ORIGINAL ARTICLE





Quantifying shortfalls in the knowledge on Neotropical Auchenipteridae fishes

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Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 302406/2019-0, 308694/2015-5, 314523/2014-6 and 434391/2016-6; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 23038.042984/2008-30

Abstract

The Neotropics harbour the greatest diversity of freshwater fish on Earth. Despite recent advances in characterizing the fish fauna, the total number of species, distributional range, evolution and ecological traits remain uncertain. Thus, we quantify shortfalls in the knowledge of taxonomy (Linnean shortfall), geographic distribution (Wallacean shortfall), evolutionary relationships (Darwinian shortfall) and feeding habits (Raunkiæran shortfall) of Auchenipteridae driftwood catfishes, one of the most representative groups of the Siluriformes family in the Neotropics. We find a steep increase in the historical accumulation of valid species over time, suggesting that 45% of the total number predicted remains to be described. Auchenipterids also remain under-collected; only 45% of the ecoregions and less than 3% of the onedegree grid cells covering the Neotropics are reasonably sampled. The topologies of recent phylogenies are more similar to each other than former ones, showing a tendency towards a robust phylogenetic hypothesis for this family. Current knowledge on feeding habits is biased towards a few genera and species and is still expanding with every new published study. Our study highlights specific knowledge gaps that need to be addressed: a considerable number of Auchenipteridae species remain to be described; and most of valid species lack reliable information on their geographic

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distribution and feeding habitat. It implies that research on fish systematic biology needs to advance and it will require a concerted effort of taxonomists, ecologists and biogeographers to reduce these gaps.

KEYWORDS

driftwood catfish, evolution, feeding ecology, geographic distribution, knowledge shortfalls, taxonomy

1 | INTRODUCTION

Discovering and describing how many species there are on Earth remain pivotal pursuits for biologists. Yet, acute changes in the Earth's environment like climate change and widespread loss of natural habitats threaten many species that remain virtually invisible to science (Zhang, 2011). The risk of losing species before even knowing them is aggravated by decreasing investments for research (Thomson et al., 2018; Troudet, Grandcolas, Blin, Vignes-Lebbe, & Legendre, 2017) and increasing threats to natural habitats (Joppa, Roberts, Myers, & Pimm, 2011). In this context, identifying and quantifying the current shortfalls in our knowledge of biodiversity can help defining priorities for future ecological and evolutionary research as well as for drawing effective biodiversity conservation programmes.

Knowledge on the distribution, ecology and evolution of most taxa on Earth is scarce or even absent (Cornwell, Pearse, Dalrymple, & Zanne, 2019; Hortal et al., 2015; Pelayo-Villamil et al., 2015). Such knowledge paucity matters because inaccurate taxonomy leads to inconsistent and/or uncertain estimates of the species' geographic ranges, phylogenetic relationships, or abundances and population dynamics (Cardoso, Erwin, Borges, & New, 2011; Hortal et al., 2015; Lomolino, 2004; Rocchini et al., 2011). Further, the lack of knowledge on species distributions precludes the identification of species feeding habits and tolerance to environmental conditions (Cardoso et al., 2011; Ferrier, 2002). These so-called knowledge shortfalls are thus related to each other (Cornwell et al., 2019; Hortal et al., 2015). Yet, most studies quantifying deficiencies in the current knowledge of species focus on specific shortfalls (e.g. Lobo, Baselga, Hortal, Jiménez-Valverde, & Gómez, 2007; Stropp et al., 2016; Troudet et al., 2017), a pragmatic approach that, however, does not provide an overall picture of how scientific progress is filling in knowledge gaps on biodiversity information.

Shortfalls in biodiversity knowledge can be defined as the gaps between realized/existing knowledge and the complete knowledge of any aspect of biodiversity within a biological domain at a given moment (Hortal et al., 2015). Given the limited resources for biodiversity research (Barber et al., 2014), it is crucial to develop scientifically sound criteria for quantifying the various knowledge shortfalls. These criteria can assist in directing a scientific effort to address persistent and/or easy-to-fill knowledge gaps. In this context, seven knowledge shortfalls covering critical aspects of biodiversity have been proposed, aiming to account for the lack of knowledge on the

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total species richness on Earth (Linnean); the geographic distribution of species (Wallacean); species abundance and population dynamics (Prestonian); the evolution and phylogenetic relationships of species or lineages (Darwinian); species tolerances to abiotic factors (Hutchinsonian); species traits and functions (Raunkiæran); and biotic interactions (Eltonian) (see Hortal et al., 2015 for a complete description).

Fishes are the most diverse group among vertebrates (Nelson, Grande, & Wilson, 2016). It is especially true for the vast Neotropical ichthyofauna (Albert, Tagliacollo, & Dagosta, 2020; Dagosta & Pinna, 2019; Lundberg, Kottelat, Smith, Stiassny, & Gill, 2000), with current estimates ranging between 8,000 and 9,000 species (Reis et al., 2016). Auchenipteridae is one of the most representative groups of the Siluriformes in the Neotropics. This family currently includes 126 species (Calegari, Vari, & Reis, 2019; Fricke, Eschmeyer, & van der Laan, 2020), 22 genera, and is composed by two subfamilies: Auchenipterinae (77 species) and Centromochlinae (49 species). The driftwood catfish family (Auchenipteridae) is widely distributed along all major cis-Andean basins, with few species in the Caribbean trans-Andean

drainages and a single species in the Pacific slope (Ferraris, 2003). Species of this family can vary in body size—a miniature species such as *Gelanoglanis* measuring about 30 mm of standard length (SL), whereas large individuals of *Ageneiosus*, *Tocantinsia* or *Trachycorystes* can reach about 600 mm SL.

Auchenipteridae have a long taxonomic history, dating back to Carolus Linnaeus (18th century) when the first species was described. However, the first suprageneric groups composed by auchenipterids were recognized almost a hundred years later by Bleeker (1862-1863; see Calegari et al., 2019 for an historical overview). Despite recurrent historical changes on taxonomy of the family, the limits and definition of Auchenipteridae are currently supported by recent phylogenetic investigations of Birindelli (2014) and Calegari et al. (2019), proceeded by other important unpublished contributions (Akama, 2004; Britski, 1972; Curran, 1989; Ferraris, 1988; Ribeiro, 2010; Royero, 1999). Auchenipteridae is the sister group of Doradidae that together compose the superfamily Doradoidea (Birindelli, 2014; Calegari et al., 2019). Members of Auchenipteridae can be morphologically distinguished from other siluriforms mainly by the synapomorphies related to secondary sexual dimorphism features such as an enlarged urogenital pore of female, ending in internal cavity for insemination; anal fin of male with intromittent organ; and anterior rays of anal fin of nuptial males larger than in non-nuptial males (Calegari et al., 2019). These morphological traits make the reproductive biology of auchenipterids very particular, as the internal insemination system allows females to carry packets of spermatozoa inside her gonads until the moment of laying eggs (and sperms) when fertilization takes place (Ferraris, 2003; Mazzoldi, Lorenzi, & Rasotto, 2007). In general, auchenipterid fishes are crepuscular and nocturnal and can be seen swimming just below the water surface in search of food items that fall from the adjacent forest (Ferraris, 2003; Freitas, Almeida, Valente, & Montag, 2011). However, diurnal species and additional feeding habits (e.g. piscivorous, frugivorous and planktonic) have been described for a handful of Auchenipteridae taxa (Corrêa, Petry, & Hahn, 2009; Ferraris, 2003; Pouilly, Yunoki, Rosales, & Torres, 2004).

In this study, we conduct a joint assessment of the Linnean and Wallacean shortfalls, and on particular aspects of the Darwinian and Raunkiæran shortfalls of current knowledge on the Auchenipteridae. Specifically, we seek to evaluate the accumulated knowledge on species richness, coverage on species' geographic distribution, the stability of phylogenetic hypotheses and the accumulation of knowledge on feeding habitats. We focus on these facets of knowledge because the accumulation of biological data on species description, georeferenced species occurrences, and phylogenetic and ecological studies on auchenipterids allows us to make a robust assessment of the Linnean, Wallacean, Darwinian and Raunkiæran shortfalls of the knowledge on this family. However, the paucity of data on species abundances and population dynamics, tolerances to abiotic factors and biotic interactions curbs the assessment of the Eltonian, Hutchinsonian and Prestonian shortfalls-which were not included in our study. Yet, we think this study provides a sound basis for prioritizing future research in this group. It may also provide a general model for the assessment of knowledge advances in Neotropical Siluriformes and/or other taxa.

2 | METHODS AND MATERIALS

2.1 | Linnean shortfall

The current status of the Linnean shortfall on Auchenipteridae was assessed by analysing the historical accumulation curve of valid species described until 2018. That is, our analysis considered herein 123 valid taxa (the current number is 126 recognized species as of July 2020). All names were checked for the most recent nomenclature, according to Calegari et al. (2019) (see also Freitas, Montag, De Marco, & Hortal, 2020). We used this information to estimate how many Auchenipteridae species remain to be described. To minimize the effect of changing rates of species description over time, we focused our analysis on the number of species described between 1974 and 2018, a contemporary period when species description rate did not show any abrupt shifts (see Results section) and comprises the recent advance in the taxonomy of the group. The year 1974 was chosen as the starting point because it contains the last abrupt leap in the description of Auchenipteridae species when nine species were described at once by Mees (1974), setting the number of species then considered as valid to 79 at that year. To assess the increment in the description of species for the before-mentioned period, we used a piecewise regression (Zar, 2010) to identify any eventual breakpoint in the description rates during this period and describe the temporal trends separately before and after such breakpoint (see Ota, Message, Graça, & Pavanelli, 2015). Breakpoints in historical species accumulation curves can be associated with historical facts that may be related to changes in the rate of species description (such as the creation of scientific journals, investments in taxonomy and field expeditions, or levels of investment in research; see Hortal, Jiménez-Valverde, Gómez, Lobo, & Baselga, 2008).

Further, we extrapolated the number of species that may remain to be discovered according to the species description rates from the period 1974 to 2018. We did so through the second-order estimator Jackknife2 (hereafter, Jack2), using the number of species described per year as samples. It assumes that yearly descriptions during this period are the outcome of relatively homogeneous levels of sampling effort. Therefore, they can be used to extrapolate the species' description curve that would be expected if the resources devoted to auchenipterid taxonomy and the effectiveness of this work would not change significantly in the future. We performed this analysis using the function *specpool* of Vegan package version 2.5–5 (Oksanen et al., 2019) in *R* environment (R Core Team, 2015). We continued by determining the year in which the predicted species richness is likely to be achieved. To do this, we adapted the original density-dependent model (Gotelli, 2008), as follows:

$$N_t = K/[1 + (K/N_0 - 1)e^{(-rt)}]$$

where K is the number of possible existent species (here computed as the sum of Jack2 plus the number of species described before 1974), N is the number of described species at a time (t), N_0 is the number of valid species described at t=0, and r is a theoretical constant species description rate. To account for different scenarios of increase in species description, we used six different rates (r=0.05, 0.1, 0.2, 0.3, 0.4 and 0.5) (see Guerra, Jardim, Llusia, Márquez, & Bastos, 2020; Ota et al., 2015).

2.2 | Wallacean Shortfall

To address the Wallacean shortfall, we first compiled a data set containing 10,421 records of the occurrence of auchenipterid catfishes, collected over ca. 180 years (from 1829 to December 2016). We retrieved these records from two online repositories: 4.983 records from SpeciesLink (on 9 May 2017) and 4,165 records from the Global Biodiversity Information Facility (GBIF, on 8 May 2017, available at http://doi.org/10.15468/dl.eyjjwt), and included only preserved specimens and published observations. We also included ichthyological records from the following Brazilian institutions, which were not available on online repositories: Museu Paraense Emílio Goeldi, Belém-Pará (1,108 records); Laboratório de Ictiologia de Altamira, Altamira-Pará (80 records); Universidade Federal da Bahia, Salvador-Bahia (44 records); Universidade Federal do Rio Grande do Norte, Natal-Rio Grande do Norte (35 records); and Universidade Federal da Paraíba, João Pessoa-Paraíba (six records). We obtained these records with the authorization of the respective collection curators. See Freitas et al. (2020) for further details on these data.

We screened all records following a three-stage data filtering process. First, we merged all duplicated records-that is records holding identical information on the fields "scientific collection" and "catalog number." Second, we selected records with reliable taxonomic identification at the species level (see the procedure in Freitas et al., 2020). For this step, we checked all taxon names in Calegari et al. (2019) for the most current nomenclature. We excluded taxon names holding incorrect nomenclature and those that we were unable to correct. Third, we selected only records with information of latitude and longitude, and the complete date of collection (i.e. day/ month/year). The whole geographic data set and the list of provider institutions are provided in Supplementary Tables S1 and S2, respectively, available on Supporting Information. After data filtering, we used all records to calculate the species accumulation curves (SACs) and used the final slopes of these curves as a proxy for inventory completeness (Hortal et al., 2008, 2011; Hortal, Garcia-Pereira, & García-Barros, 2004; Yang, Ma, & Kreft, 2013). Survey completeness is typically scale-dependent (Lobo et al., 2018). Therefore, we calculated SACs for two sets of geographic features, representing two spatial scales: Freshwater Ecoregions of the World (Abell et al., 2008) and geographic grid cells of one-degree resolution. We calculated the SACs and obtained the slopes only for ecoregions that contained at least 50 records, and for grid cells with at least

20 records. Ecoregions and cells with slopes lower than or equal to 0.01 were considered well-sampled. Ecoregions and cells with slope values between 0.01 and 0.05 were considered as "reasonably sampled." Here, a slope of 0.01 means that for every 100 records added to the ecoregion or grid cell, one new species would be registered, while a slope equal to 0.05 means adding a new species to the inventory with every 20 records. Such reference values describe the relationship between sampling effort and species inventorying (Hortal et al., 2004; Yang et al., 2013).

Finally, we established historical species range accumulation curves (see Lobo et al., 2007) to explore the temporal evolution of sampling effort for the most recorded species. These curves assess the accumulation of occurrence records in new grid cells through time for the following species: *Trachelyopterus galeatus* (712 records), Auchenipterichthys longimanus (335 records), Ageneiosus ucayalensis (334 records), Ageneiosus inermis (312 records), Centromochlus heckelii (294 records) and Auchenipterus nuchalis (271 records).

2.3 | Darwinian shortfall

We assessed the Darwinian shortfall by evaluating the temporal variations in the similarity of all available phylogenetic hypotheses. We assumed that a higher degree of convergence (i.e. higher similarity) between phylogenies indicates a well-established set of evolutionary relationships among different lineages within the family. On the contrary, increasing dissimilarity would show incongruent phylogenetic patterns and therefore unstable (i.e. uncertain) knowledge about evolutionary models of the group. To this end, we compiled all phylogenies available for Auchenipteridae that represented relationships at the family level (Akama, 2004; Birindelli, 2014; Britski, 1972; Calegari et al., 2019; Curran, 1989; Ferraris, 1988; Ribeiro, 2010; Royero, 1999). These phylogenetic hypotheses involve different types of input data (e.g. morphological or molecular data), phylogenetic reconstruction methods (e.g. gradist, cladist, molecular) and coverage of taxa within the family.

We first retrieved the phylogenetic relationships through the illustrations of the phylogenies using the software TreeSnatcher Plus (Laubach, von Haeseler, & Lercher, 2012). Then, we computed the similarities between each pair of phylogenies as the correlation between the patristic distances of common taxa present in both phylogenies. Given that branch length in a phylogenetic tree varies between phylogenies depending on the criteria and class of data applied, we first converted all branch lengths to one (i.e. patristic distances were based on the number of phylogenetic nodes separating two tips). The phylogenies include different taxa, but we only focused on patristic distances between genera. Notwithstanding, the number of shared taxa between phylogenies varies, which might affect the correlation coefficients between topologies. Given this potentially confounding effect, we conducted a resampling procedure, where we used as a baseline the lowest number of common genera observed for any pair of phylogenies (n = 12). Then, for a phylogeny pair, ten shared genera were randomly selected to calculate the correlation between phylogenetic

distances. We repeated this procedure ten thousand times per phylogeny pair, and we calculated the mean correlation coefficient. This approach yields a similarity matrix between phylogenies based on the topological congruence among shared genera. We used Spearman's ρ correlation coefficient, which was transformed into a dissimilarity index (D = 1 – ρ), to classify the phylogenies according to the UPGMA algorithm. We expect a higher degree of congruency within the most recent phylogenies. We computed all analyses in the R environment (R Core Team, 2015), using the "ape" package (Paradis & Schliep, 2019). All phylogenetic trees are provided as images in Supplementary Appendix S1 available on Supporting Information.

2.4 | Raunkiæran shortfall

We assessed the quality and completeness of current knowledge about the trophic ecology of Auchenipteridae fishes. To do this, we searched scientific literature about the description of feeding habits in three online databases: ISI Web of Science (www.webofknowl edge.com), SciELO (www.scielo.org) and Google Scholar (www.schol ar.google.com). This survey considered only scientific literature published before December 2017. We used the keywords "diet," "feeding," "feeding ecology" and "trophic ecology," in combination with "Auchenipteridae" or the names of genera (e.g. "Auchenipterus AND feeding"). To cover the wide range of specialized scientific journals of international and national relevance, we searched for keywords in Portuguese, English, Spanish and French.

All publications with any information on feeding habits of auchenipterid fishes were then classified into eleven categories according to the dietary niche: aquatic insects, terrestrial insects, crustaceans, other invertebrates, fish, other vertebrates, fruits and seeds, vegetal matter, zooplankton, algae and detritus. If a species A has been reported to consume two different food items (e.g. terrestrial insects and crustaceans), then we added two entries with feeding habits for that species: "species A x terrestrial insects" and "species A x crustaceans," no matter whether these records were in two different publications or just one. Then, we evaluated the extent of the Raunkiæran shortfall in trophic habits by establishing a trophic habit accumulation curve using the combination of varying feeding habits per species as a function of the cumulative number of published papers. Based on this, we aimed to verify whether new feeding habits are documented as new studies are published. In case there is a reasonable knowledge of feeding habits for the Auchenipteridae fishes, we expect to obtain an asymptotic rarefaction curve. We performed this analysis in EstimateS software version 9.1 (Colwell, 2013).

3 | RESULTS

3.1 | Linnean shortfall

A total of 123 currently valid species names have been assigned to the Auchenipteridae between 1766 and 2018 (Figure 1a). The

first species were described in 1766 as Siluris inermis and S. galeatus (see section 4.1 below), and until 1974, one new species was described approximately every three years (0.4 species per year). The species description rate shows a threefold increase from 1974 to 2018, with 1.2 new species per year on average. The piecewise regression conducted on species descriptions after 1974 estimated a breakpoint around 2000, when 93 species had already been described (Figure 1b). Therefore, the historical species accumulation curve was described by two quadratic polynomial functions in both intervals (Figure 1b), with 24 species described in the period 1974-2000 and 29 more between 2001 and 2018. Considering only the period between 1974 and 2018 (53 species described), the estimator Jack2 predicted a total of 152 species for the Auchenipteridae family, which added to the 70 valid species discovered before 1974, and renders a predicted total richness of 222 species for the family. According to this estimation, 99 new Auchenipteridae species remain to be described (~ 45% of the total). The scenarios of future species description using the six theoretical constant growth rates forecast that all species in the family will be described by the years 2,170 (r = 0.05), 2,100 (r = 0.1), 2059 (r = 0.2), 2046 (r = 0.3), 2039(r = 0.4) or 2035 (r = 0.5), respectively (Figure 1c).

3.2 | Wallacean shortfall

Only 5,467 (52.5%) out of the original 10,421 records were deemed suitable for our analyses after the data filtering process (see Materials and Methods section). We also reduced the original 469 taxonomic entities (i.e. different text strings at the column "species") to 117 valid species names. So, the results we described henceforth reflect only the data resulting from the filtering procedure. Auchenipterid catfishes were recorded in 42 out of the 50 freshwater ecoregions of the Neotropics based on our sample. The number of records per ecoregion ranged from 1 to 1,170 (median of 66.5 records; Table 1). Species richness ranged from 1 to 55 per ecoregion, with 12 species on average (and a median of six species). The richest ecoregion was Amazonas Lowlands with 1,170 records of 55 species, followed by Amazonas Estuary & Coastal Drainage (600 records for 36 species), Rio Negro (372 records for 43 species) and Orinoco Llanos (243 records for 34 species). We observed the lowest auchenipterid richness in three ecoregions with one species each: the Amazonas High Andes (Duringlanis perugiae), Santa Maria (Trachelyopterus amblops) and Fluminense (Trachelyopterus striatulus).

We calculated the species accumulation curves for the 24 ecoregions that contained at least 50 records (57% of all ecoregions), rendering slopes ranging from less than 0.01 to over 0.99 (Table 1). Seven ecoregions (i.e. 16.7% of the total) were considered as well-sampled (SAC slopes lower than 0.01): Amazonas Estuary & Coastal Drainages, Amazonas Lowlands, Guianas, Lower Uruguay, Paraguay, Upper Parana and Xingu. Another 12 ecoregions (28.6% of ecoregions with occurrence data) can be considered reasonably sampled (slopes between 0.01 and 0.05) and five as poorly sampled (slopes larger than 0.05: Amazonas Guiana Shield, Magdalena—Sinu,

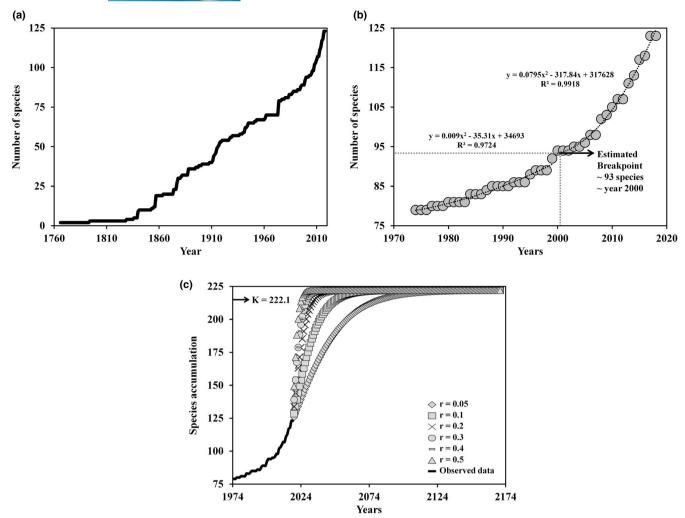


FIGURE 1 Assessment of the Linnean shortfall for the family Auchenipteridae. (a) Historical accumulation curve of species description. (b) Piecewise regression on species descriptions rates for the period 1974–2018, indicating the estimated breakpoint. (c) Predictions of the accumulated number of species described for six different scenarios of species description using theoretical constant growth rates (r)

Orinoco Guiana Shield, Orinoco Llanos, Tapajos-Juruena) (Table 1, Figure 2).

We found that 1,353 out of 1,968 cells did not have a single record of auchenipterid fishes, whereas 615 (i.e. 31.2% of all grid cells) contained at least one record. The number of records and species per cell ranged from 1 to 197 records and 1 to 28 species. When considering cells with at least one record, we found a median of four records and two species per cell. The richest cell showed 97 records for 28 species, whereas 231 cells contained only one species (records varying from 1 to 31). Seventy cells held at least 20 records, which represented only 11.4% of all cells with records. The final slopes of the species accumulation curves in these cells ranged from less than 0.01 to 0.42. From these, only three cells (0.5% of cells with records) can be considered as well-sampled (slope \leq 0.01), and 18 (2.4% of cells with occurrence) were reasonably sampled (slope > 0.01 to \leq 0.05) (Figure 2).

The species *Trachelyopterus galeatus* showed the broadest geographic distribution, being recorded in 245 grid cells (39.8% of the cells with records), followed by *Ageneiosus inermis* (121 cells,

19.7%), A. ucayalensis (112 cells, 18.2%), Auchenipterus nuchalis (97 cells, 15.8%), Centromochlus heckelii (93 cells, 15.1%) and Auchenipterichthys longimanus (64 cells, 10.4%). Forty-one species were recorded in five or less grid cells, implying that the known distribution of one-third of the auchenipterid species is restricted to very few areas. After over 180 years of sampling (1829–2016), occurrences of auchenipterid fishes are still accumulating as the sampling of new areas (grid cells) expands. That is, the known geographic distribution of auchenipterid fishes is still expanding, at least for the most conspicuous species (Figure 3).

3.3 | Darwinian shortfall

All phylogenetic studies were based on the analysis of morphological data, except for Calegari et al. (2019), which conducted the phylogenetic reconstruction based on a combined molecular and morphology data set. All phylogenetic trees of the evaluated studies were estimated by Parsimony criteria, except for the Britski's (1972)

TABLE 1 Summary of the inventory completeness for auchenipterid fishes. Number of species occurrence records, species richness and final slope of the species accumulation curves for the 42 ecoregions with Auchenipteridae records. Well-sampled ecoregions are highlighted in bold. We also show the number of grid cells that are either well- or reasonably sampled in each ecoregion (slopes \leq 0.01 or > 0.01 and \leq 0.05, respectively). Ecoregion IDs correspond to the unique identifiers attributed to freshwater ecoregions by Abell et al. (2008).

Tocantins-Araguaia 324 310 26 0.03 - 2 2 2 2 2 2 2 2 2	Ecoregion	ID	Records	Species	Slope	Well-sampled cells	Reasonably sampled cells
Color Colo	Amazonas Lowlands	316	1,170	55	< 0.01	-	2
Total Name State	·	323	630	36	0.01	1	1
Upper Parana 344 284 12 < 0.01 - 2 Orinoco Lalnos 307 243 34 0.06 1 2 Paraguay 343 217 16 < 0.01	Rio Negro	314	372	43	0.02	-	-
Orinoco Llanos 307 243 34 0.06 1 2 Paraguay 443 217 16 < 0.01	Tocantins-Araguaia	324	310	26	0.03	-	2
Paraguay 343 217 16 < 0.01 - 1	Upper Parana	344	284	12	< 0.01	-	2
Madeira Brazilian Shield 321 208 26 0.03 - 2 Essequibo 310 196 23 0.02 Northeastern Mata Altantica 328 186 9 0.02 Northeastern Mata Altantica 328 181 20 0.02 Northeastern Mata Altantica 328 181 38 0.01 Northeastern Mata Altantica 329 182 183 3 0.04 Northeastern Cadating & Coastal 309 181 30 8 3 181 26 0.04 Northeastern Cadating & Coastal 309 181 30 8 3 0.04 Northeastern Cadating & Coastal 309 31 8 9 0.05 Northeastern Cadating & Coastal 309 31 8 9 0.05 Northeastern Cadating & Coastal 310 8 3 9 0.05 Northeastern Cadating & Coastal 310 8 3 9 0.05 Northeastern Cadating & Coastal 310 8 3 9 0.05 Northeastern Cadating & Coastal 310 8 3 0.05 Northeastern Cadating & Coastal 329 35 3 0.02 Northeastern Cadating & Coastal 7 3 0.05 Northeastern Cadating & Coastal 7 3 0.05 Northeastern Cadating & Coastal 7 0.06 Northeastern Cadating & Coastal 7 0.06 Northeastern Cad	Orinoco Llanos	307	243	34	0.06	1	2
Sesequibo 310 196 23 0.02 - - -	Paraguay	343	217	16	< 0.01	-	1
Northeastern Mata Atlantica Altantica Altantic	Madeira Brazilian Shield	321	208	26	0.03	-	2
Atlantica Mamore-Madre de Dios Piedemont Ningu 322 135 16 0.01 - 1 Tapajos-Juruena 320 123 17 0.06 1 - 1 Tapajos-Juruena 320 123 17 0.06 1 - 1 Tapajos-Juruena 320 115 8 0.01 - 2 Lower Uruguay 332 115 8 0.01 - 2 Torninages Orinoco Delta & Coastal 309 112 15 0.04 - 1 Drainages Orinoco Guiana Shield 308 111 26 0.06	Essequibo	310	196	23	0.02	-	-
Pledmont		328	186	9	0.02	-	-
Tapajos-Juruena 320 123 17 0.06 1 - Iguassu 346 117 6 0.03 - - Lower Uruguay 332 115 8 0.01 - 2 Orinoco Delta & Coastal Drainages 309 112 15 0.04 - 1 Orinoco Guiana Shield 308 111 26 0.06 - - Guianas 311 106 16 0.01 - - Amazonas Guiana Shield 315 89 22 0.11 - - Magdalena-Sinu 302 73 3 > 0.99 - - Guapore-Itenez 319 71 15 0.04 - 1 Laguna dos Patos 334 62 4 0.02 - - Western Amazon 313 61 9 0.05 - 1 Northeastern Caatinga & Coastal Drainages 326 48 3	Mamore-Madre de Dios Piedmont	318	181	20	0.02	-	-
Section Sect	Xingu	322	135	16	0.01	-	1
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Drinoco Delta & Coastal Drainages 112 15 15 0.04 - 1 1 1 1 1 1 1 1 1	lguassu	346	117	6	0.03	-	-
Drainages Orinoco Guiana Shield 308 111 26 0.06 - - -	Lower Uruguay	332	115	8	0.01	-	2
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Guapore-Itenez 319 71 15 0.04 - 1 Laguna dos Patos 334 62 4 0.02 Western Amazon Piedmont São Francisco 327 56 5 0.02 Northeastern Caatinga & Coastal Drainages Upper Uruguay 333 37 6 Paraiba do Sul 329 35 3 North Andean Pacific Slopes-Rio Atrato Ribeira de Iguape 330 19 3 Chaco 342 13 5 Parnaiba 325 9 2 Parnaiba 325 9 2 Parnaiba 325 9 2 Parnaiba 325 9 2 Parnaiba 325 9 3 3 Parnaiba 325 9 2 Parnaiba 325 9 3 3 Parnaiba 325 9 3 3 Parnaiba 325 9 3 3 Parnaiba 325 9 2 Parnaiba 325 9 2 Parnaiba 325 9 2 Parnaiba 335 7 3	Amazonas Guiana Shield	315	89	22	0.11	-	-
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Western Amazon Piedmont 313 61 9 0.05 - 1 São Francisco 327 56 5 0.02 - - Northeastern Caatinga & Coastal Drainages 326 48 3 - - - Upper Uruguay 333 37 6 - - - Paraiba do Sul 329 35 3 - - - North Andean Pacific Slopes-Rio Atrato 301 23 3 - - - Ribeira de Iguape 330 19 3 - - - Ribeira de Iguape 342 13 5 - - - Chaco 342 13 5 - - - Lower Parana 345 10 4 - - - Parmaiba 325 9 2 - - - Fluminense 352 8 1 - - <t< td=""><td>Guapore-Itenez</td><td>319</td><td>71</td><td>15</td><td>0.04</td><td>-</td><td>1</td></t<>	Guapore-Itenez	319	71	15	0.04	-	1
Piedmont	Laguna dos Patos	334	62	4	0.02	-	-
Northeastern Caatinga & Coastal Drainages Upper Uruguay 333 37 6 - Paraiba do Sul 329 35 3 - North Andean Pacific Slopes-Rio Atrato Ribeira de Iguape 330 19 3 - Chaco 342 13 5 - Chaco 345 10 4 - Parnaiba 325 9 2 - Parnaiba 335 7 3 - Chaco 342 13 5 - Chaco 342 13 5 - Chaco 345 10 4 - Chaco 345 10 4 - Chaco 345 10 4 - Chaco 10 - Chaco 10 - Chaco 11 - Chaco 12 - Chaco 13 - Chaco 14 - Chaco 15 - Chaco 16 - Chaco 17 - Chaco 18 - Chaco 19	Western Amazon Piedmont	313	61	9	0.05	-	1
Coastal Drainages Upper Uruguay 333 37 6 - - - - Paraiba do Sul 329 35 3 - - - - North Andean Pacific Slopes-Rio Atrato 301 23 3 - - - - Ribeira de Iguape 330 19 3 - - - - Chaco 342 13 5 - - - - Lower Parana 345 10 4 - - - - Parnaiba 325 9 2 - - - - Fluminense 352 8 1 - - - - Tramandai-Mampituba 335 7 3 - - - - South America Caribbean Drainages-Trinidad 304 6 3 - - - - -	São Francisco	327	56	5	0.02	-	-
Paraiba do Sul 329 35 3 - - - - North Andean Pacific Slopes-Rio Atrato 301 23 3 - - - - Ribeira de Iguape 330 19 3 - - - - Chaco 342 13 5 - - - - Lower Parana 345 10 4 - - - - Parnaiba 325 9 2 - - - - Fluminense 352 8 1 - - - - South America Caribbean Drainages-Trinidad 304 6 3 - - - - -	Northeastern Caatinga & Coastal Drainages	326	48	3	-	-	-
North Andean Pacific Slopes-Rio Atrato Ribeira de Iguape 330 19 3	Upper Uruguay	333	37	6	-	-	-
Slopes-Rio Atrato Slop	Paraiba do Sul	329	35	3	-	-	-
Ribeira de Iguape 330 19 3		301	23	3	-	-	-
Chaco 342 13 5 - - - Lower Parana 345 10 4 - - - Parnaiba 325 9 2 - - - Fluminense 352 8 1 - - - Tramandai-Mampituba 335 7 3 - - - South America Caribbean Drainages-Trinidad 304 6 3 - - - -	Ribeira de Iguape	330	19	3	-	-	-
Parnaiba 325 9 2 - - - - Fluminense 352 8 1 - - - - Tramandai-Mampituba 335 7 3 - - - - South America Caribbean Drainages-Trinidad 304 6 3 - - - -	Chaco	342	13	5	-	-	-
Fluminense 352 8 1	Lower Parana	345	10	4	-	-	-
Tramandai-Mampituba 335 7 3 South America Caribbean 304 6 3	Parnaiba	325	9	2	-	-	-
South America Caribbean 304 6 3 Drainages-Trinidad	Fluminense	352	8	1	-	-	-
South America Caribbean 304 6 3 Drainages-Trinidad	Tramandai-Mampituba	335	7	3	-	-	-
	South America Caribbean	304	6	3	-	-	-
	Orinoco Piedmont	306	5	5	-	-	-

TABLE 1 (Continued)

Ecoregion	ID	Records	Species	Slope	Well-sampled cells	Reasonably sampled cells
Maracaibo	303	5	3	-	-	-
Rio Tuira	210	5	2	-	-	-
Southeastern Mata Atlantica	331	5	2	-	-	-
Ucayali—Urubamba Piedmont	317	2	2	-	-	-
Amazonas High Andes	312	1	1	-	-	-
Santa Maria	208	1	1	-	-	-

Note: Names and IDs of freshwater ecoregions without records of Auchenipteridae are as follows: Orinoco High Andes = 305; Central Andean Pacific Slopes = 336; Titicaca = 337; Atacama = 338; Mar Chiquita—Salinas Grandes = 339; Cuyan—Desaguadero = 340; South Andean Pacific Slopes = 341; Bonaerensean Drainages = 347; Patagonia = 348; Valdivian Lakes = 349.

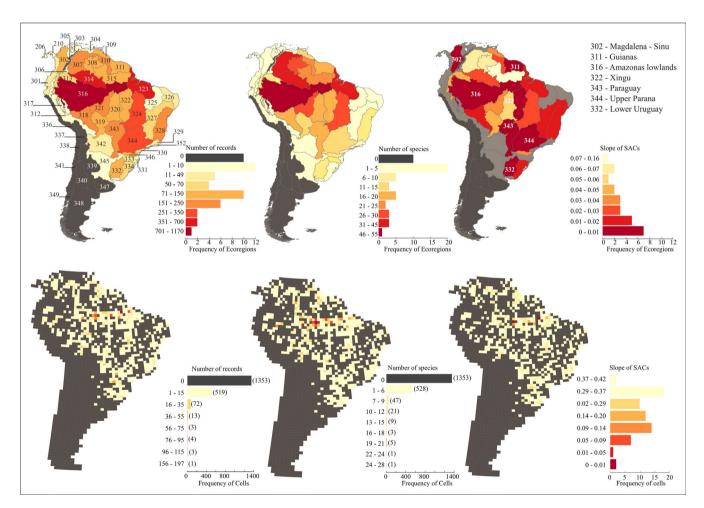


FIGURE 2 Inventory completeness for the Auchenipteridae fishes across South America. Maps depict the number of records, species observed and final slope of the species accumulation curves (SACs) for freshwater ecoregions (upper row) and one-degree resolution grid cells (lower row). Numbers in the upper-left map indicate the unique identifier (ID) attributed to freshwater ecoregions, as in Abell et al. (2008). Names and IDs of freshwater ecoregions with ≥ 1 record of Auchenipteridae fishes are given in Table 1. Figure appears in colour in the online version only

hypothesis that used phenetic approach, and Calegari et al. (2019), that estimated the trees also under Bayesian inference as a comparative approach to the Parsimony analysis.

Given the number of valid species at the year of each study, the phylogenies covered, on average, 46% of valid species. Birindelli (2014) used the lowest proportion of species among all valid species

(20%, 23 out of the 113 valid species in 2014; Figure 4b), followed by Akama (2004; 27% of valid species, 26 out of 95), Ribeiro (2011; 33%, 33 out of 107), Curran (1989; 46%, 39 out of 85), Bristki (1972; 52%, 36 out of 69) and Ferraris (1988; 67%, 56 out of 84). In the most recent phylogenetic study, Calegari et al. (2019) included 97 out of the 124 valid species (at the moment of publication), representing 77% of the valid names at the time.

The analysis of similarity between phylogenies showed that the topologies of Birindelli (2014) and Ribeiro (2010) were the most similar (mean Spearman's $\rho=0.77$), followed by the topologies of Akama (2004) and Calegari et al. (2019) (mean Spearman's $\rho=0.72$) (Figure 4a). On the other hand, the less similar phylogenies were Britski (1972) and Curran (1989) (mean Spearman's $\rho=0.25$). In fact, Britski and Curran's topologies showed, on average, 24% and 19% of similarity to the other phylogenetic trees.

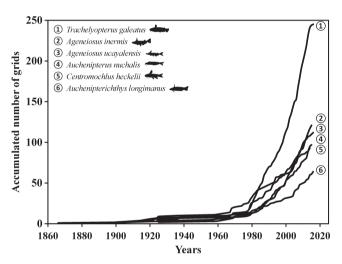
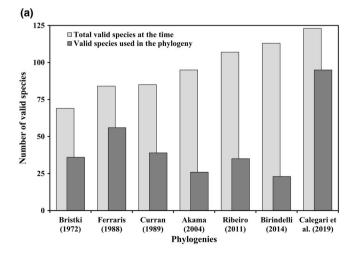


FIGURE 3 Temporal accumulation of the number of grid cells with occurrence records for the six most recorded Auchenipteridae species (period 1829–2016)

3.4 | Raunkiæran shortfall

We compiled 67 published studies that recorded the feeding habits of 54 auchenipterid species. Among them, we registered 244 records of species diet habits, with a total of 142 unique combinations of diet and species (i.e. each single feeding habit recorded for a certain species in a published study). The final slope of the feeding habit accumulation curve shows that the dietary knowledge on Auchenipteridae catfishes is still expanding at a nearly constant pace of 1.5 unique combinations of feeding habits and species per published study (Figure 5a). The species with best-documented feeding habits was Trachelyopterus galeatus (17 papers provided data on its diet, rendering 40 single feeding combinations, out of which ten appeared a single time in the literature), followed by Ageneiosus ucayalensis (13 combinations, four unique, in six articles), Trachelyopterus striatulus (14 combinations, five unique, in seven papers) and Auchenipterus nuchalis (13 combinations, four unique, in nine papers). For Entomocorus gameroi, we obtained six feeding habits and six unique combinations. From the 54 species with data on feeding habits, 14 species showed only a single record of feeding habit.

The distribution of species studied among genera shows that although the most speciose genera hold data for more species, there are some significant biases. While the two genera with more species (*Tatia* and *Trachelyopterus*) have data for around one-fourth of their species, many less speciose genera are much better represented (in particular *Ageneiosus*) (Figure 5b). Strikingly, while five genera had records of feeding habits for their representatives (*Asterophysus*, *Auchenipterichthys*, *Epapterus*, *Tocantinsia* and *Trachycorystes*), seven genera presented no documented feeding habit (*Gephyromochlus*, *Liosomadoras*, *Pseudepapterus*, *Pseudotatia*, *Spinipterus*, *Trachelyichthys* and *Trachelyopterichthys*). The list of feeding habits per species and the consulted literature are provided in Supplementary Tables S3 and S4 available on Supporting Information.



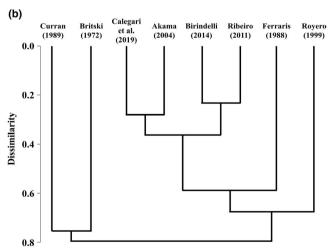


FIGURE 4 (a) Number of species included in the phylogeny studies and the number of valid species at the time of reconstruction. (b) Dendrogram of dissimilarity between phylogenetic topologies of the family Auchenipteridae

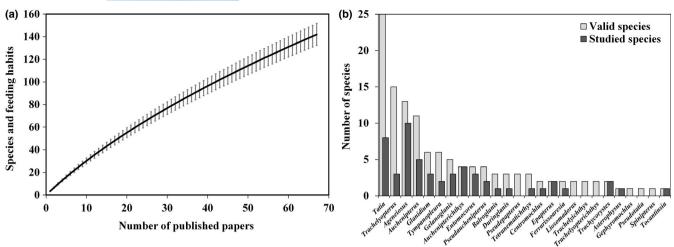
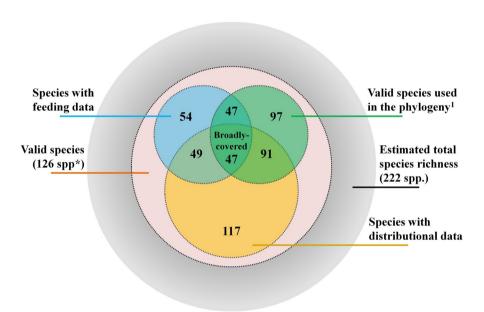


FIGURE 5 Current status on the knowledge of feeding habits for Auchenipteridae species. (a) Accumulation of observed feeding habits per species with an increasing number of publications (vertical lines represent the standard variation). (b) Distribution of species with documented feeding habits among the currently valid genera, compared with the number of species in each one of these genera



of the Auchenipteridae catfish family (order Siluriformes) at the species level. The Linnean shortfall (i.e. undescribed species) surrounding our current knowledge is represented in grey. The area outside each circle represents the species in a lack of knowledge. Broadly covered species (shown in the overlap area) are those for which there are data on their distribution, phylogenetic relationships (from Calegari et al., 2019) and feeding habits. Figure appears in colour in the online version only

Lastly, an overall picture of the results showing the overlap among the studied knowledge shortfalls reveals a relatively broad coverage of data for c.~40% of the species (Figure 6). A similar proportion of species holds both phylogenetic and diet data, and there is phylogenetic and distributional information for more than 70% of the species. See Supplementary Table S5 available on Supporting Information for the complete list of species and their data availability.

4 | DISCUSSION

The knowledge of taxonomy, geographic distribution, evolutionary relationships and feeding habits of Auchenipteridae catfishes has increased substantially in the last decades. Our results indicate that the historical accumulation of species description sharply

increased between 1974 and 2018, thereby suggesting that a sound knowledge about the family's total richness is not yet on the horizon. It implies that an increased effort to in inventory and describe auchenipterid catfishes from South American freshwater environments is needed to attain a fair knowledge of the overall diversity of this group. Despite such undersampling, the similarities between the most recent phylogenies suggest that current evolutionary hypotheses for this family are fairly robust, at least in their most basal topology. It is not the case for the knowledge about the feeding habits and diet of auchenipterids, which is still in a phase of expansion. Our results highlight the need for further efforts in describing species and/or developing taxonomic reviews, field explorations and ecological investigations for this diverse group of fishes. Below, we discuss the impact of each of the studied shortfalls and pinpoint historical events contribution to such temporal dynamics.

4.1 | Linnean shortfall

Increasing taxonomic efforts typically leads to increments in species description rates, rather than to levelling-off the accumulation of new taxa. The number of descriptions and estimated species richness increase as taxonomy improves (Troudet et al., 2017). This is the case for the Auchenipteridae: our results show a remarkable increase in species descriptions in recent years. Despite such efforts, a substantial proportion of taxa may remain to be described to science (almost 50% according to our estimation), corroborating that Auchenipteridae is a poorly sampled family (Ota et al., 2015).

The taxonomic history of auchenipterid fishes started in 1766 with the description of Silurus inermis and S. galeatus (currently valid as Ageneiosus inermis and Trachelyopterus galeatus, respectively) by Carolus Linnaeus in the twelfth edition of "Systema Nature" (see Calegari et al., 2019). But the first real improvement in the description of auchenipterid species was promoted by Achille Valenciennes in 1,840, a French zoologist who explored South America in the early nineteenth century and described species of Ageneiosus, Auchenipterus and Trachelyopterus. In the late nineteenth century, the known auchenipterid diversity increased substantially due to the studies of Rudolf Kner (1857) and Franz Steindachner (between 1881 and 1915) (see Calegari et al., 2019). After a period of intense taxonomic contributions by Carl H. Eigenmann and Alípio de Miranda Ribeiro in the early twentieth century, Gerloff Mees published "The Auchenipteridae and Pimelodidae of Suriname (Pisces, Nematognathi)" in 1974, one of the most valuable monographs on auchenipterid systematics where he described several new species of Centromochlus and Tatia, as well as the genera Pseudotatia, Tocantinsia and Trachelyichthys. This monograph set up the basis for the recent increase in taxonomic effort (1980-2017), thanks to the work of dozens of researchers around the world, especially the North Americans Carl J. Ferraris, Richard Vari and Stephen Walsh, and the Brazilians José Birindelli, Luiza M. Sarmento-Soares, Frank Ribeiro and Bárbara B. Calegari. This high rate of description continues to date, with the recent description of Spinipterus moijiri Rocha, Rossoni, Akama, & Zuanon, 2019, Tatia caudosignata DoNascimiento, Albornoz-Garzón & García-Melo 2019, and Tatia akroa Souza, Sarmento-Soares, Canto & Ribeiro 2020, which we did not include in the analyses.

The breakpoint in the species description curve identified by our analyses may highlight the change from a classical opportunistic taxonomic process to a more systematized selection of habitats and areas for surveys, combined with a higher sampling effort. According to Ota et al. (2015), three factors may be responsible for the increase in description rates of siluriforms from 2001 onwards: the creation of the specialized biennial meeting *Encontro Brasileiro de Ictiologia* (Brazilian Meeting of Ichthyologists); the indexing of the specialized journal *Neotropical Ichthyology* by ISI Web of Knowledge in 2003; and the onset of the U.S. NSF-funded project "All Catfish Species Inventory" (http://silurus.acnatsci.org/) also in 2003, which increased by 24% the volume of data on Siluriformes. All these factors may have promoted a higher taxonomic effort. Indeed, the number of active taxonomists was higher in this second period. While 21

authors described species between 1974 and 2000, 31 participated in species descriptions during 2001–2018 (see Table S1 in Freitas et al., 2020). Moreover, the development of survey techniques and protocols during this latter period may have increased the effectiveness of the surveys in finding new species. It is also necessary to highlight the importance of being cognizant of intrinsic features of the natural history of species to better understand what is contributing to the knowledge gaps. The Auchenipteridae family is known by its distinctive habit of using submerged trunks as diurnal shelters (in genera such as *Balroglanis*, *Liosomadoras*, *Tatia* and *Trachelyichthys*; Birindelli & Zuanon, 2012) or by foraging at twilight and during the night on the surface of the water (such as the miniature species of *Gelanoglanis*; Calegari & Reis, 2017). Because of these peculiarities, collecting fish from this family requires using diverse methods such as manual collecting inside trunks or ichthyoplankton nets.

The Linnean shortfall is made of unknown species from two distinct categories (Hortal et al., 2015): species yet to be sampled and those already collected but not described. The latter condition can be represented by either species previously known as a new form by the specialist but not yet formally described, as well as unidentified specimens deposited in scientific collections, or particular cases of misidentification. The taxonomy of groups with many species in these situations often benefits from beta taxonomy (i.e. revisionary work). In Auchenipteridae, the revisionary studies published in the last decade significantly contributed to the description of new species. Around 40% of auchenipterid species described between 2001 and 2018 resulted from taxonomic revisions (e.g. Reis & Borges, 2006; Ribeiro, Rapp Py-Daniel, & Walsh, 2017; Sarmento-Soares & Martins-Pinheiro, 2008). Indeed, several of the better-known auchenipterid species could be hiding records for several species. For instance, "catch-all-names" species as T. galeatus and A. ucayalensis (the first and the third most recorded species) may be holding specimens from at least three additional species each (J. Zuanon, pers. comm.; see Akama, 2004; Ribeiro et al., 2017). In this sense, revisionary studies are responsible for re-identifying material deposited in the collections, including older and recent specimens sampled, also contributing to updating the database collection and the geographic distribution of species (Lundberg et al., 2000; von Staden, Raimondo, & Dayaram, 2013).

Conversely, the taxonomic gap represented by the not-yet-sampled species depends on inventory surveys (mainly in poorly known regions), which are of paramount importance for registering species new to science (Hortal et al., 2015; Mora, Tittensor, & Myers, 2008; Wheeler, 2004). In the case of Auchenipteridae, 60% of the species described in the last decade resulted from field inventories (e.g. Akama & Ferraris, 2011; Sarmento-Soares, Cabeceira, Carvalho, Zuanon, & Akama, 2013; Sarmento-Soares, Lazzarotto, Py-Daniel, & Leitão, 2016). The high number of species recently discovered in the field may be related to the inconspicuousness of Auchenipteridae catfishes. The development of new collecting techniques, new technologies and exploration of new habitats can lead to a substantial increase in the species description for a group of organisms (see Winston, 1999). In this context, many Neotropical fish families have

been revised through studies focused on delimitating species by molecular techniques (e.g. Characidae—García-Melo et al., 2019; Curimatidae—Melo & Oliveira, 2017; Loricariidae—Roxo, Ochoa, Costa-Silva, & Oliveira, 2015). Therefore, the noteworthy scarcity of species delimitations from genetic sequences in Auchenipteridae (with the exceptions of Calegari et al., 2019; Cooke, Chao, & Beheregaray, 2012; Hashimoto, Py-Daniel, & Batista, 2020) is likely to result in the description of large numbers of new species with the progressive implementation of molecular techniques.

4.2 | Wallacean shortfall

The analysis of inventory completeness reveals that the geographic distribution of Auchenipteridae along South American freshwaters is largely undersampled. According to our criteria, only 17% of the ecoregions auchenipterid records are well-sampled, and 29% are reasonably sampled. That is, more than half of the ecoregions are largely under-collected for these catfishes. This pattern is even more striking when looking at one-degree grid cells: only three and 18 cells were either well or reasonably sampled, respectively. It implies that the spatial coverage of species distributions is unknown even in the ecoregions with relatively well-established inventories. Many second- and third-order basins could be holding unknown species or larger distributions of the already known ones. This precludes determining whether the geographically restricted distributions shown by a third of the known species are due to true endemism or simply to undersampling.

The degree of inventory completeness changes with the spatial resolution analysed (Ferrier, 2002; Lobo et al., 2018; Yang et al., 2013). In our case, reducing the scale from ecoregion to one-degree grid cells resulted in progressively lower degrees of inventory completeness; while many ecoregions show either high or moderately high levels of inventory completeness, only a handful of one-degree cells from the Amazonas Lowlands are reasonably sampled. Intensive local inventories are associated with specific research projects, long-term ecological studies, historically relevant localities repeatedly visited by taxonomists (Guerra et al., 2020; Hortal et al., 2008; Sastre & Lobo, 2009) and/or the proximity to research centres and taxonomists' home ranges (Dennis & Thomas, 2000; Lobo & Martin-Piera, 2002; Rodrigues et al., 2010). For instance, the three anecdotally well-sampled grid cells, which are placed near two well-established scientific research centres, the Instituto Nacional de Pesquisas da Amazonia (INPA) and the Museu Paraense Emilio Goeldi (MPEG), in the Amazonian cities of Manaus and Belém (Brazil), respectively. Indeed, biodiversity occurrence data are historically biased towards locations that offer easier logistics, such as roads, and nearby cities or villages (Hortal, Lobo, & Jiménez-Valverde, 2007; Lobo et al., 2007; Meyer, Kreft, Guralnick, & Jetz, 2015). This is particularly important in areas with access difficulties, for example in the Amazon region, where considerable effort is needed to study local biodiversity patterns (see Dutra et al., 2020; Jézéquel et al., 2019, 2020).

The temporal evolution in the accumulated number of grid cells with occurrences registered for the most recorded species shows that despite the taxonomic problems (see topic 4.1), the yearly increase in geographic coverage of sampling location was generally low before 1980, increasing conspicuously after the 1980s. We observed such steep increase in the number of records from the 80s and 90s for many biological groups around the world (e.g. angiosperms, Canhos et al., 2015; invertebrates, Hortal et al., 2008; Isaac & Pocock, 2015; Lobo et al., 2007; birds, Amano, Lamming, & Sutherland, 2016; small mammals, Escribano, Ariño, & Galicia, 2016). This increase is generally associated with the development of universities, scientific facilities and conservation efforts. Similar increases in inventory rates, however, appeared earlier for better-studied groups (e.g. amphibians, Guerra et al., 2020; Rodrigues et al., 2010) or may even decrease in many areas after historical colonial inventories (Stropp et al., 2016). In Brazil, we can associate several factors with the increase in the records of fauna and flora during this period, such as creating protected areas and increasing the number of more stringent environmental impact studies (Pott & Estrela, 2017). Such studies require the collection and deposit of biological material in scientific collections. Additionally, funds for field expeditions increased around the 60s, favouring the creation of important scientific fish collections, such as the INPA fish collection (Rapp Py-Daniel et al., 2015), and the expansion of other already established ichthyological collections, such as the collections of MPEG (Silva et al., 2017) and the Museu de Zoologia da Universidade de São Paulo (MZUSP; Marinho et al., 2019; Menezes, Fig ueiredo, & Britski, 1997).

4.3 | Darwinian shortfall

The knowledge of Auchenipteridae evolution has advanced considerably since the first phylogenetic studies of this family and now seems to be largely settled. The four most recent phylogenetic hypotheses showed the highest similarity among them. It is not surprising since all of them included in their analyses similar sets of morphological characters that were initially described by Ferraris (1988) and Royero (1999). Indeed, the phylogenetic trees of Akama (2004), Ribeiro (2010), Birindelli (2014), and Calegari et al. (2019) show congruence in the composition and relationships within the subfamily Auchenipterinae (sensu Calegari et al., 2019). The consistency in the most recent phylogenies contrasts with the older ones (Britski, 1972; Curran, 1989; Ferraris, 1988), which in general were hampered by inclusion of comparatively low numbers of species. Thus, the first phylogenies sought to establish relationships among genera accounting for only a few auchenipterid representatives. Some recent auchenipterid phylogenetic studies resulted from revisionary studies focused on a particular genus (Akama, 2004; Ribeiro, 2010; Royero, 1999), increasing the number of taxa sampled.

Despite the increase in phylogenetic studies, a full understanding of the evolutionary relationships of these driftwood catfishes persists. The most important basal differences between these evolutionary hypotheses come from the composition of the clade "(Auchenipterichthys

+ (Trachelyopterichthys + Trachelyichthys)," which was considered monophyletic by Akama (2004) and Calegari et al. (2019), while Ribeiro (2010) and Birindelli (2014) also included Trachycorystes and Trachelyopterus within it. These discrepancies occur because the different hypotheses have been based on incomplete sampling biased towards several genera, using even mostly different sets of species. This incongruity is the biggest obstacle for the fulfilment of phylogenetic gaps (Assis, 2018; Diniz-Filho, Loyola, Raia, Mooers, & Bini, 2013; Hortal et al., 2015) and calls for an even more comprehensive survey of the family. The recent species-level phylogeny of Calegari et al. (2019) is the first to include a large proportion of the species of the family (97 out of 124 valid species; updated to 126 species after Rocha et al., 2019: Souza, Sarmento-Soares, Canto, & Ribeiro, 2020). It is also a pioneer in the use of molecular data under a total evidence approach, in contrast to all former hypotheses based only on morphological data. The availability of molecular data is indeed providing a better understanding of the evolutionary relationships among living beings (Diniz-Filho et al., 2013; Gascuel & Steel, 2020; Moritz, 1995), also rendering essential insights into the description of biodiversity (Hime et al., 2020; Sheth & Thaker, 2017).

4.4 | Raunkiæran shortfall

Knowledge of fish diet offers a consistent approach to assessing interactive processes within aquatic communities (Winemiller, 1989), enabling predictions about the roles of particular trophic groups and fish species in the system (López-Rodríguez et al., 2019). Such ecological data are desirable for developing conservation strategies and are a key element in protecting species and ecosystems (Abelha, Agostinho, & Goulart, 2001; Braga, Bornatowski, & Vitule, 2012). Examining the amount, patterns and trends of the study of species traits allows us to identify knowledge gaps and to guide future research strategies (Guerra et al., 2018). Despite such importance, current knowledge on feeding habits presents significant biases across auchenipterid genera and species. The first feeding habit of an auchenipterid (Ageneiosus militaris) was published in the Anales del Museo de Historia Natural de Montevideo by Devincenzi and Teague (1942). After our compilation, we concluded that less than 50% of the known species has some published information on diet. Additionally, information on the diet of auchenipterid fishes is still accumulating with every new study published. Particular attention should focus on the genera underrepresented in our survey (e.g. Tatia, Trachelyopterus), as well as towards those with no available information on feeding habits (Gephyromochlus, Liosomadoras, Pseudepapterus, Pseudotatia, Spinipterus, Trachelyichthys and Trachelyopterichthys). In general, we lack comprehensive knowledge on the trophic ecology of fishes (Braga et al., 2012), as well as other vertebrates such as amphibians (Solé & Rödder, 2000). The vast fish diversity and the limited standardization of the methods applied hamper to fill this gap in this group (Bennemann, Casatti, & Oliveira, 2006), compared to other groups such as primates (Hanya & Chapman, 2013).

A noteworthy aspect of our results was the majority of unique combinations of diet and species registered in the consulted literature. For instance, as unique combinations we have, in Rodrigues et al. (1990), *Entomocorus gameroi* fed exclusively on plankton; in Dary, Ferreira, Zuanon, and Röpke (2017), the diet of *Ageneiosus inermis* was entirely composed by aquatic insects (see Supplementary Table S5 for all feeding combinations). Given the known dietary plasticity of auchenipterids, we highlight the limited nature of the records obtained in the literature. Therefore, more comprehensive studies are needed to retrieve a reliable picture of auchenipterid's feeding habits. Although we are dealing with one ecological trait (feeding habit), this shortfall is certainly vast for other functionally important features of this group that are even more difficult to measure (e.g. behaviour, and reproductive aspects such as fecundity, oocyte size).

4.5 | Interactions between shortfalls

One way or another, all shortfalls are intimately related to each other, but all of them are necessarily tied to the Linnean shortfall (Hortal et al., 2015). The basic alpha-taxonomic process of the Auchenipteridae species description is far from complete. Failing to distinguish species—the basic units of ecological and evolutionary studies-prevents attributing any characteristic to them accurately, whether it is geographic distribution, phylogenetic relatedness or a functional trait. Filling in the Linnean shortfall with a formal description of species allows assigning at least one location to a taxon, thus beginning to fill in the Wallacean shortfall. For instance, some species are known only from the type locality, such as the auchenipterid Pseudotatia parva, known from the lower course of the Rio São Francisco (north-east Brazil) (Mees, 1974). As new biological inventories are carried out, it would be more likely to record a species from other locations. Such is the case of Spinipterus acsi, for which a new record extended its geographic distribution to almost 2,000 km by river from the type locality (Calegari, Akama, & Reis, 2018). Notwithstanding, the uncertainties in the Darwinian shortfall in Auchenipteridae can be reduced with the advances in taxonomic research. Still, they will remain limited by the vast extent of the Linnean shortfall, which, as new species are described (or waiting for a formal description), they will not be included in phylogenetic hypotheses immediately. This generalized interaction between shortfalls hampers the development of knowledge on evolutionary patterns (Assis, 2018; Hortal et al., 2015).

Wallacean shortfalls can also have pervasive impacts on Raunkiæran gaps (Hortal et al., 2015). The lack of geographic coverage can also affect the knowledge about within-species variation of trophic habits, as the frequency of feeding on different sources can be highly influenced by where fishes are caught. For instance, *Tocantinsia piresi* showed carnivorous and frugivorous habits in two different Amazonian river basins (compare Mérona, Santos, & Almeida, 2001 with Dary et al., 2017). Indeed, species with larger distributions (e.g. *Trachelyopterus galeatus* and *Auchenipterus nuchalis*) showed a greater number of feeding studies and thus feeding

combinations (not shown). Widely distributed species commonly show trophic generalism (Abelha et al., 2001), and because they are easier to collect, they are also better-studied. On the other hand, the feeding habits of auchenipterid species with restricted distributions (e.g. Ferrarissoaresia meridionalis) or recently described (e.g. Ageneiosus apiaka, Spinipterus acsi) have been seldom studied. Darwinian shortfalls can also contribute to the Raunkiæran shortfalls as a novel phylogenetic arrangement can create-or rather make evident—new gaps on the knowledge of traits. For instance, Calegari et al. (2019) recovered as a separated lineage the monotypic genus Gephyromochlus, which was previously recognized as Glanidium. Thus, no information of feeding habit is available for Gephyromochlus, while previous to this taxonomic change, feeding habit for the taxa could be extrapolated from Glanidium species. In this sense, well-resolved phylogenetic hypotheses may be crucial to inferences about the relationships between traits and ecological functions, and/or whether they are the result of other evolutionarily correlated features (Hortal et al., 2015; Thompson, Davies, & Gonzalez, 2015).

4.6 | Concluding remarks

The compilation of biodiversity data at regional and global scales has shown enormous advances in recent years (Cornwell et al., 2019; Funk & Richardson, 2002; Hortal et al., 2015; Siracusa, Gadelha, & Ziviani, 2020). The growing availability of information and the development of bioinformatics have enabled large-scale analyses and aided in the interpretation of biodiversity data (Maldonado et al., 2015; Soberón & Peterson, 2004). Many initiatives have provided data that are being used in ecological and evolutionary studies, such as the Global Biodiversity Information Facility (GBIF) or NIH genetic sequence database (GenBank) (Canhos et al., 2015). These global database projects are essential for reducing the extent of the biodiversity knowledge shortfalls (Hortal et al., 2015). On the one hand, they mobilize information previously hidden and/or inaccessible in grey literature. But importantly, they can also serve as a way of identifying which are the biases in our current knowledge and where the gaps remain, allowing identifying specific regions, taxa or clades in need of further work. Specifically for auchenipterids, our study highlights knowledge gaps that need to be addressed: 1) a considerable number of species remain to be described, either through taxonomic revisions (e.g. revision of Trachelyichthys is being conducted by B.B. Calegari and collaborators), and reidentification of samples already stored in collections or possibly coming from new field surveys; in fact, some genera have no published taxonomic revisions (e.g. Centromochlus, Glanidium, Trachelyopterichthys, Trachelyopterus); 2) the limited geographic extent of collections requires sampling new areas, especially in ecoregions with high numbers of auchenipterid species but still considered undersampled (e.g. Amazonas Guiana Shield, Orinoco Guiana Shield and Orinoco Llanos); and 3) most described species lack reliable information regarding their feeding habits; this is even more evident for Trachelyopterus, which is one of

the most diverse auchenipterid genera, but knowledge on the diet of its representatives is almost inexistent, not to mention the genera with no information available on feeding habit (e.g. *Pseudepapaterus*, *Liosomadoras* or *Trachelyichthys*). Based on this, future research on the driftwood catfishes should put special attention in focusing special efforts to cover the taxonomic and geographic gaps mapped in this work. This will increase the effectiveness of future works in the task of providing a more complete overview of the distribution, evolution and ecology of auchenipterids.

There is, however, a limit to the value of currently available biodiversity data. As our results exemplify, in general, the diversity of most living groups is mostly unknown due to limited taxonomic knowledge. Here, the continuous increase in the number of formally described species suggests promising scientific advances for the coming years. It implies that research on systematic biology needs to advance intensively and continuously as new species are expected to be described. Additionally, most of the described species lack reliable information on geographic distribution, evolutionary relationships, functional traits and other vital ecological aspects. Filling these gaps is crucial to evaluating broad-scale biodiversity pattern and process (Hortal et al., 2015). Reducing these gaps will require a concerted effort of taxonomists, ecologists and biogeographers, using evaluations of knowledge shortfalls such as the one conducted here to guide field, experimental and laboratory work towards covering specific knowledge gaps.

ACKNOWLEDGEMENTS

We thank J. Zuanon, L. Juen, J.A.F. Diniz-Filho, G. Tessarolo, F.B. Teresa and C. Guisande for their discussions and comments on an earlier draft of this manuscript. This work was financially supported by grants from the Brazilian Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES—Finance Code 001; TMSF—23038.042984/2008-30); and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; PDM—308694/2015-5; LFAM—302406/2019-0; JH—PVE 314523/2014-6, JS—Post-Doctoral fellowship 434391/2016-6). JS also benefited from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie Action (grant agreement #843234; project: TAXON-TIME); and LFAM from the PROCAD (UFPA/UFG/UNESP: Ecologia, Genética e Conservação do Cerrado, Amazônia e Mata Atlântica).

DATA AVAILABILITY STATEMENT

Data are available at the Zenodo repository (http://doi.org/10.5281/zenodo.3962901).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Freitas TMS, Stropp J, Calegari BB, et al. Quantifying shortfalls in the knowledge on Neotropical Auchenipteridae fishes. *Fish Fish*. 2020;00:1–18. https://doi.org/10.1111/faf.12507