of such studies, it is fundamental that genetic data be obtained to distinguish their phylogeographic patterns.

The genus Pionus has eight species of parrots, four of which are allopatrically distributed in mountain forests from northern Mexico to South America, and four others are in the lowlands (Juniper & Parr 1998, Ribas et al. 2007). This is consistent with speciation patterns caused by vicariance, since mountain groups are limited by boundaries related to topographic diversity isolating the mountain forests surrounded by lower, warmer lands (Ribas et al. 2007). The genus Pionus diversified in the late Miocene and early Pliocene, approximately 4.7 to 5.8 million years ago (Ribas et al. 2007). The white-crowned parrot is the only species in the genus that is distributed in northern Middle America, and it expands from Mexico (from southern Tamaulipas along the Gulf of Mexico coastline to the Yucatan Peninsula and Chiapas) to the west of the Isthmus of Panama. Mexican laws have cataloged it as a Threatened species (NOM-059, SEMARNAT 2010), whereas the International Union for Conservation of Nature has it listed as of Least Concern (IUCN 2016).

Spix described the species *Pionus senilis* in 1824 from a specimen that was later determined to have been obtained from Veracruz, Mexico. The species was considered monotypic until Griscom (1929) described *P. s. decoloratus* from the populations in southern Quintana Roo (Mexico), Guatemala, Honduras, and western Panama. The latter is distinguished by the darker purple, less blue, plumage on the chest and throat; the abdomen and sides are an olive green instead of a bright green, and the primary feathers are mostly bright blue with little green. The typical *P. senilis* is greener and has a green stripe between the blue and dark areas of the inner vanes of the external primary feathers. The above description explains that the southern populations (southeastern Nicaragua, Costa Rica and Panama) are differentiated by these characteristics, and that those in Quintana Roo (Mexico), Belize, Honduras, and northern Nicaragua are intermediate.

This species' populations have dwindled in Mexico and have even vanished from western Quintana Roo and several areas along the Gulf of Mexico (Salinas-Melgoza & Renton 2008). This is mostly due to the impact that human activity has had on its habitat (evergreen tropical forest, oak forest, and lower mountain forest), which has been highly deforested for farming. As a result, it inhabits only 48% of its original area, and only 16.2% of this surface is protected (Monterrubio-Rico et al. 2016). Further, this species is illegally sold as a pet (Cantú et al. 2007). There is little data on the species in Central American countries.

Given its progressive depletion and possible population fragmentation, a conservation plan for the species is important because it would then be possible to keep the populations comprising evolutionary units safe and flag them as of high conservation priority (Ryder 1986). To achieve this goal, we investigate population differentiation patterns with three mitochondrial markers applied at the intraspecific level with genealogy analyses. These data would facilitate the study of population evolution, deductions concerning lineage colonization, diversification and extinction, and the identification of geological or ecological causes that influenced the populations (Avise 1998, Domínguez-Domínguez and Vázquez-Domínguez 2009).

Following this need to learn more about the white-crowned parrot (*Pionus senilis* [Von Spix 1824]), we decided to perform a phylogeographic analysis with these main objectives: a) identifying genetic lineages within the entire distribution area of the species, b) revealing the likely geological events that allowed the current distribution of the distinct haplotypes, and c) identifying the geographic barriers that have influenced the distribution of genetic lineages.

#### **Material and Methods**

#### 1. Biological samples

Blood samples were taken from white-crowned parrot specimens between 2017 and 2019 using collection permit SGPA/DGVS/05058/17. Each sample was georeferenced. One 0.1-ml blood sample was taken from each parrot, conserved on an FTA card, and placed in the National Bird Collection at the Institute of Biology of the National Autonomous University of Mexico (Universidad Nacional Autónoma de México, UNAM). We collected and analyzed samples from 59 individuals from 11 localities ranging from northern Mexico (state of Tamaulipas) to Costa Rica (Table 1, Figure 1). The capture of wild samples was unsuccessful because of the challenge of catching the parrots while foraging, the difficulties in finding and climbing to their nests, and time constraints. We resorted to collecting samples of captive individuals in the locations studied with the certainty that these individuals were captured in the area. This conclusion was based on the information provided by owners, and on the fact that many rural people collect nestling's locality. They keep them as pets and perhaps sell them to people that look for them illegally, but they cannot afford to buy them in the illegal trade, a situation more likely in cities. Additional samples were facilitated by the Macaw Mountain Bird Park (Honduras), and Rescate Animal Zoo Ave (Costa Rica). Each sample was georeferenced. One 0.1-ml blood sample was taken from each parrot, conserved on an FTA card, and placed in the National Bird Collection at the Institute of Biology of the National Autonomous University of Mexico (Universidad Nacional Autónoma de México, UNAM). We collected and analyzed samples from 59 individuals from 11 localities ranging from northern Mexico (state of Tamaulipas) to Costa Rica (Table 1, Figure 1).

## 2. DNA extraction, PCR amplification and marker sequencing

Genome DNA was obtained using a modified technique to extract DNA from animal tissue using phenol-chloroform. We amplified mitochondrial fragments *NADH dehydrogenase II (ND2), NADH dehydrogenase 4 (ND4),* and *cytochrome oxidase I (COI).* We were able to amplify 55 individuals with the three genes. The ND2 gene was amplified using L5215 (Hackett 1996) and H6313 primers (Bonaccorso et al. 2010), ND4 and LEU primers were used for ND4 (Arévalo et al. 1994), and COI was amplified using COIbird F1 and COIbird R1 primers (Hebert et al. 2004).

The amplification reactions caused by the polymerase chain reaction (PCR) (12.5  $\mu$ L) were prepared with 6  $\mu$ l 10% trehalose,

Country	State	Locality	Samples	ID	Latitude	Longitude
Mexico	Tamaulipas	El Cielo	9	RCRA1 – RCRA3, RCRA25 – RCRA30	23.024	-99.148
Mexico	San Luis Potosí	El Naranjo	2	RCRA4, RCRA5	22.572	-99.343
Mexico	San Luis Potosí	Aquismon	1	RCRA6	21.624	-99.028
Mexico	San Luis Potosí	Xilitla	2	RCRA7, RCRA8	21.375	-99.990
Mexico	San Luis Potosí	Santos	1	RCRA9	21.572	-99.961
Mexico	Oaxaca	Chalchijalpan	3	RCRA14 - RCRA16	17.057	-94.656
Mexico	Chiapas	Tecpatan	3	RCRA17 - RCRA19	17.137	-93.318
Mexico	Tabasco	Tenosique	5	RCRA20 - RCRA24	17.256	-91.133
Honduras	Copán	Macaw Mountain	11	Hon-23 – Hon-33	14.851	-89.154
				Nica 13-1, Nica 14-2, Nica 15-4, Nica 16-3, Nica 17-5, Nica 18-6, Nica 19-7, Nica 20-8,		
Nicaragua	Jinotega	Wiwili	10	Nica 21-9, Nica 22-10	13.584	-85.803
Costa Rica	Alajuela	Zoo Ave	12	Avezoo1 – Avezoo 12	10.012	-88.276

Table 1. Localities and number of collected the white-crowned parrot (Pionus senilis) samples.



Figure 1. Sampling areas of the white-crowned parrot (*Pionus senilis*) along its distribution Centroamerica. A. El Cielo, Tamaulipas; B. El Naranjo SLP; C. Xilitla SLP; D. Aquismon, SLP; E. Santos, SLP; F. Chalchijalpan, Oaxaca; G. Tecpatan, Chiapas; H. Tenosique, Tabasco; I. Macaw Mountain, Copán; J. Wiwili, Jinotega and K. Zoo Ave, Alajuela. The colors represent the three unique genetic lineages of this work: Northern (blue), Center (green) and Southern (red).

2  $\mu$ l distilled water, 10 mM PCR buffer, 0.2 mM of each dNTP, 1.5 mM MgCl2, 0.3  $\mu$ M of each primer, 0.5 units of Taq DNA polymerase, and approximately 50 ng of genome DNA. Both DNA chains were sequenced using the amplification primers and the dideoxi method (Sanger et al. 1977). The PCR products were sent for sequencing to the Biodiversity and Human Health Genome Sequencing Laboratory (Laboratorio de Secuenciación de la Biodiversidad y de la Salud) at the UNAM Institute of Biology and to Macrogen (Maryland, USA).

#### 3. Sequence analysis

Sequences were edited using BioEdit v7.2 software (Hall 1999), and chromatograms were manually checked using FinchTV v1.4 software. In addition, each sequence was compared to the information available at GenBank using the basic local alignment search tool (BLAST), which made it possible to establish a 96–99% identity in each sequenced case. MEGA v10 software was used to read sequences (Tamura et al. 2011).

Genetic diversity indicators, such as number of mitochondrial haplotypes (h), number of polymorphic sites (Sn), genetic diversity (H), average number of differences between pairs of sequences ( $\pi$ ), and nucleotide diversity (k), were calculated using DNAsp v10 software (Rozas & Rozas 1999). Different summary statistics were also implemented to determine whether the markers assume a neutral evolution model: Tajima's D (Tajima 1989), Fu (Fu & Li 1993) and Fs (Fu 1997). We used MEGA v10 software to identify the genetic distances between groups (Tamura et al. 2011) and individuals were assembled into groups established by phylogenetic trees using the Kimura two-parameter substitution model.

An analysis of molecular variance (AMOVA) (Excoffier et al. 2005) was conducted to determine whether genetic variation and differentiation between the groups had a structured distribution. This analysis breaks variance down into (a) differences in haplotype composition among individuals from individual populations (variance within a population); (b) differences in haplotype composition of individuals from different populations (variance between populations); and (c) differences in haplotype composition between groups of populations (variance between FST regions). We performed this analysis using GenAIEx v6.0 software (Peakall & Smouse 2006) with 9999 permutations. To know whether a species' gene flow follows an isolation by distance model (i.e., whether the geographic distances and genetic distances between different pairs of populations are correlated), we performed a Mantel test using GenAlEX v6.0 software (Peakall and Smouse 2012). This analysis assumes that genetic distances increase with geographic distance. The test computes the correlation between a geographic distance matrix versus a genetic distance matrix, then permutes the matrices and computes the same test statistic under each permutation and compares the original test statistic with the distribution of the test statistic from the permutation to generate the p-value.

## 4. Relationships between haplotypes and genealogical analyses

We constructed a haplotype network in PopART v1.7 (Leigh & Bryant 2015) using the MJN algorithm, to represent the relationships between haplotypes at each sampling locality. PopART v1.7 software

starts from the number of paired substitutions to introduce medium vectors that represent the haplotypes the concatenated 55 individuals. An analysis was also performed with Split Tree v4 software (Huson & Bryant 2006) using Neighbor Net with the GTR substitution model and 400 bootstrap replicas.

We reconstructed genealogical relationships using Bayesian inference (BI) and maximum likelihood (ML). The matrix for these analyses included 55 sequences of COI, ND2 and ND4 from the samples collected in the field, in addition to sequences belonging to Pionus chalcopterus (GenBank Access: MF784450.1) that we included as an external group. Molecular evolution models were estimated with jModelTest v2.1.1 (Posadas 2008), using the corrected Akaike's Information Criterion (AICc) (Alfaro and Huelsenbeck 2006). TN93 was the best model for ND2 (Tamura and Nei 1993 + 3 rates), TIM1 for ND4 (Posada, 2008), and HKY for COI (Hasegawa et al. 1985). The best model for the concatenated sequences (COI + ND2 + ND4) was TIM3 (Posada 2008). We used MrBayes v3.2 (Ronquist and Huelsenbeck 2003) and RAxML v7.8 software (Stamatakis 2014), respectively, to reconstruct Bayesian inference and maximum likelihood. MrBayes made two independent runs of 30,000,000 generations and four Markov chains (Markov Chain Monte Carlo), testing a tree every 2,000 generations at a temperature of 0.3 and burning 30% of the generated data. The remaining trees were summarized as majority consensus. In RAxML, the ML+ through bootstrap search was performed with 10 searches and 10,000 replicas. Trees were displayed in FigTree v1.4.0 (Rambaut 2014).

#### 5. Molecular clock

We analyzed the molecular clock by implementing the BEAST v.1.6.1 program (Drummond & Rambaut 2007) to estimate the divergence time in a tree of species. We used the 55 concatenated sequences of the three-mitochondrial markers, calibrating with Pionus chalcopterus to 2.2 million years in the past when the two species branched off (Ribas et al. 2007). We ran a simulation to determine when the three white-crowned parrot lineages separated, using GTR as the substitution rate, with estimated base frequencies, gamma shape distribution (with 4 categories), proportion of invariant sites, a relaxed molecular clock with uncorrelated lognormal distribution and a Yule tree prior. We performed the BEAST analysis three times with 100 million generations each time and took a sample every 1000 steps using the Yules speciation tree, an uncorrelated relaxed clock model with log-normal distribution. After running the analyses through BEAST, we used TRACER v.1.6 to observe the parameters of the results. We then combined the tree files (.tree) using LOGCOMBINER and summarized them as a maximum clade credibility tree produced by TREEANNOTATOR (Drummond & Rambaut 2007) after burning 30%. This tree was displayed in Figtree.

#### 6. Historical demography

To evaluate whether the data were consistent with the occurrence of selection at a molecular level or with past demographic expansion, we calculated the observed distribution of the number of differences between pairs of haplotypes using DnaSP v5.10 software to distinguish whether the populations, Northern (14), Central (30), and Southern (11) were in demographic equilibrium (Librado & Rozas 2009).
#### Results

#### 1. Analysis of genetic diversity and differentiation

We obtained amplification products with the COI gene from 59 individuals, with the ND2 gene from 55 individuals, and with the ND4 gene from 58 individuals, though only 55 individuals simultaneously exhibited all three fragments. No insertions or deletions were found, and the start and stop codons were at the expected sites. Base composition patterns were those expected for avian mtDNA. No compositional bias was found in the bases. The three genes were concatenated in 55 individuals, resulting in a total dataset of 2222 base pairs. Seventeen variable sites, 16 informative sites and five haplotypes were found. General haplotype diversity (h) was 0.706 and nucleotide diversity ( $\pi$ ) was 0.00254. Tajima's D was D = 1.412 (P > 0.10). Statistical data Fu and Li's F = 1.64 and Fu's Fs 1.65 (P > 0.10) were not significant (Table 2).

We detected four haplotypes with COI and ND2, three with ND4, and five with the concatenated sequences when all of the samples were analyzed as a single group. Almost every population exhibited a single haplotype, even those with a larger sample size (Nicaragua, Costa Rica, and Honduras). Nucleotide diversity was also low (Pi = 0.00254) (Table 2). The genetic distances between groups were less than 1%: 0.23% between populations in northern Mexico and Central America, 0.58% between northern Mexico and Costa Rica, and finally 0.54% between Central America and Costa Rica.

The comparison by pairs of the FST values showed high differentiation between the population groups (Table 3). The comparison of central populations (southern Mexico, Honduras, and Nicaragua) with those from the south (Costa Rica) had the highest FST value (0.992), while the comparison of populations from the north (northeastern Mexico) with those from the south had an FST value of 0.956. The lowest FST value was obtained when the populations from the north were compared with those from the center (0.904). AMOVA results showed that the greatest genetic difference occurs between the population groups with 99.5% of differences, whereas the

difference within the populations is 0.18%. The correlation between the geographic distance matrix and the genetic distance matrix was moderately significant (r = 0.568, p < 0.05, Figure 2), indicating that partly a process of isolation by distance undergone by this species' populations (Table 4).

## 2. Relationships between haplotypes and their geographic distribution

The haplotype network showed the relationships of the three haplogroups and their frequencies found in the 55 individuals (Figure 3). In the network, the green haplogroups of the Costa Rican specimens are separated by 12 mutations from the other two groups (Hap 1, southern group). All of the specimens from the populations in northeastern Mexico are included in a single haplogroup (blue) (Hap 5, northern group). The populations in southern Mexico, Honduras and Nicaragua are in the pink-cherry-purple haplogroup and are widely distributed (Haps 2-4, central group). The latter group has three haplotypes: haplotype 2, which is common, haplotype 4 in three individuals from Tenosique, and haplotype 3 in a specimen from Nicaragua (Figures 3 and 4).

The Red Split Tree analysis also produced three groups (Figure 5), which are similar to those reported by prior analyses. The first southern group included individuals from Costa Rica, the second central group had individuals from southern Mexico (Tecpatan, Tenosique, and Chalchijalpal localities) and northern Central America (Honduras and Nicaragua), and specimens from northeastern Mexico (states of Tamaulipas and San Luis Potosí) comprised the third northern group.

#### 3. Genealogical analysis

Phylogenetic analyses were performed to estimate the genealogical relationships between the detected groups (Figure 6). The tree constructed from Bayesian inference coincides with the topology obtained by maximum likelihood. The analyzed samples were grouped into three clades: the first with 11 specimens from Costa Rica; the second

Table 2. Genetic diversity indices obtained for the white-crowned parrot (Pionus senilis).

Gene fragment	Ν	Nt	Н	S	Hd	Pi	Dt	Fu y Li	Fs fu
COI	60	677	4	12	0.655	0.00297	0.90837	1.23	1.53
ND2	56	767	4	12	0.674	0.00222	0.90837	1.04	1.23
ND4	58	778	3	10	0.627	0.00283	2.488	1.14	1,21
Concatenated	55	2222	5	34	0.706	0.00254	1.412	1.64	1.65

N =sample size, Nt =base pairs, H =haplotypes, S =polymorphic sites, Hd =haplotype diversity, Pi =nucleotide diversity, Dt = D Tajima significant at p < 0.10.

Table 3. Genetic differentiation for the white-crowned parrot (Pionus senilis) groups.

		%	<b>F</b> <sub>ST</sub>	G <sub>st</sub>	N <sub>st</sub>
Northern	Southern	0.4%	0.956	0.785	0.956
Northern	Central	0.3%	0.904	0.793	0.904
Southern	Central	0.5%	0.992	0.894	0.992

% genetic distance F<sub>SP</sub> genetic differentiation between populations; G<sub>SP</sub> genetic differentiation between populations; N<sub>ST</sub> nucleotide diversity between populations.



Figure 2. Concatenated Mantel test for all populations of the white-crowned parrot (*Pionus senilis*). The AMOVA test produced genetic diversity distribution values of 99.5% between the groups; the rest is distributed among the populations.

Table 4. AMOVA summary for the white-crowned parrot (Pionus senilis) populations using concatenated mitochondrial gene sequences.

Source	df	SS	<b>Components variation</b>	% variation
Among groups	2	1687.759	45.610	99.5
Among populations within groups	8	4.136	0.085	0.32
Within groups	49	6.889	0.14	0.18
Total	59	1698.78	45.835	100%



**Figure 3.** Concatenated haplotype network of the white-crowned parrot (*Pionus senilis*) for populations in Mexico, Honduras, Nicaragua, and Costa Rica using nucleotide sequences ND2, ND4 and COI. Dashes on haplotype network branches indicate mutations between haplotypes and the sizes of circles are proportional to the number of samples for each haplotype.

with 30 specimens from Nicaragua, Honduras, and the localities of Tecpatan, Tenosique, and Chalchijalpa, Mexico; and the third with 14 individuals from the populations in northern Mexico, namely El Cielo, El Naranjo, Xilitla and Santos.

#### 4. Molecular clock

The BEAST analyses produced a high effective sample size (ESS) (200) for all parameters, indicating that the posterior distribution



Figure 4. Geographical distribution and statistical parsimony network of concatenated haplotypes of white-crowned parrot (*Pionus senilis*) overlaid on a map of Centro America. Pie charts represent haplotypes found in each sampling locality.



Figure 5. Concatenated Split Tree of the white-crowned parrot (*Pionus senilis*) for populations in Mexico, Honduras, Nicaragua, and Costa Rica using nucleotide sequences ND2, ND4 and COI. The distance between taxa represents the sum of weights of all splits that separate taxa.



Figure 6. Consensus (ND4, COI and ND2) tree showing the genealogical relationships between 55 individuals of white-crowned parrot individuals (*Pionus senilis*) with *Pionus chalcopterus* as outgroup obtained with Bayesian inference (BI) and maximum likelihood analysis (ML). Node values represent posterior probabilities and bootstrap values (PP / BP). The scale bar below is a reference of branch length, and branch length is proportional to the amount of evolutionary change. Populations groups: Northern (blue), Center (green) and Southern (red).



Figure 7. Estimates of divergence time in years shown by lineages of the white-crowned parrot (*Pionus senilis*) populations based on the concatenated 2222 bp data from mtDNA sequences. Blue bars on the tree correspond to the 95% credibility intervals of the estimated node ages. The colors represent the three outstanding genetic lineages of this work: Northern (blue), Central (green) and Southern (purple).

was adequately sampled. This result concurred with the Bayesian inference and maximum likelihood analyses. The tree from BEAST (Figure 7) with mtDNA data strongly supported (PP = 1.0) a division between the Costa Rican (Southern) lineage and the other two lineages that occurred 1.33 Mya (95% highest posterior density [HPD]), as well as the differentiation between the other two lineages (PP = 0.53) at 1.19 Mya (95% HPD). The Central lineage was dated at 840,000 years and the Northern lineage at 700,000 years. Results from the mitochondrial data suggest that both lineages branched away during the Pleistocene.

#### 5. Historical demography

Distribution analysis of concatenated paired differences (Figure 8) showed a distribution that would be expected of a constant population size. This result fits the population expansion of the global sample

analyzed for populations of the white-crowned parrot. Specifically, for haplogroups only the central group fits a stable distribution model.

#### Discussion

We conducted the first complete phylogeographic study for a charismatic, but least studied, parrot in Middle America. Our mtDNA data revealed three genetic groups. The first group corresponded to individuals from the states of Tamaulipas and San Luis Potosí in northern Mexico (Northern), the second to populations in southern Mexico, Honduras, and Guatemala (Central), and the third exclusively to specimens from Costa Rica (Southern). These white-crowned parrot groups are separated by a short genetic distance (0.5–0.3%, Table 3). *P. senilis* branched away from *P. cyanescens/P. chalcopterus* about 2.2 – 1.2 million years ago (Ribas et al. 2007). This finding, and the



Figure 8. Mismatch distributions of the white-crowned parrot (*Pionus senilis*) populations: concatenated (A), Northern (b), Central (C), Southern (D). Dashes lines indicates the observed distribution of pairwise differences (red and solid lines show the expected distribution (green) under a model of sudden expansion.

fact that *P. senilis* is mostly distributed in lowlands at present, strongly implies an ancestral distribution across Central American lowlands (Ribas et al. 2007).

White-crowned parrots have a wide geographic distribution, yet no studies have been made of the connectivity between its populations. Our mtDNA data show consistent levels of phylogeographic structure among the three population groups, though it must be determined whether this result stems from their historical biogeography (i.e., it is caused by geographic boundaries) or from gaps in sampling. We discovered that the genetic structure in all three groups was consistent, even when the isolation by distance analysis was taken into consideration. Moreover, the highest Fst values point to a greater genetic differentiation between the Central and Southern groups (0.992), which are geographically closer to each other, and the Fst values (0.956) for the Northern-Southern and Northern-Central groups are extremely high compared to any other species (Table 3).

Although the Northern and the Southern groups each presented a unique haplotype, three unique haplotypes were found in the Central populations, indicating high haplotype diversity (Hd) in total (h = 0.706). These data are similar to those reported by other studies on Psittacidae, such as *Cyanoliseus patagonus* with a haplotype diversity of 0.943, *Eolophus roseicapilla* with Hd: 0.817, *Anodorhynchus hyacinthinus* with Hd: 0.604, *Eclectus roratus* with Hd: 0.500 and *Lophochroa leadbeateri* with Hd: 0.602 (Masello et al. 2011; Engelhard et al. 2015; Presti et al. 2015; Astuti 2020; Ewart et al. 2021). Low nucleotide diversity values ( $\pi < 0.0025$ ) and a small number of haplotypes are characteristic of the effects of population demographic expansion over a relatively recent period (Hamilton 2009). This has been attributed to expansion following a small effective size period in the population, since

rapid growth in a population increases its retention of new mutations (Avise et al. 1984, Watterson 1984).

Tajima's D and Fu's Fs neutrality tests were performed to measure the effect of the population's demographic changes on sequences of mtDNA. The Fs test is more powerful at detecting recent or selected population growth and demographic expansion than Tajima's D (Tajima 1989), and it usually produces high negative values. The analyses showed that both Fu's, Fs, and Tajima's D tests had non-significant values (Table 2), indicating that the mutations neither favor nor hinder the organism and thus do not exert selection pressure (Ramos-Onsins and Rozas 2002).

We recovered a clear phylogeographic structure even though the genetic groups are separated by few mutations. The geographic distribution of genetic variation is not entirely random (as indicated by the AMOVA and  $F_{st}$  values), suggesting a scenario in which the groups have been diverging in isolation and then expanding their distribution range. Furthermore, the low nucleotide diversity but high haplotype diversity we found in *P. senilis* is consistent with populations with small effective sizes that undergo rapid population growth (Grant and Bowen 1998). Although they are similar, the different haplotypes in the populations suggest that there is no detectable gene flow between the three *P. senilis* population groups. This is also supported by the AMOVA results, which indicate that the largest percentage of genetic variation is spread throughout the population groups (99.5). There is little variation within lineages.

The  $F_{ST}$  and  $R_{ST}$  values (Table 2) and the haplotype networks (Figure 3) show that the populations of *P. senilis* are separated into three lineages with geographic distributions that do not overlap. In this study, the pattern observed in the haplotype network and the results from

molecular dating point to the diversification of the different haplotype groups 1.3 million years ago, even when a small number of haplotypes exist in the geographically distant groups (e.g., samples from southern Mexico and Nicaragua) with low levels of nucleotide diversity. Since the displacement range of this species has not been studied, it would be interesting to determine the displacement range of the populations throughout their territory, showing how dispersion capacity affects the genetic structure of their populations.

An analysis of endemism using four different groups of fauna found that after the Trans-Mexican Volcanic Belt separates the highest amount of biota between N and S Mexico and Central America, the Isthmus of Tehuantepec and the Nicaraguan depression are the following marked barriers (Miguez-Gutierrez et al. 2013). Correlating geologic and genetic studies to elucidate the patterns of biogeographic and evolutionary history in Central America, four tectonic blocks appear, Maya, Chortis, Chorotega, and Chocó, and three evolutionary groups separated by the barriers between these tectonic blocks emerge, the Mayan, Mid-CA, and Panamian. After the Great American Biotic Interchange (3.1 to 2.5 Ma) after the formation of the Isthmus of Panama, new migrations or colonizations prompted by the Pleistocene climatic fluctuations and local volcanic activity followed (Gutiérrez-García and Vázquez-Domínguez, 2013).

Prior studies based on mtDNA have revealed a strong differentiation between the populations of different vertebrates inhabiting Middle America. In the case of the glass frog *Hyalinobatrachium fleischmanni* six concordant genetic lineages have been described with geographical barriers of the Sierra Madre del Sur, the Tehuantepec isthmus, Motagua–Polochic–Jocotán fault system, Hess escarpment, and the Panama Isthmus (Mendoza et al. 2019). Regarding some clades of snakes, genetic divergences correspond to the depression of Nicaragua, the Chortis block, the Maya block, and the Isthmus of Tehuantepec. (Daza et al. 2010).

The Isthmus of Tehuantepec is undoubtedly an important barrier in the distribution of genetic lineages, as is the case of rodents of the genus *Reithrodontomys* (Sullivan et al. 2000), *Peromyscus* with 5.7% of divergence between its different groups (Kilpatrick et al. 2021), salamanders (Rovito et al. 2012; Rovito and Parra-Olea 2016), the toad *Incilus valliceps* (Mulcahy et al. 2006) and bats (Guevara-Chumacero et al. 2013, Hernández-Canchola and León-Paniagua 2017). Even the genetic structure of mammals with a higher dispersion capacity has been influenced by the Isthmus of Tehuantepec, as is the case of the coati *Nasua narica* (Nigenda-Morales et al. 2019).

Geological information (Barrier et al. 1998; Manea and Manea 2006) suggests that a highland corridor spanned the Isthmus of Tehuantepec during the Miocene, then collapsed due to extreme Pliocene tectonic activity (about 3.5 million years ago). This event separated the mountain ranges on either side of the isthmus. The genetic differences between the white-crowned parrot individuals on both sides of the isthmus match a more recent divergence after the geological events causing lowlands to form in the Isthmus of Tehuantepec; as observed in local mountain species (González et al. 2011; Ortiz-Ramírez et al. 2016).

The Nicaragua Depression determines a site that marks significant changes in the communities of Middle American birds (Patten and Smith-Patten 2008; Sánchez-González et al. 2008), acting as a barrier for other taxa that inhabit Central American rainforests. This pattern suggests that the dispersion and vicariance of lineages due to this barrier have occurred numerous times, even after the Pliocene (Bonaccorso et al. 2010; Gutiérrez-García and Vázquez-Domínguez 2012). This area also holds sway over vicariant events in Central America, being proposed as a region of numerous changes in the distribution patterns of many groups that it bars from the Middle American highlands (Marshall and Liebherr 2000). The Nicaragua Depression has also played a relevant role in the distribution of the bat *Sturnira hondurensis*, separating the continuous Mexico-Nicaragua area from another ideal habitat in the mountain regions of Costa Rica and Panama (Torres-Morales 2019). This pattern is evident in the rodent *Ototylomys phyllotis* since the depression acted as a barrier that influenced the rodent's phylogeographic pattern (Gutiérrez-García and Vázquez-Domínguez 2012). Daza et al. (2010) propose that hypotheses be generated and tested by combining phylogeographic studies with geological-tectonic data.

Throughout the distribution area of the white-crowned parrot, its phylogeographic structure matches that of other species of birds in this area of Middle America (Barber and Klicka 2010; Barrera-Guzmán et al. 2012; Rocha-Méndez et al. 2018; Castillo-Chora et al. 2021). The Middle American Turdus assimilis populations bared low genetic differentiation with a difference of 0.03 between individuals from northern Mexico and Central America, including the state of Chiapas, Mexico; this indicates that the Isthmus of Tehuantepec may be the boundary between these populations (Nuñez-Zapata et al. 2016). However, many examples of similarly distributed bird species exhibit a more pronounced genetic differentiation in almost the same range. The magnificent hummingbird Eugenes fulgens, whose phylogeographic pattern associated with Middle American highlands revealed three principal lineages: E. f. fulgens to the west of the Isthmus of Tehuantepec, and two groups of E. f. viridiceps to the east of the Isthmus, isolated from each other by the Motagua-Polochic-Jocotán fault system (Zamudio-Beltrán et al. 2020).

Not only geographical barriers can determine the population structure of Central American birds but also foraging ecology. Species that depend on seasonally variable plant reproductive parts present less geographic genetic differentiation compared to those that rely primarily on insectivorous diets (Miller et al. 2021). However, for the whitecrowned parrot, being a seedeater mainly, they still exhibit a divergence pattern in these areas. We can also see a division between the whitecrowned parrot individuals from Costa Rica and the other populations, which coincides with the lowlands of the Nicaragua Depression.

The evolutionary impact of the Nicaragua Depression on birds is also evident in several sets of taxa found on either side of the region. Such is the case of *Lepidocolaptes affinis*, whose phylogeographic pattern indicates that the Nicaragua Depression has prevented gene flow, even though the populations on both sides of the Isthmus of Tehuantepec did not show high genetic differentiation (Arbeláez-Cortés et al. 2010). On the other hand, *Catharus frantzii* at the Isthmus of Tehuantepec and populations on either side of the Nicaragua Depression presented a phylogeographic pattern (Ortiz-Ramírez et al. 2016). Another case is *Habia fuscicauda*, which has two clades: one that genetically corresponds to the region from southeastern Mexico to the Nicaragua Depression, and the other from the Nicaragua Depression to Central Panama (Castillo-Chora et al. 2021).

The estimated mean divergence time produced by BEAST analysis indicates that white-crowned parrot branched away from *P. chalcopterus* 1.33 Mya and that the other two clades differentiated

1.19 Mya. The Central lineage is dated at 840,000 years, and the Northern at 700,000 ys. Results from mitochondrial data suggest that these lineages parted during the Pleistocene, whose paleoclimatic dynamics and geological events were the main cause for swift, recent diversification in neotropical biota (Hackett and Lehn 1997; Haffer 1997).

Our work enabled us to reconstruct the phylogeographic pattern and evolutionary history of the white-crowned parrot, whose populations form into three distinct lineages. The Southern lineage is located to the south of the Nicaragua Depression, a geographic barrier for different species of birds. Comparison of the genetic variation in the populations from southern Mexico to Nicaragua against those from northern Mexico leads us to infer that the Isthmus of Tehuantepec is the barrier that keeps these two lineages apart. Our results prove that even though this divergence occurred during the Pleistocene, geographic barriers play an active role in the genetic structuring of a species.

Given the differences in plumage detected when the subspecies were named, and the marked genetic structure found with an absence of gene flow in the last 0.7–1.7 million years between the three metapopulations, it would be relevant to complete a study that included the vocalizations, morphology, and nuclear sequences of these three groups to determine whether they must continue to be treated as one species.

The strong genetic differentiation of the white.crowned parrot populations in three genetic lineages at the mitochondrial level requires the need to use independent conservation status for each. It is critical considering that the Northern and Central groups have decreased to the point of being eliminated in western Quintana Roo and some areas in the Gulf of Mexico (Salinas-Melgoza and Renton 2002). It is well-known that deforestation rates in tropical moist forests, oak groves, and lower montane forests are high, mainly because of the land transformation into agricultural activities (Rosete-Verges et al. 2014). In addition, it is unknown how biological mechanisms, physiological traits, phenotypic plasticity, local adaptations, interactions between species, dispersal capabilities, or food availability influence the permanence of populations (Hoffmann and Sgro 2011).

The three genetic groups detected in this study have a geographic concordance, which indicates that each group can be considered an Evolutionarily Significant Unit (ESU). ESUs are based on sequence marker-based phylogeographic analyses, defining ESUs as reciprocally monophyletic mitochondrial DNA (mtDNA) clusters with divergence (Moritz 1994). They can also be explained as intraspecific lineages with highly restricted gene flow between them, allowing the delimitation of the ESUs without reciprocal monophyly (Fraser y Bernatchez 2001). Our results on the genetic structure of the populations of the whitecrowned parrot have implications for conservation since most of the sites we studied represent very isolated and small populations, which need efficient protection actions at the regional level to preserve them, along with their habitats, and its genetic heritage. We propose that these three groups be considered a reference for the conservation programs of the white-crowned parrot in the countries where they are distributed including the maintenance of genetic connectivity between different populations with its effects on sustaining gene flow, to preserve this ESUs. It is also necessary to carry out a study in which the impact of habitat fragmentation is evaluated and that allows the establishment of more natural protected areas.

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#### Associate Editor

Luis Fabio Silveira

#### **Author Contributions**

Canek Rivera-Arroyo: conceptualization; resources; methodology; writing – original draft; writing – review & editing.

Patricia Escalante-Pliego: conceptualization; resources; methodology; writing – review & editing.

Damián Aguilar-Torres: methodology.

Milton F. Úbeda-Olivas: methodology.

## **Conflicts of Interest**

The authors declare that they have no conflict of interest related to the publication of this manuscript.

#### **Ethics**

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

#### **Data Availability**

The raw data for the samples collected under this study are available in this link: https://doi.org/10.48331/scielodata.TYSDUZ, SciELO Data.

All the gene sequences have been submitted to GenBank under accession numbers OP491996-OP492050, OP566431-OP566485, OP583596-583650.

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# Spatial and seasonal variation of benthic fish assemblages in whitewater rivers of Central Amazon

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Abstract: Despite the high number of fish species described for the Amazon region, the ichthyofauna that inhabits the depths of the main channels of large tropical rivers is one of the least known. In order to know the diversity patterns of these fish in whitewater rivers of the Central Amazon, we used data from the main channel benthic fish assemblage of the Japurá, Purus and Madeira rivers and tested the hypothesis that there are marked spatial and seasonal differences in the composition of the fish community among them. For this, we used a multivariate dispersion test, total  $\beta$  diversity and its decomposition into local (LCBD) and species contribution to  $\beta$  diversity (SCBD). Additionally, we tested for relationships between LCBD values and richness, total abundance, and environmental variables. We categorized species with higher SCBD values into resident or migratory to investigate the potential importance of floodplains to benthic fish assemblage of the main channel of whitewater rivers. Our results corroborate the proposed hypothesis, showing that there are seasonal and inter-river differences in benthic ichthyofauna, being more evident for the Purus River. LCBD showed strong negative relationships with species richness and total abundance, particularly in the Japurá and Madeira rivers in rising season, indicating that rivers and season with high uniqueness in their composition also had low richness and abundance. LCBD was negatively correlated with conductivity and pH, which increased with declining these environmental variables, as observed mainly in Japurá River in both seasons. Approximately one third of the species had higher than average SCBD values and were considered major contributors to  $\beta$  diversity, as well as classified as migratory. This demonstrates the importance of conducting studies that use spatial and seasonal variables, in addition to including the background fish fauna in conservation studies, expanding the protected area and taking into account the different patterns of diversity between rivers. Furthermore, these differences in assemblage composition might be explained by the asymmetrical spatial use of habitats during different seasons, strongly suggesting the importance of the flood-pulse cycle for maintaining diversity in this environment. Keywords: Ichthyofauna; distribution; composition; species richness.

## Variação espacial e sazonal de assembleias de peixes bentônicos em rios de água branca da Amazônia Central

*Resumo:* Apesar do elevado número de espécies de peixes descritas para a região amazônica, a ictiofauna que habita as profundezas dos principais canais de grandes rios tropicais é uma das menos conhecidas. Para conhecer os padrões de diversidade desses peixes nos rios de águas brancas da Amazônia Central, utilizamos dados da assembleia de peixes bentônicos do canal principal dos rios Japurá, Purus e Madeira e testamos a hipótese de que existem

marcadas diferenças espaciais e sazonais na composição da comunidade de peixes. Para isso, nós usamos um teste de dispersão multivariada, diversidade β total e sua decomposição em local (LCBD) e contribuição de espécies para diversidade  $\beta$  (SCBD). Além disso, testamos as relações entre os valores de LCBD e riqueza, abundância total e variáveis ambientais. Nós categorizamos as espécies com valores mais altos de SCBD em residentes ou migratórias para investigar a importância potencial das planícies de inundação para a assembleia de peixes bentônicos do canal principal dos rios de águas brancas. Nossos resultados corroboram a hipótese proposta, mostrando que existem diferenças sazonais e entre rios na ictiofauna bentônica, sendo mais evidente para o rio Purus. O LCBD apresentou fortes relações negativas com a riqueza de espécies e abundância total, principalmente nos rios Japurá e Madeira no período de enchente, indicando que rios e períodos com alta singularidade em sua composição também apresentaram baixa riqueza e abundância. O LCBD correlacionou-se negativamente com a condutividade e o pH, aumentando com o declínio dessas variáveis ambientais, como observado principalmente no Rio Japurá em ambos os períodos. Aproximadamente um terço das espécies apresentou valores de SCBD acima da média e foram considerados os principais contribuintes para a diversidade  $\beta$ , além de terem sido classificadas como migratórios. Isso demonstra a importância da realização de estudos que utilizem variáveis espaciais e sazonais, além de incluir a ictiofauna de fundo nos estudos de conservação, ampliando a área protegida e levando em consideração os diferentes padrões de diversidade entre os rios. Além disso, essas diferenças na composição da assembleia podem ser explicadas pelo uso espacial assimétrico dos habitats durante as diferentes estações do ano, sugerindo fortemente a importância do ciclo do pulso de inundação para a manutenção da diversidade neste ambiente.

Palavras-chave: Ictiofauna; distribuição; composição; riqueza de espécies.

## Introduction

The plurality of Amazonian environments shelters a high diversity of the freshwater ichthyofauna, being the most diverse in the world (Albert & Reis 2011). South America alone contains more than 5,000 described freshwater fish species, of which approximately half are found in the Amazon Basin (Jézéquel et al. 2020, Reis et al. 2016). Despite the high number of fish species described for this region, the fish assemblages that inhabit the bottom depths of the main channels of large tropical rivers are among the least known ichthyofauna due to difficulties obtaining samples from this biotope (Duarte et al. 2019a, b). Thereby, studies performed in this type of environment have often led to the discovery of new taxa and records of rare species (*e.g.*, De Santana & Vari 2012, Lundberg et al. 2013, Walsh et al. 2015).

The high tropical diversity has been attributed to many factors, including seasonal flood-pulse dynamics, which affect many ecological and environmental processes, by allowing lateral connectivity to adjacent floodplain habitats (Kong et al. 2017, Lowe-McConnell 1987, Tockner et al. 2000). This seasonality shapes many interconnected community and population dynamics (Lowe-McConnell 1987), including animal movements, feeding, growth and reproductive activity (Cox-Fernandes 1997, Winemiller & Jepsen 1998, Röpke et al. 2016).

Given that seasonality in tropical rivers induces major changes in water levels, such changes can potentially promote species coexistence, and therefore high species richness (Lowe-McConnell 1987, Henderson et al. 1998, Albert & Reis 2011). Consequently, strong spatio-temporal variations in community structure and compositions are expected within flood-pulse systems. Thus, understanding such seasonal effects and identifying which factors may be involved in their variation is critical for quantifying biodiversity patterns and may contribute to improve conservation strategies (Kong et al. 2017).

Several methods have been developed to measure variation spatio-temporal in species composition, *i.e.*  $\beta$  diversity (Anderson et al. 2011, Legendre 2008). Conceptually,  $\beta$  diversity beta is the variation in species composition among sites within a geographical area of interest (Whittaker 1960). It brings information about local and regional diversity. In this sense, Tuomisto (2010a, b) states that beta diversity can be applied in studies involving communities in a regional macro scale. This approach can be seen in other studies (Qian et al. 2005, Mondal & Bhat 2022). Recently, the proposal by Legendre & de Cáceres (2013) allows the total  $\beta$  diversity (BD<sub>total</sub>) estimated from a site-by-species abundance matrix to be partitioned into components of local contribution to  $\beta$  diversity (LCBD) or species contribution to  $\beta$ diversity (SCBD). LCBD indicates sampling sites with high ecological uniqueness, that is, with quite different species composition from the others and, therefore, contributing more to  $\beta$  diversity. SCBD represents the relative importance of each species in influencing patterns of  $\beta$ diversity, signaling those species that present high variation between sites in the study area or that are abundant in the few places where they occur (Legendre & de Cáceres 2013). Instead of relying solely on total β diversity values, a decomposition into site and species contribution provides more detailed insights on the spatio-temporal patterns of community composition variation (Kong et al. 2017, Leão et al. 2020).

Furthemore, studies that seek to identify the species that inhabit a particular environment and the factors that affect the dynamics of this community become fundamental for future management programs and conservation (Magurran & Dornelas 2010), mostly, in face of anthropogenic activities, including resource overexploitation, habitat loss and climate change, that are currently causing profound transformations in ecosystems and unprecedented loss of biological diversity (Tedesco et al. 2013, Frederico et al. 2021). Among these activities is commercial fishing, which is carried out in the lower reaches of the main whitewater rivers of the Brazilian Amazon, such as Japurá, Purus and Madeira, comprising the 'main commercial fishing region' (Goulding et al. 2018).

Using data from benthic fish assemblage of the main channel of whitewater rivers of Central Amazon (Japurá, Purus and Madeira rivers), we tested the hypothesis that there are marked spatial and seasonal differences in community composition. Despite being rivers with similar characteristics, their origins and basin formation can offer different conditions that are reflected in the composition of fish species (Lundberg et al. 1998, Nakamura et al. 2021). In addition, current fishing pressures on species, as mentioned, and even environmental changes caused by rising and receding water levels during the flood pulse can lead to changes in the biotic communities present in each river. For this, we assessed  $\beta$  diversity patterns across a receding and rising season in each river. To test our hypothesis, we (i) investigated whether there was variation in species composition between rivers and between seasonal periods; (ii) evaluated the contribution of sites and species to overall  $\beta$  diversity along habitat gradient (spatial) and seasons; and (iii) investigated the potential importance of floodplains to benthic fish assemblage in the main channels of whitewater rivers of Central Amazon.

#### **Material and Methods**

#### 1. Study area and sampling

This study was carried out in the mainstem channels of the lower reaches of the major whitewater rivers of Central Amazon: Japurá, Madeira and Purus rivers (Figure 1). Amazonian waters are classified into three distinct biogeochemical categories (Bogotá-Gregory et al. 2020, Ríos Villamizar et al. 2020): (1) blackwater, (2) clearwater and (3) whitewater: (1) nutrient-poor, low-sediment, high-transparency with humic-stained, and acidic blackwaters originating from deeply weathered soils overlying lowland tropical forests; (2) nutrient-poor, low-sediment, high-transparency, and neutral clearwaters originating from upland shield formations dominated by Precambrian rocks; (3) nutrient-rich, low-transparency, neutral whitewaters, with high loads of fertile alluvial suspended sediment. The Amazon River and its tributaries possessing their headwaters in the Andes, such as the Madeira and Japurá rivers, or those draining the western lowlands, such as the Purus River, constitute the so-called white- or muddy-water rivers, with a high load of sediments and dissolved inorganic solids (Goulding et al. 2003). The whitewater rivers show as general characteristics, a low transparency (0.10 to 0.60 m) due to erosion processes in their headwaters. These regions are mostly composed of alkaline soil and it is relatively rich in mineral salts, which result in almost neutral pH (6.5 to 7.5) and relatively high conductivity (40 to 300  $\mu$ S cm<sup>-1</sup>) (Bogotá-Gregory et al. 2020). However, the physico-chemical characteristics are strongly influenced by seasonal variations in water level as well (Ríos Villamizar et al. 2020).

We established 10 sampling sites along each river course, separated by ~30 km (Figure 1). Sampling took place during rising and receding water seasons (Figure 1), from 2012 to 2014: Madeira River, September 2012 (receding) and March 2013 (rising); Japurá River, April 2013 (rising) and August 2013 (receding); Purus River, September 2013 (receding) and April 2014 (rising). Fish were sampled using a bottom trawl net with an external mesh size of 4 cm and an internal net in the form of a "funnel" (0.5 m height, 3 m long and 3 m wide; 5 mm mesh size). A parallel trawl was performed at each sampling site, following the current direction, with 10 min total duration time per trawl. It is highlight that despite the collections having been carried out in a standardized way, some sampling sites no fish were collected (see Table 1). The fishes collected were euthanized in eugenol solution (clove oil) and fixed in 10% formalin solution, before being transported to the laboratory. At the Laboratory of Systematics and Ecology at the National Institute of Amazon Research (INPA), samples were sorted, identified to species level, counted, washed to remove formalin and then preserved in 70% ethanol. Voucher specimens were deposited in the INPA Fish Collection.

#### 2. Environmental data

We measured several environmental variables in each site, namely depth, distance between the riverbanks, current velocity, temperature,



Figure 1. Maps showing the location of Japurá, Purus and Madeira rivers with sampling sites. Note the left panels indicates boundary of the Amazon basin with respective sampling sites in the Central Amazon.

**Table 1.** Sampling sites with their LCBD (local contribution to beta diversity) indices in each river-season: Jap = Japurá River; Mad = Madeira River; Pur = Purus River; Ris = Rising; Rec = Receding. Bold indicates significant values (P < 0.05). Sampling sites not listed here mean that no fish were collected.

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Mad-Rec 10	0.015	0.976
Pur-Rec 1	0.015	0.974
Pur-Rec 2	0.019	0.401
Pur-Rec 3	0.014	0.995
Pur-Rec 4	0.016	0.936
Pur-Rec 5	0.016	0.895
Pur-Rec 6	0.014	0.999
Pur-Rec 7	0.017	0.831
Pur-Rec 8	0.014	0.996
Pur-Rec 9	0.015	0.963
Pur-Rec 10	0.014	0.994

dissolved oxygen, pH and conductivity, since these variables can potentially show seasonal variation in tropical rivers (Thomé-Souza & Chao 2004, Röpke et al. 2016, Duarte et al. 2019a) (Table S1). Depth (m) was monitored during each trawl using a portable echo sounder, with measurements taken every minute for calculation of the mean depth per trawl. Distance between the riverbanks (m) was assessed using a global positioning system (GPS). Current velocity (m s<sup>-1</sup>) was measured near the bottom using a digital flow meter (Flowatch FL-K2) with a sensor coupled to a 15 m cable, for this measurement, the boat engine was turned off and following the current direction (downstream). Temperature (°C), dissolved oxygen (mg mL<sup>-1</sup>), pH and conductivity ( $\mu$ S cm<sup>-1</sup>) were assessed from three measurements taken along the transect travelled by each trawl. Measurements were taken using a multiparameter device (U-50, Horiba) using water samples collected near the bottom with a Van Dorn horizontal bottle sampler (5 L).

#### 3. Statistical analyses

To investigate whether one or more rivers and seasons was more variable than the others in terms of species composition, we used homogeneity of multivariate dispersion method to determine whether the dispersion (degree of variability among sites) of each group (riverseason) around their group centroid was significantly different from one another. Non-Euclidean distances between objects and group centroids are handled by reducing the original distances to principal coordinates. Additionally, this analysis creates a set of confidence intervals on the differences between the mean distance-to-centroid of the levels of the grouping factor with the specified family-wise probability of coverage, the Tukey's 'Honest Significant Difference' method. Thus, this method provides a measure of the  $\beta$  diversity of groups (*i.e.*, rivers and seasons in our analysis) and was implemented using the *betadisper* call in the *vegan* package, PERMDISP2 procedure (Anderson et al. 2006).

To calculate  $\beta$  diversity, we followed the approach proposed by Legendre & de Cáceres (2013), which quantifies the total variance in a species-by-site community matrix as an estimate of the total dissimilarity (BD<sub>total</sub>). First, the species abundance data were subjected to a Hellinger transformation, which is adequate for dissimilarity assessments (Legendre & de Cáceres 2013). We quantified total  $\beta$ diversity (BD<sub>total</sub>) combining all sites and seasons. The generated index ranges from 0 to 1, where 1 indicates maximum dissimilarity (*i.e.*, all sites have completely different composition) and 0 indicates maximum similarity between sites. In addition, we calculated the local contribution to beta diversity (LCBD), and the species contribution to beta diversity (SCBD). For both LCBD and SCBD, the sum of the indices is equal to 1, since they represent a relative contribution to total dissimilarity. BD<sub>total</sub>, LCBD and SCBD indices were computed using the function *beta.div* in the *adespatial* package (Dray et al. 2021). Significance of individual LCBD values was tested for using the permutation procedure of Legendre & de Cáceres (2013). In addition, for investigating the potential importance of floodplains to benthic fish assemblage of the main channel of whitewater rivers, we categorized species with higher SCBD values into resident or migratory based on some studies of fish diversity, description and record of these species in distinct habitats such as floodplain lakes or adjacent wetlands (*e.g.*, Cox-Fernandes 1997, De Santana & Vari 2012, Lundberg et al. 2013, Duarte et al. 2022).

To test for differences in sites contribution (LCBD) between rivers and seasons, we used a One-way Analysis of Variance (ANOVA) followed by Tukey's test (P < 0.05) for multiple comparisons, with the assumptions of normality and homogeneity of the variances being test, using the R function aov. In addition, to investigate whether LCBD could be linked to community-level metrics, we performed Spearman correlations with species richness and total abundance of the assemblage in each river and season. Thus, it was possible to assess if the rivers and seasons that contributed the most to  $\beta$  diversity (higher values of LCBD) were more or less rich and/or numerical abundant (Heino & Grönroos 2017). Finally, the local scale environmental variables described above (Table S1) were used to assess possible relationships with LCBD. First, these variables were normalised (log<sub>10</sub>) and we used the Variance Influence Factor (VIF) to verify multi-collinearity between all these predictive environmental variable candidates. Those that presented a VIF  $\geq$  10 were considered strongly correlated. In this step, we excluded distance between the riverbanks and current velocity. The VIF analysis was performed using the function vif.cca in the vegan package and the correlations between LCBD and local environmental variables were examined using the corrplot package (Wei et al. 2021). We also used the dbRDA (distance-based redundancy analysis), which is a constraint ordination method using non-Euclidean distance measures that reveals relationships between community structure, sites and environmental variables (Legendre & Anderson 1999). Significance of each variable was assessed using 999 permutations in ANOVA. For this analysis we used log-transformed (log10 (x+1)) species abundance data, using only species with SCBD values higher than the mean, which a total of 30 species. The environmental variables were also normalized  $(\log_{10})$  and had been previously selected using the *stepwise* method with permutation tests. All statistical procedures were conducted in R (R Core Team, 2018).

#### Results

#### 1. Fish sampling

Sampling yielded a total 7,289 individual fish from 107 species, 18 families and 7 orders (Table S2). The order Siluriformes represented the largest number of species (62) followed by Gymnotiformes (36). The family Apteronotidae represented 21 species and Doradidae represented 19 (Table S2). *Sternarchella calhamazon* (Lundberg, Cox Fernandes, Campos da Paz & Sullivan, 2013) was the most abundant species in the Japurá and Purus rivers, representing 45.7% and 16.3%, of the total collected, respectively. For the Madeira River, the doradidae *Opsodoras boulengeri* (Steindachner, 1915) was the most abundant species, with 19.2% of the total collected in this river (Table S2). More species and more individuals were captured in Purus River in receding season, while the smaller number of species and total abundance in Madeira River in rising season (Table S2). Overall, sampling revealed that many of benthic fish species were rare in terms of numerical abundance, whereby 29 species (27% of the total) only yielded one individual each (Table S2).

#### 2. Beta diversity, LCBD and SCBD

We detected marked variation in overall species composition between rivers and seasons (PERMDISP2, F = 6.93, P < 0.001; Figure 2). The Purus seasons were not distinct from one another in terms of species composition, but differed from the other rivers (Figure 2 and Table 2).

The total  $\beta$  diversity was 0.843 and local contribution to beta diversity (LCBD) ranged between 0.026 and 0.014 (Table 1). We found a strong difference between rivers and seasons (ANOVA: LCBD:  $F_{(5.47)} = 6.552$ , P < 0.001), with the highest values observed for Madeira River in rising season (sampling sites 4 and 10), Japurá River in rising season (sampling sites 2, 8, 9 and 10) and Japurá River in receding season (sampling sites 2 and 10) with significant LCBD indices (P < 0.05) (Table 1), making these sampling sites, in respective rivers and seasons, the



Figure 2. Plot of the groups (river-season) and distances (Bray-curtis) to centroids on the first two PCoA axes. PERMDISP2 multivariate analysis determines the degree of dispersion among sites of each group around their centroid. Jap = Japurá River; Mad = Madeira River; Pur = Purus River; Ris = Rising; Rec = Receding.

**Table 2.** Result of Tukey multiple comparisons of means with 95% familywise confidence level among the rivers and seasons. Bold indicates significant values (P < 0.05). Jap = Japurá River; Mad = Madeira River; Pur = Purus River; Ris = Rising; Rec = Receding.

	Jap-Ris	Jap-Rec	Mad-Ris	Mad-Rec	Pur-Ris	Pur-Rec
Jap-Ris	*	0.9999	0.9939	0.9649	0.0029	0.0032
Jap-Rec	0.9999	*	0.9989	0.9885	0.0069	0.0073
Mad-Ris	0.9939	0.9989	*	0.9999	0.0306	0.0322
Mad-Rec	0.9649	0.9885	0.9999	*	0.0306	0.0324
Pur-Ris	0.0029	0.0069	0.0306	0.0306	*	0.9999
Pur-Rec	0.0032	0.0073	0.0322	0.0324	0.9999	*

largest contributor to  $\beta$  diversity. The pairwise comparison showed that Purus River in receding season were significantly different (P < 0.01) from Japurá River (both seasons) and Madeira River in rising season. All other comparisons were not significant (P > 0.05) (Table S3). LCBD showed strong negative relationships with both species richness (r = -0.821, P < 0.001) and total abundance (r = -0.806, P = 0.001). This indicates that overall, sites that presented high uniqueness in their composition also had low number of species and/or individuals, a pattern observed primarily in Japurá and Madeira rivers in rising season.

Species contribution to beta diversity (SCBD) ranged between 0.0642 and 0.0002, with values higher than the mean (0.0093) for 30 species (28% of the total captured; Table S2). The electric fish Steatogenvs elegans (Steindachner, 1880); catfish Calophysus macropterus (Lichtenstein, 1819) and Pimelodus blochii (Valenciennes, 1840), were the three largest contributors to  $\beta$  diversity (0.0642, 0.0596, and 0.0546, respectively; Table S2). Rare species with only one individual, such as Magosternarchus duccis (Lundberg, Cox Fernandes & Albert, 1996); Platyurosternarchus macrostoma (Günther, 1870) and 'black piraíba' Brachyplatystoma capapretum (Lundberg & Akama, 2005), presented extremely low contributions to beta diversity  $(\leq 0.0003$ ; Table S2). Of these 30 species with SCBD values exceeding the mean, most were categorized as migratory (28 species), only the Loricariidae Apistoloricaria ommation (Nijssen & Isbrücker, 1988) and the Apteronotidae Orthosternarchus tamandua (Boulenger, 1898) were categorized as resident (Table S2).

#### 3. Environmental conditions

The environmental variables measured varied both by river and seasonal period (Table S1). According to our analyses, among the environmental variables selected, only conductivity and pH showed significant correlations with LCBD (P < 0.05, Figure 3). Specifically, LCBD increased with declining conductivity and pH (Figure 3), as seen at Japurá River in both seasons (Table S1).

The dbRDA model testing the association between species with SCBD values higher than the mean and environmental variables was significant (F = 2.99, P = 0.001), explaining 26% of variation. All environmental variables tested, except for distance between the riverbanks and current velocity, had a significant (P < 0.05) effect on fish assemblage (Figure 4). According to these results, species like catfishes *Calophysus macropterus* (Lichtenstein, 1819) (Cama) and *Pimelodus blochii* (Valenciennes, 1840) (Pibl) were associated with higher values of depth and dissolved oxygen (Figure 4), as seen at Purus River in



Figure 3. Correlations between environmental variables (see legend in Table S1) and local contribution to beta diversity (LCBD). Size of symbol is proportional to the maximum absolute value of the correlation coefficient (i.e., 1). The cross symbol means that the given correlation is not statistically significant at  $\alpha = 0.05$ .



Figure 4. Redundancy analyses (dbRDA) relating species with SCBD values higher than the mean and environmental variables: Depth, temperature (Temp), dissolved oxygen (DO), conductivity (Cond) and pH. Only significant variables (P < 0.05) are shown in the figure. Details about the environmental variables and species are given in Tables S1 and S2 respectively.

rising season (Table S1). However, the environmental variables were not determinants of the distribution of the most species for rivers and seasons once the species closer to the center of the ordination exhibited very low scores on the dbRDA.

#### Discussion

Our results support our hypothesis of marked spatial and seasonal differences in community composition of benthic fish assemblages in whitewater rivers of Central Amazon. We further detected marked variation in community composition between rivers and seasons, with Purus River in both seasons being distinct from the other rivers and seasons in terms of species composition. Approximately one third of the species contributed to overall  $\beta$  diversity and most were classified as migratory. LCBD values revealed differences between seasons, while sites' contributions were related to different environmental variables.

Studies carried out in the lower stretches of the whitewater rivers have been considered as highly important biological areas as they shelter a great diversity of fish species (e.g., Cox-Fernandes et al. 2004, Silva et al. 2010, Duarte et al. 2019a, Duarte et al. 2022). Our results show that this diversity also extends to the bottom depths of the main river channel. Here we confirm that information showing a high diverse bottom-dwelling ichthyofauna, with 107 species representatives of the main Amazonian fish orders (57.9% Siluriformes and 33.6% Gymnotiformes). These numbers correspond to  $\sim 4\%$  of the fish species richness estimated for the entire Amazon Basin, estimated to be  $\sim$  2,400 fish species (Jézéquel et al. 2020). No other broad study has been conducted in the main channel of these rivers, except for the Calhamazon Project (1992-1997), which was the first study to investigate the bottom-related ichthyofauna of these rivers. During that project, a broad sampling of the fish species from each of the main river channels of the Brazilian Amazon basin was performed using benthic trawls. In one of the studies conducted as part of that project, Cox-Fernandes (1999) noted that whitewater rivers, including the Japurá, Madeira and Purus rivers, are largely responsible for the great diversity of electric fishes in the Solimões-Amazonas system.

Seasonal variations in water levels can cause temporal changes in the benthic fish assemblages from the channels of the Amazonian rivers (Thomé-Souza & Chao 2004, Duarte et al. 2019a, Duarte et al. 2022). During the rising season, when the marginal areas are flooded, many fish migrate laterally towards these areas, where they may find better feeding conditions and refuge from predators (Duarte et al. 2019b). Conversely, during the receding season, when the water level declines, the fish follow this movement towards the river channels, which results in a high concentration of fish in these areas (Cox-Fernandes 1997, Duarte et al. 2019a, b). Thus, a high concentration of fish in the main channel explains their higher capture rates during the receding seasons, both in terms of the number of species and the number of individuals, as well as the greater similarity between these assemblages (Cox-Fernandes 1997, Duarte et al. 2019a). These continual disassembly and reassembly cycles of local communities across a spatially heterogeneous landscape are responsible for the high local fish diversity in Amazonian floodplains (Arrington & Winemiller 2004). However, it is also worth mentioning that the rising season may be more unpredictable in terms of fish species composition due to the species reassembling process or sampling limitations, because it is more difficult to catch fish in this season when the water depth is higher and the ichthyofauna is more dispersed (Duarte et al. 2019a).

Our results are consistent with the expectation that fish community composition varies within floodplain systems (Arrington & Winemiller 2004, Kong et al. 2017), with Purus River species composition being most distinct than that of the other rivers and seasons. For instance, Röpke et al. (2016), studying the seasonal dynamics of the fish assemblage in a floodplain lake at the confluence of the Negro and Amazon rivers, observed that assemblage composition was strongly influenced by the seasonality of these rivers. Consequently, temporal  $\beta$  diversity was high, and the assemblage was dominated by seasonally transient species. Both short- and long-distance movement capabilities of species affect the composition of local assemblages. Short movements between the main watercourses and seasonally available habitats have been reported for Amazonian fishes, from headwater ecosystems (*e.g.*, temporary pools; Espírito-Santo et al. 2017) to floodplain rivers (Cox-Fernandes 1997, Mormul et al. 2012). Specifically, the spatial distribution of fish species is linked to their dispersal capability and ability to colonise new environments, as well as their ability in responding to variations in water depth (Espírito-Santo et al. 2017). The movement of fishes in the rising season is certainly higher than in the receding season due to expansion of the river to the floodplain, leading to a mixture of species from different habitats (*e.g.*, river channel and floodplain; Cox-Fernandes 1997).

Large LCBD values indicate sites that have highly different species compositions (Legendre & de Cáceres 2013). From a conservation planning perspective, large LCBD values may indicate sites that have unusual species combinations and thus have potentially high conservation value - or conversely, degraded and species-poor sites in need of ecological restoration, or even those with invasive species. While LCBD may be inversely correlated with species richness and abundance, as observed in our results, as well as in several other groups (e.g., freshwater insects; Heino & Grönroos 2017; dung beetles and mammals; Da Silva et al. 2020), these patterns remain relatively unexplored, and there are also studies with different results (Vilmi et al. 2017, Santos et al. 2021). Determining the factors that influence local contribution to beta diversity (LCBD) is a complex task, as the processes that govern this contribution are difficult to predict (Legendre & de Cáceres 2013). Indeed, different studies have found support for positive and negative effects of different variables in different systems (e.g., Kong et al. 2017, Leão et al. 2020). Thus, whether these patterns of site contributions and their relationships with community characteristics and environmental variables will show some degree of generality across taxa and habitats remains unanswered and will require further research.

Among the environmental variables assessed, two were important in explaining the spatial and temporal (seasonal) contribution to compositional differences. Conductivity and pH presented a negative relationship with LCBD. This indicates that ß diversity received a higher contribution from sites with lower conductivity and pH, as observed in Japurá River in both seasons. According to Ríos Villamizar et al. (2020) depending on the sampling date (i.e., season), whitewater river like Japurá can have intermediate chemical characteristics between white and black water. In the case of Japurá River, it is characterized as a river of low conductivity water that receives seasonal inputs from major connecting channels to the Solimões River during the rising season (Goulding et al. 2003, Bogotá-Gregory et al. 2020). During a study to investigate how Amazonian fish community composition and species richness are influenced by water type, Bogotá-Gregory et al. (2020) observed that whitewater communities' structure were distinct from those of blackwaters and clearwaters, with community structure correlated strongly to conductivity and turbidity. Studies conducted in similar tropical aquatic environments have shown that the ichthyofauna richness and biomass were positively related to the electrical conductivity and nutrient concentration in the water (Saint-Paul et al. 2000), pH, concentration of silicate, and the basin drainage

area, as Cox-Fernandes (1999) noted for the main whitewater tributaries of the Amazon River, including the Japurá, Purus and Madeira rivers.

Species contribution to beta diversity (SCBD) showed that relatively ubiquitous species that occur at variable abundances across sites contributed most to  $\beta$  diversity, being represented by approximately one third of the species, this value is higher than that found in other studies (Legendre & de Cáceres 2013, Leão et al. 2020, Santos et al. 2021). In view of that higher values of SCBD indicate heterogeneous distribution of taxa throughout the sites, rare species with low occurrence and abundance have extremely low contributions to  $\beta$  diversity (Legendre & de Cáceres 2013). This may reflect factors such as: individual characteristics of each species, dispersion abilities or interaction with abiotic variables (Siegloch et al. 2018, Leão et al. 2020). Previous studies indicated that physical changes in aquatic environments due to temporal variation appear to influence the abundance and richness of benthic fish species in the channels of the Amazonian rivers (Thomé-Souza & Chao 2004, Duarte et al. 2019a). During the extreme drought of 1997-98 following an El Niño event in the Negro River, Thomé-Souza & Chao (2004) observed reductions in both the abundance and richness of benthic fish species, which may have been caused by predation or migration. These authors argued that as the water recedes and becomes more transparent in the dry season, predation pressure on benthic fishes may be amplified, and some species may also perform longitudinal migrations (Thomé-Souza & Chao 2004). Furthermore, the width and depth of the main channel may have important effects on the reproductive biology of catfish that use the river channels to reproduce, as well as on the development and distribution of their larvae (Leite et al. 2007). In our study, the larvae and juveniles of the Pimelodidae catfish *Calophysus macropterus* – one of the largest contributors to  $\beta$ diversity (SCBD= 0.0596) - were collected in Purus River during the rising season, and a previous study has shown that the seasonal growth in C. macropterus is correlated with the flood pulse, especially in periods of rising and falling waters (Pérez & Fabré 2009). Additionally, the physical and chemical characteristics of the channels may have spatial and seasonal variations affecting the larvae of the main migratory catfish species in the Amazon basin (Leite et al. 2007). However, conditions that are considered optimal for one species can vary with their lifecycle stage (Matthews 1998), which is associated with diet changes during ontogeny, the use of different water column depths for protection against predation or the availability of food resources.

In summary, we show that the community composition of benthic fish assemblages varies spatial and seasonally, which highlights the importance of studying temporal variations in future ecological studies, especially in the still understudied Amazon region (Arrington & Winemiller 2004, Duarte et al. 2019a, Duarte et al. 2022). It is also important to point out that several areas in these rivers have been set aside to protect and conserve biodiversity, as in the protected areas (PAs) of this study (e.g., Piagaçu-Purus Sustainable Development Reserve in Purus River and Mamirauá Sustainable Development Reserve in Japurá River). The deep-river channels have generally been used as boundaries for these protected areas, so the deep-river communities may not be specifically included within protected areas. Generally, the large whitewater rivers extend well upstream from the protected areas, so the deep-river habitats may be vulnerable to human disturbances upstream, such as dams, agricultural intensification and deforestation (Couto et al. 2021, Duponchelle et al. 2021). Furthermore, maintaining lateral

connectivity (including the river and its floodplain) and connectivity between upstream and downstream habitats is essential for many migratory fishes (short- and long-distance migrants). If migratory fishes of commercial importance spawn in these river channels, then habitat degradation may adversely affect the future of commercial fishing (Duponchelle et al. 2021). For these reasons, the whitewater rivers and other Amazonian systems need to be managed as watersheds with careful attention to downstream effects of development activities.

#### **Supplementary Material**

The following online material is available for this article:

Table S1 - Mean  $\pm$  SD, minimum and maximum range for the environmental variables measured per river and season: Depth, Distance between the riverbanks (DBRB), Current velocity, Temperature (Temp), Dissolved Oxygen (DO), pH and Conductivity (Cond).

Table S2 - Number of individuals of each species sampled per river and season. In parenthesis, the species used in the dbRDA analysis, with respective acronyms. Total abundance (N) and number of species (S) are shown at the end of the table. Asterisks indicate species with their SCBD values (species contributions to beta diversity) above the overall mean (0.0093) and bold shows the three species with the highest values (SCBD). The letters on the side SCBD values refers to categorization of species into resident (R) or migratory (M).

Table S3 - Pairwise comparisons of LCBD (local contribution to beta diversity) among the rivers and seasons using ANOVA. Bold indicates significant values (P < 0.01). Jap = Japurá River; Mad = Madeira River; Pur = Purus River; Ris = Rising; Rec = Receding.

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#### **Author contributions**

Cleber Duarte: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Thatyla Luana Beck Farago: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Camila Saraiva dos Anjos: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Natasha Rabelo dos Santos: Contribution to data collection; Contribution to manuscript preparation. Lindaura Maues do Nascimento: Contribution to data collection; Contribution to manuscript preparation.

Ariana Cella-Ribeiro: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Cláudia Pereira de Deus: Substantial contribution in the concept and design of the study; Contribution to critical revision, adding intellectual content.

#### **Conflicts of Interest**

The authors declare that they have no conflict of interest related to the publication of this manuscript.

#### Ethics

The collects were made under the license of the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO) nº. 22121-1 and 37632-2.

#### **Data Availability**

The data used in our analysis is available at Biota Neotropica Dataverse

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