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Knowledge status and trends in description of amphibian species in Brazil

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ABSTRACT

Overcoming the Linnaean and Wallacean shortfalls is an urgent task for biologists. It has been estimated that only a small fraction of the biodiversity on Earth is known, while geographic ranges of already described species are poorly documented. We performed a systematic review and modeling on species descriptions of Brazilian amphibians to evaluate the taxonomic knowledge on this group, to estimate the number of new species that remain to be described, and to identify description trends and relevant information for guiding future studies. All descriptions made between 1758 and 2017 of amphibian species and anuran tadpoles in Brazil, the country with the richest amphibian fauna, were gathered and characterized (species, year of description, number of authors per article, and coordinates of the collecting site). We found 1,119 amphibian species reported occurring in Brazil. The number of descriptions of both amphibian species and anuran tadpoles, as well as the number of authors per article, has exponentially increased over time. Phylogenetic regression analysis revealed that species with smaller body length and distribution area were described later, and that these two species traits are also correlated. According to two predictive models and several scenarios, we estimated that at least 25% of the Brazilian amphibian species have not yet been described. Our findings highlight the maintenance of significant Linnaean and Wallacean shortfalls in the knowledge of Brazilian amphibian species, despite of the increasing research efforts. The northern (Amazon) and central region (Cerrado) of Brazil should be priority areas for herpetological research. Society and the scientific community must commit to a greater investment in biodiversity knowledge to improve conservation strategies before the described and undescribed species become extinct.

1 Introduction

The estimated number of non-microbial species in the world currently ranges from 2 to 50 million (Scheffers et al., 2012), implying that the number of already described species (1.8 million species; Roskov et al., 2019) is a small fraction of the species diversity on Earth. The uncertainty about the number of species in a taxon, also termed Linnaean shortfall (Hortal et al., 2015), has been investigated using taxonomic knowledge and statistical techniques (May, 1988; Guiry, 2012; Costello, Wilson and Houlding, 2012; Nabout et al., 2013). Besides, deficient knowledge on the geographic distribution of the species generates an additional shortfall, termed Wallacean shortfall (Lomolino and Heaney, 2004; Whittaker et al., 2005), which affects the parameters used to quantify biodiversity and examine biogeographic patterns, such as species richness, endemism and beta-diversity (Bini et al., 2006; Yang, et al., 2013).

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Causes and consequences of knowledge shortfalls on biodiversity are diverse and can affect taxa differently (Hortal et al., 2015). New methods that enable the modeling of species discovery curves have recently been used as a major tool for estimating global and regional species richness (Wilson and Costello, 2005; Solow and Smith, 2005; Bebber et al., 2007; Costello and Wilson, 2011; Joppa et al., 2011b). These methods should take into account historical, economic and technological contexts, as well as the effect of taxonomic efficiency (Gaston et al., 1995b; Essl et al., 2013; Randhawa et al., 2015; Lu and He, 2017).

Systematics and taxonomy provide an empirical basis for conducting biodiversity inventories and understanding biological evolution, but multiple challenges still hamper the progress of the taxonomic study ("taxonomic impediment"; de Carvalho, 2005; Ebach et al., 2011). Understanding morphological diversity, mastering taxonomic descriptions, and clarifying phylogenetic and biogeographic relationships requires time, advanced study, professional training, and institutional commitment (Ebach et al., 2011). Analysis of species description in some animal groups has shown that larger or conspicuous species are discovered earlier than species with small body size or narrow distribution ranges (Gaston et al., 1995a; Cardoso et al., 2015; Higgs and Attrill, 2015). Some species currently known to be widely distributed may belong to groups of cryptic species that have similar or identical morphological characteristics (e.g., Gehara et al., 2014). Many species are known only by the type locality, and there are still many taxonomic uncertainties among sympatric species, especially in highly biodiverse groups, as is the case of amphibians (e.g. Thomé et al., 2012). Moreover, despite the necessity of increasing our knowledge on biology, distribution and phylogenetic relationship among taxa, in terms of conservation it is also necessary to know more about the number of species on different scales (Adams and Muths, 2019).

Most of the new species recently described have been discovered in Asia and South America (Costello et al., 2013). Tropical regions gather the highest species diversity, with South America being the richest continent in amphibian species (Vasconcelos et al., 2019a) and Brazil the country with the highest occurrence and rate of description of amphibian species in the world (Segalla et al., 2019). In amphibians, it is foreseeable that the large number of species annually described indicates a noticeable Linnaean shortfall, especially in the tropics, where wide areas remain unsampled (Oliveira et al., 2016). Moreover, amphibian species are sensitive to environmental changes (Becker et al., 2007; Blaustein et al., 2011; do Amaral et al., 2019) and many species can become extinct without being described (Fouquet et al., 2012).

The amphibians from the Neotropical region are a suitable model to represent the Linnaean and Wallacean shortfalls, since they contain a large number of species and new species are annually described. Here, we used Brazilian amphibians as models both to verify the effectiveness of taxonomic research and to estimate the total number of remaining undescribed species in this group. Based on an extensive systematic review and statistical modeling (general and phylogenetic regressions and species discovery curves), we characterized all descriptions of amphibian species and anuran tadpoles occurring in Brazil, published between 1750 and 2017, and we answered the following specific questions: (i) have the descriptions of new species and tadpoles increased over time? (ii) do body size and range size influence the timing of species description? (iii) what is the estimated number of undescribed amphibian species in Brazil? (iv) when is this Linnaean shortfall likely to be overcome? Our findings were analyzed with regard to the regions in which species were described and general guidelines for future taxonomic and herpetologist research provided.

2 Materials and methods

2.1. Literature search

Scientific literature about the species of amphibians and anuran larvae with distribution ranges in Brazil was searched in databases of published articles, textbooks, and online sources. As we were only interested in the general patterns of species description, we selected the amphibians described until 2017. The amphibian species list was gathered from Segalla et al. (2019). Tadpole species descriptions were gathered from Supplementary material of Provete et al. (2012), which was frequently updated in an online spreadsheet by the authors. We also carried out an additional search on described species in the Institute for Scientific Information database (ISI; www.isiknowledge.com), Scientific Electronic Library online (Scielo; www.scielo.org), Google (www.google.com), Google Scholar (www.scholar.google.com), and Amphibia web (http://www.amphibiaweb.org/). We searched scientific articles using keywords combining the taxon name, including synonyms according to Frost (2019), with the following terms: "amphibian" AND "Brazil" OR "Brasil" OR "tadpole" OR "larvae" OR "girino" OR "larva". Only studies on external morphology of the tadpoles were considered. No filters (e.g. range of years) were used during the search. The data were collected from July 2018 through January 2019. We standardized taxonomic names according to Frost (2019), which follows the more recent classifications. For each study, the following metadata were recorded: name of the species, coordinates of each described species (when available), year of species description (first publication) and number of authors. When the exact coordinates of the described species (type locality of the holotype) were not specified in the study, we recorded the coordinates of the collection sites (e.g., one locality of paratype) or of the municipality in which it was collected (when available).

We also gathered data on body size of adult males (snout-vent length, SVL) for each species from articles of species descriptions (checked in Frost, 2019), of call descriptions (checked in the Supplementary material of Guerra et al., 2018), natural history studies (e.g. Heyer et al., 1990; Lescure and Marty, 2000; Duellman, 2005; Duellman, 1978) and specialized textbooks (e.g. Kwet, 2001; Haddad et al., 2013). The species distribution areas were obtained from the International Union for Conservation of Nature's Red List of Threatened Species (IUCN, 2017) database. The polygons representing the distribution range of the Brazilian amphibian species were downloaded from the IUCN website, and the areas (Km^2) were subsequently calculated using the Quantum GIS software (QGIS, 2011). Although, in some cases, the polygons used for the analysis may have outdated data regarding the distribution of species, they provide suitable estimates in general and are still widely used by researchers to assess general patterns in ecological studies (e.g. Kemppinen et al., 2020). The species that lacked data on SVL, distribution range or phylogenetic relationships, as well as exotic species, were excluded from the statistical analyses. The data and literature used in this study are available in Supplementary materials S1 and S2.

2.2. Data analysis

2.2.1. Trends in description of Brazilian amphibians

To evaluate whether the number of described species and number of authors in the description studies of amphibians from Brazil increased over the years, we applied Generalized Linear Models (GLM) with Poisson log-link function (McCullagh and Nelder, 1989). Specifically, four GLMs were fitted using the annual number of described amphibians (1 – all species and 2 – anuran tadpoles) and the number of authors per study (3 – all species and 4 – anuran tadpoles) as response variables and the year of publication as a fixed variable. Considering that more than one species can be described in the same study, for the analysis of the number of authors per year, each article was counted only once (amphibians, n = 718; tadpoles, n = 372). The statistical assumptions were carefully checked for each model. Leverage values as well as DFBeta values indicated no obviously influential cases (Quinn and Keogh, 2002; Field, 2005). Overdispersion was identified in the models that verified trends in the annual number of descriptions of species and tadpoles (dispersion parameter = 5.36, chi-2 = 837.6, df = 156, $p < 0.001$; dispersion parameter = 4.12, chi-2 = 255.6, df = 62, $p < 0.001$, respectively), but not in the other two models. To correct for overdispersion, estimated regression coefficients were multiplied by the square root of the overdispersion parameter and then the statistics and the p-value were recalculated. All models were fitted in R version 3.5.3 (R Core Team, 2019) using the function *glm*. We assumed $p \leq 0.05$ as significance levels for our analyses.

2.2.2. Bias in the description of Brazilian anuran species

To estimate the effect of body size (cm) and range size (Km^2) on the description date of Brazilian anurans, we used a phylogenetic generalized least squares (PGLS) regression (Grafen, 1989). As most species of the Orders Caudata and Gymnophiona are classified by IUCN as Data Deficient and lack data on distribution range, we used only species of the Order Anura for these analyses. To control for the phylogenetic relationships among species and to test the presence of potential phylogenetic signal, we used PGLS and estimated Pagel's λ parameter on the residual phylogenetic covariance matrix (Pagel, 1999; Freckleton et al., 2002). When λ is closed 0, no phylogenetic structure on regression residuals is observed, whereas λ closed 1 indicates phylogenetic structure on residuals as expected by a stochastic Brownian motion process of evolution. Thus, we allowed the model to automatically control for phylogenetic structure when it was necessary, correcting the potential Type 1 error of regression coefficients (Revell, 2010). The phylogenetic covariance matrix was calculated according to the phylogeny of Amphibians proposed by Pyron and Wiens (2011). Previously, we had pruned from the phylogeny all the species not included in our database, and thus we applied the PGLS on 300 species (Supplementary material S3). We checked for homoscedasticity and normal distribution on model residuals, and log-transformed the SVL and distribution area to meet the assumptions (Zar, 1999). The PGLS was performed using the *Caper* package (Orme et al., 2014) implemented in software R version 3.5.3 (R Core Team, 2019). We assumed $p \leq 0.05$ as significance levels for our analyses.

2.2.3. Brazilian amphibian species estimation

We used two different approaches to estimate the expected total number of species occurring in Brazil. In the first approach, we fitted two non-linear models of species descriptions that control for taxonomic effort. These models improve fitting in species description curves since they account for historical contexts and changes in taxonomic effort (Costello et al., 2012; Lu and He, 2017). They are based on the negative exponential model ($\Delta S = k\,(S_{tot} - S_{cum})$), in which ΔS is the number of species described within a time span, S_{tot} is the estimated total species richness, S_{cum} is the accumulated described species and k is a description efficiency parameter. If $k = T\,(a + bt)$, where T is the number of taxonomists within the time span, and t is the year of description, this model becomes the Joppa model $\Delta S = T\,(a + bt)\,(S_{tot} - S_{cum})$. If the Joppa model (Joppa et al., 2011b) is modified by substituting bt by bS_{cum}, this becomes the Lu & He model (Lu and He, 2017). We fitted the models using generalized nonlinear squares implemented in *gnls* function of R package *nlme*.

Residual variance was fitted as a power function of residual mean to account for overdispersion or underdispersion of residuals. We ranked the model by second-order Akaike Criterion Information (AICc) and inferred the total species richness (S_{tot}) and the cumulative species description curve by averaging the four models using their AICc weights (Burnham and Anderson, 2002; Dormann et al., 2018). Thus, we considered the uncertainty of model estimates. Our analyses were run by removing the procedure of fitting model by time slices of the original script of Lu and He (2017). We fitted the models considering all time series since 1758 until 2017.

In the second approach, we estimated the total number of species by Jackknife2 estimator, and then we used a logistic model to simulate different scenarios of species description in order to estimate the time when all species would be described (for more details, see Gotelli, 2008; Ota et al., 2015). For this, we considered the amphibian species described between the years 1960 and 2017. We chose that period as most of the Brazilian amphibian species were described after 1960, and it was also when studies on natural history (call and tadpole descriptions in anurans) began to be most frequently published (Guerra et al., 2018). The logistic model was simulated in two periods of time until all species description had been completed (50 or 100 years) and six scenarios (0.05, 0.1, 0.2, 0.3, 0.4 and 0.5) of description rates constructed (r). The curve that showed a sigmoid form when the simulated and real values converged was considered the most realistic scenario (Ota et al., 2015). All analyses were implemented in R version 3.5.3 (R Core Team, 2019).

3 Results

3.1. Trends in description of Brazilian amphibians

The species list amounted to a total of 1,119 amphibian species in Brazil (until December 2017), five of which were salamanders (Caudata), 38 caecilians (Gymnophiona) and 1076 anurans (Anura). Two anuran species are considered exotic (*Eleutherodactylus johnstonei* Barbour, 1914 and *Lithobates catesbeianus* (Shaw, 1802)) and were thus excluded from further analyses. We found three studies providing descriptions of Caudata species that were published between 1874 and 2013, 33 studies with descriptions of Gymnophiona species published between 1802 and 2015, and 718 studies with descriptions of anuran species between 1758 and 2017. Furthermore, we found 437 studies on tadpole descriptions between 1876 and 2017, of which 372 first described the larvae of an anuran species. Among the Brazilian anuran species described until 2017, 82.3% (919 spp.) have a larval stage (indirect development), within which only 57.9% (532 spp.) have a description of their tadpoles, with 19.4% (103 spp.) having the tadpole description included in the original species description. In species that did not have the larvae described in the original description, the tadpole was described an average of 69.5 years later ($\pm$55.6; range 0–220). The first described tadpole was *Pipa pipa* (Linnaeus, 1758) in the work of Parker (1876), and the first tadpole description together with the species was for *Scinax rizibilis* (Bokerman 1964).

An exponential increase in the number of descriptions of new Brazilian amphibian species (estimate $\pm$ SE = 0.009 $\pm$ 0.0001, z = 16.17, $p < 0.001$, df = 156) and anuran larvae (estimate $\pm$ SE = 0.01 $\pm$ 0.002, z = 9.04, $p < 0.001$, df = 62) has been observed over time (Fig. 1a). The annual discovery rate in the first decade of the 21st century was on average 18 species per year, while between 2008 and 2017 this rate increased to 25 species per year. The annual number of authors per article also followed a similar historical pattern (Fig. 1b). An increase in the number of taxonomists authoring the studies that describe amphibian species (estimate $\pm$ SE = 0.008 $\pm$ 0.0004, z = 17.04, $p < 0.001$, df = 1112) and anuran tadpoles (estimate $\pm$ SE = 0.004 $\pm$ 0.0005, z = 9.77, $p < 0.001$, df = 529) was found. From all amphibian species with distribution area in Brazil, 847 species (78.9%) were described within the country (Fig. 2), mainly in the southeastern region (398 species – states of Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo), and in the northeastern (93 species – state of Bahia), northern (51 species – state of Amazonas) and southern regions (51 species – state of Santa Catarina). Peru was the country with the second highest number of described species (57 species) that occurred in Brazil. Thus, most of the species were described in the Atlantic Forest and Amazon rainforest (Fig. 2). In 2013, the greatest number of new amphibian species described (32 spp.) was reached, followed by 2012 and 2015 (30 spp.). In 1978, the greatest number of tadpole descriptions (33 spp.) was reached, followed by 1990 (29 spp.), 2007 (23 spp.) and 2015 (22 spp.). The study by Spix (1824) presented the highest number of amphibian species descriptions, with a total of 28 new anuran species for Brazil.

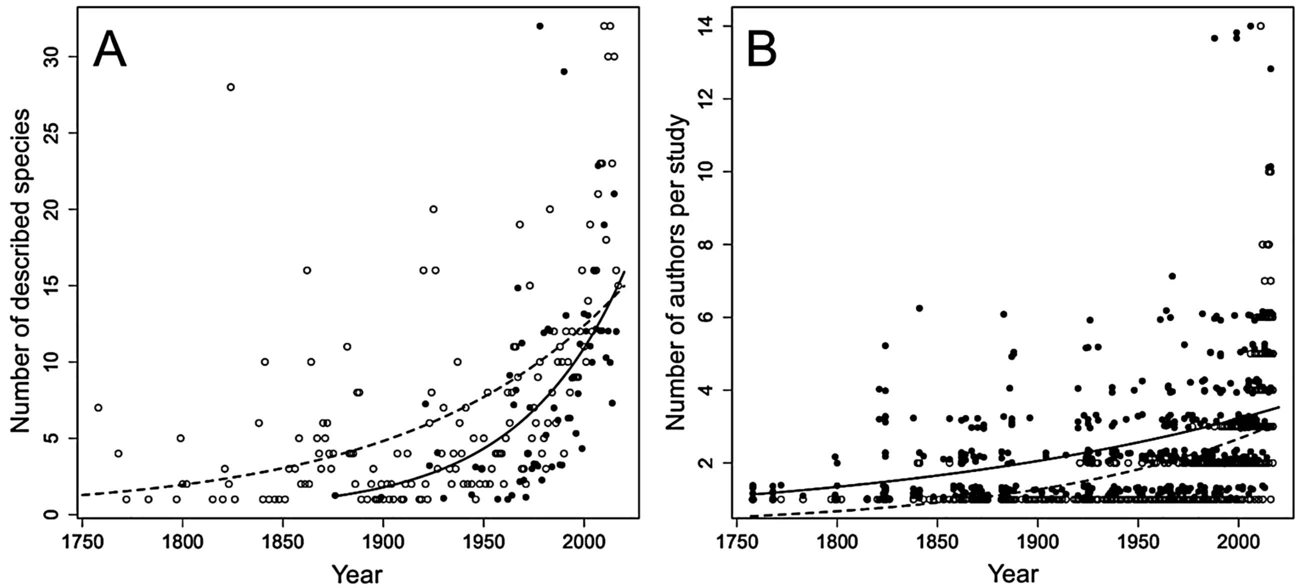

Fig. 1. The annual number of descriptions of Brazilian amphibian species (A) and the annual number of authors in each study of species description (B) published between 1750 and 2017. Regression lines fitting the number of new described species over the years are shown. Adults (Amphibia) depicted as filled circles and dashed line. Tadpoles (Anura) depicted as unfilled circles and continuous line.

3.2. Bias in the description of Brazilian anuran species

Phylogenetic Generalized Least Squares (PGLS) regression analysis showed a significant positive linear relationship between body size and distribution range size of Brazilian anuran species (estimate ± SE = 0.012 ± 0.005; t = 2.409; r^2 = 0.015; F = 5.806; df = 1, 295; p < 0.01; Fig. 3A), with phylogenetic signal in the model residuals (λ = 0.98). Large-sized species mostly occupy wider distribution ranges, whereas small-sized species are distributed across all range sizes. We also found a negative relationship between body size and the year of species description (estimate ± SE = −0.001 ± 0.001; t = −5.34; r^2 = 0.08; F = 28.52; df = 1, 298; p < 0.01; Fig. 3B), and between distribution and the year of species description (estimate ± SE = −0.019 ± 0.001; t = −9.74; r^2 = 0.24; F = 94.91; df = 1, 295; p < 0.01; Fig. 3C). Both body size (λ = 0.97) and distribution (λ = 0.83) presented a phylogenetic signal in the model residuals.

3.3. Brazilian amphibian species estimation

In the first approach, the Joppa model concentrated all support to explain the species description curve (Table 1). Consequently, the average model is, in fact, inferred from the Joppa model, as can be visualized in Fig. 4. The average model estimated a total of 1473 species (CI = 1259–1687), suggesting that 76% (CI = 0.66 – 0.89) of the total number of species had been already described. By plotting the cumulative number of described species weighted by taxonomic effort, it is seen that the rate of description of new described species is decreasing and the ratio of new species to taxonomists is beginning to stabilize (Fig. 5).

According to the second approach, Jackknife2 estimated a total of 2073 amphibian species in Brazil. If we add 414 species discovered before 1960 (prior to our time series), the absolute total would be 2487 species. Hence, this model predicts a description of 1370 (55.1%) additional new species. For both time possibilities (50 and 100 years), the best description rate (r) to describe the observed species accumulation curve was 0.1 (a line that showed the overall shape of the curve closer to a sigmoid; Fig. 6). However, for the 50-year period, it is only with an r value of 0.15 that the curve reaches an asymptote (approximately in the year 2060). For the 100-year period, the asymptote is reached about year 2095 (Fig. 6).

4 Discussion

4.1. Trends in description of Brazilian amphibians

Brazil is the richest country in amphibian species in the world, and the anurans are the most representative group. Admittedly, many efforts have been made to know more about the existing species diversity, as shown by the exponential-like increase in the number of taxonomists and subsequent accumulation curve of described species over time. A similar pattern was found when considering South American amphibians (Vasconcelos et al., 2019a), likely guided by Brazilian description efforts. However, many gaps still need to be filled. For instance, more than 40% of Brazilian anurans with aquatic free-swimming larvae still lack a description of the tadpole (Provete et al., 2012). Guerra et al. (2018) verified that there is a significant lack of knowledge on the advertisement calls of the Brazilian anuran species, suggesting a Raunkiaeran shortfall (see Hortal et al., 2015) regarding an important trait for reproduction and territory defense. Overall, the lack of knowledge on species diversity and traits affects groups other than amphibians, and many taxa have shown a similar pattern (Bebber et al., 2007; De Clerck et al., 2013; Ota et al., 2015).

Since Linnaeus proposed his taxonomic classification (Linnaeus, 1753), which is currently used, scientists have been working for more than 200 years in an attempt to describe all species on the planet. Species delimitation has traditionally been based on morphological differences, but an integrative taxonomic approach, including bioacoustics, ecology, behavioral, morphology, biochemical, ultrastructural analyses and molecular genetics (barcoding and phylogeography) has been used to taxonomically facilitate a complete appraisal of biodiversity, especially on identifying cryptic species (Ortega-Andrade et al., 2015; Ferrão et al., 2016; Komarek, 2006; Rojas et al., 2016; Vacher et al., 2017). The emergence of technological (e.g., tools for genetic and call analysis) and interdisciplinary research has resulted in an increase in the number of scientists involved in species descriptions (Costello et al., 2012; Bebber et al., 2007). Consequently, the number of authors in the studies has increased, despite the evidence of a decrease in resource effort and number of taxonomists over time (Nabout et al., 2015). Recently, amphibians have undergone major taxonomic changes, including the revision and adjustment of taxonomic classification (Duellman et al., 2016; Dubois, 2017), and several groups of amphibians encompassing species of very similar morphology have also been recently reviewed due to the existence of cryptic species (e.g.

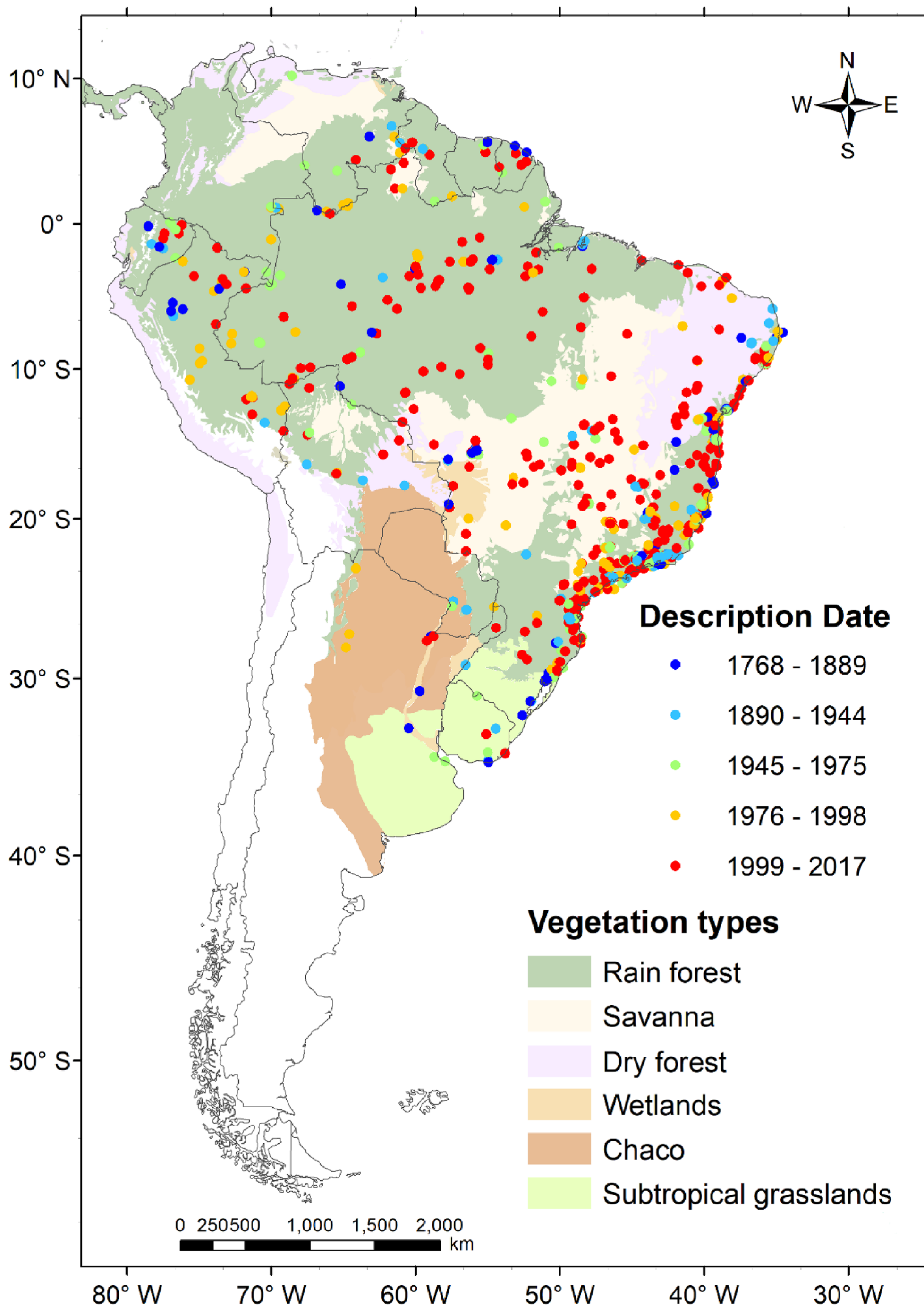

Fig. 2. Map showing the collection site of 879 species of amphibians that have been described between 1768 and 2017, and with distribution range in Brazil.

Pimenta et al., 2014; Ribeiro et al., 2015). All those efforts, such as taxonomic revision and complexity in species description, have become more common and easily accessible among researchers because of digital communication, which improves the stability of species hypothesis and enables more reliable estimates of total species richness (Bebber et al., 2007).

Overall, most of the amphibian species occurring in Brazil were described in the southeast region (states of Rio de Janeiro, São Paulo, and Minas Gerais) and in the northeast region (state of Bahia), mainly in the Atlantic Forest biome. The southeast and northeast regions of Brazil were colonized earlier and have the oldest universities, museums, and research institutes, and hence those regions were the target of the first scientific expeditions by researchers. In addition, the Atlantic Forest has one of the highest species richness and endemism rates of the continent (Carnaval et al., 2009; Haddad et al., 2013; Guerra et al., 2018). The northern (states of Acre, Amapá, Roraima, Rondônia, and Tocantins) and northeast (states of Ceará, Maranhão, Paraíba, Pernambuco, and Piauí) regions of the Brazil, particularly in the Amazon and Caatinga Biomes, are those with the fewest described species. Consequently, it can be expected that species descriptions will increase in the coming years if more research efforts are allocated to these unsampled areas. Moreover, there is also a high bias in species descriptions and species distribution knowledge concerning the location of access routes (Oliveira et al., 2016), with a general pattern of amphibian species being described along the rivers. Large sampling gaps are observed in the northern, central, and southern states of Brazil,

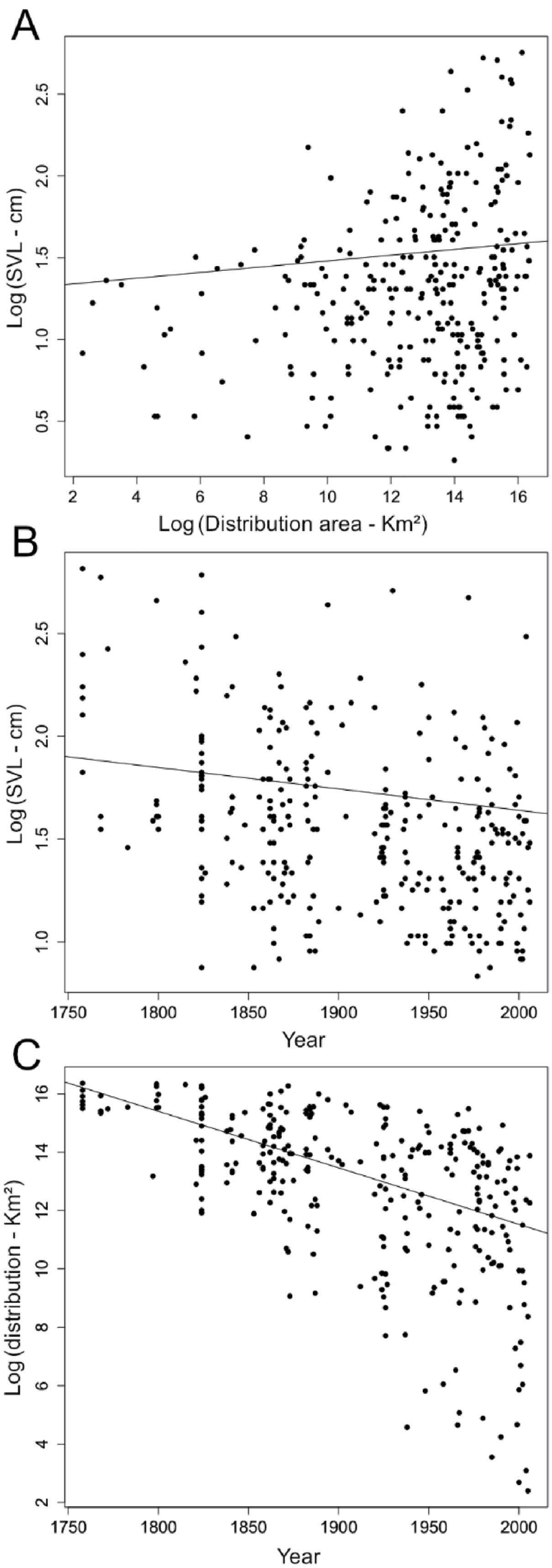

Fig. 3. Phylogenetic Generalized Least Squares (PGLS) regression analyses showing the relationship between (A) body size (cm) and distribution range size area (Km^2), (B) body size (cm) and year of species description, and (C) distribution range size area (Km^2) and year of species description for a total of 300 Brazilian anuran species.

corresponding to the Amazon, Cerrado and Pampa Biomes and other transition zones that are challenging to access.

Since Brazil is a country with large territorial size and much diversity in phytogeographic regions, there are still broad areas that have not been sampled for amphibians (de Affonso et al., 2015; Oliveira et al., 2016; Guerra et al., 2018; Vasconcelos et al., 2019b). The lack of data on species distribution is also a major problem in the implementation of public policies and conservation programs for amphibians (Young et al., 2004), especially in regions that are suffering severe habitat destruction (Becker et al., 2007). Even in known vertebrate groups, the least conservative estimates of the known species distribution were lower than potential distribution predicted by species distribution models (Oliveira et al., 2016). Consequently, journals publishing distribution notes and natural history attributes of species, such as Herpetology Notes and Check List, have been gaining prominence, as they are important vehicles of publication of these observational studies.

As previously reported, we found that the number of authors of species descriptions has been increasing over the years (Guerra et al., 2018; Vasconcelos et al., 2019a). Decreasing travel and communication costs, as well as the increasing number of researchers, have likely stimulated collaboration in studies encompassing different areas (Hsu and Huang, 2011; Vermeulen, Parker and Penders, 2013). Collaboration among multiple authors allow researchers to address more complex biological questions, to reduce research costs, and even to build multi-taxa studies with other researchers specialized in different taxonomic groups (Nabout et al., 2015; Guerra et al., 2018). As data on the biology of the species have become easier to acquire, mainly because of the easy access to new technologies, it is possible to make more detailed analyses on diversity: such as by assessing how anthropogenic impacts affect species directly (e.g., urbanization; Scheffers and Paszkowski, 2012) and indirectly (e.g., global warming; Llusia et al., 2013). Even so, almost all tropical amphibians still lack basic information about their natural history.

4.2. Bias in the description of Brazilian anuran species

As shown by regression models, Brazilian amphibians follow a long-established macroecological pattern, i.e. body size is positively correlated with species distribution area. This allometric relationship may have several mechanistic explanations. It might be expected that larger species generally show higher dispersion capacity (Gaston and Blackburn, 1996; Wollenberg et al., 2011), greater fertility (Van Bocxlaer et al., 2010) and broader diet (Brown and Maurer, 1989). As proposed by the energy constraint on minimum range size hypothesis (Agosta and Bernardo, 2013), larger species require larger areas to obtain resources for their survival, implying larger geographic territories to maintain viable population sizes (Brown and Maurer, 1989). In addition, it is expected that larger species have open populations with a high gene flow (Diniz-Filho et al., 2005).

It might be argued that another explanation for this pattern is the fact that the first species described could accumulate more records over time and therefore show a greater geographic distribution (Costello and Wilson, 2011). However, as found in marine species (Higgs and Attrill, 2015), we believe that this is not the case for Brazilian amphibians, since there are many endemic groups, such as brachycephalids in the Atlantic Forest. Our results also support the hypothesis that the range size–body size pattern occurs on a macroevolutionary scale, since these characteristics showed a significant phylogenetic signal. These factors directly affect conservation strategies, since large-bodied species with a relatively small geographical range are expected to be more prone to extinction risk due to the low total size of the population (Gaston and Blackburn, 1996; Diniz-Filho et al., 2005).

We also found that larger-sized species, consequently widely distributed, have a tendency to be described sooner than small species, and this is in accordance with studies carried out in other animal groups

Table 1
Descriptive statistics of Joppa (Joppa et al., 2011a,b) and Lu and He (Lu and He, 2017) species discovery models for Brazilian amphibian species described from 1758 to 2017. Abbreviations: S_{tot} = estimated total species richness, 95% CI = 95% confidence interval, a and b = estimated parameters, ΔAIC = Akaike Criterion Information, WAIC = AIC weights.

Model	S_{tot}	Lower 95% CI	Upper 95% CI	a	b	ΔAIC	WAIC
Joppa's model	1473.23	1257.48	1688.98	$1.64*10^{-2}$	$-7.69*10^{-6}$	0	$99.9*10^{-3}$
Lu and He's model	1230.58	1165.01	1296.16	$1.45*10^{-3}$	$1.61*10^{-5}$	15.4	$4.6*10^{-4}$
Average model	1473.12	1258.93	1687.31	–	–	–	–

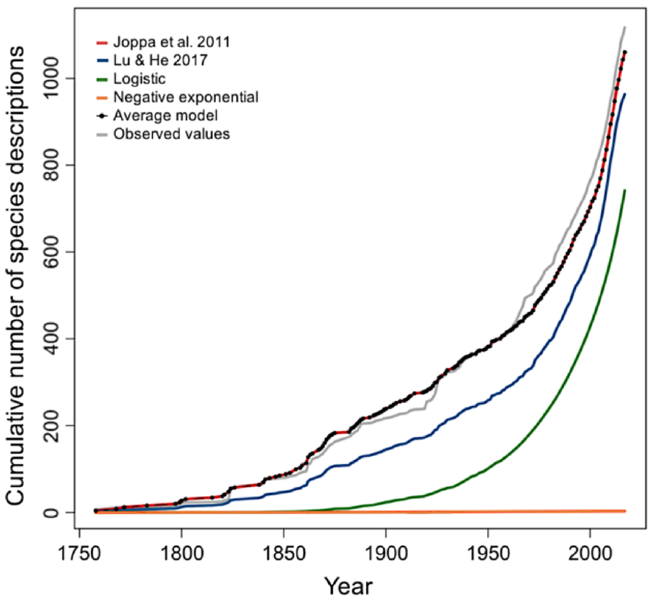

Fig. 4. Observed and predicted accumulation curve of descriptions of Brazilian amphibian species over time. Lines depict curves based on different predictive models, namely that constructed by Joppa et al. (2011), by Lu and He (2017) and an average model.

(e.g. Gaston et al., 1995a; Cardoso et al., 2015; Higgs and Attrill, 2015). In addition, although we have not analyzed the taxonomic status, we can assert that as was found for North American butterflies (Gaston et al., 1995a), the amphibian species described earlier have a greater number of synonymies than those most recently described and therefore they have been more intensely studied. Overall, most species with an easier description (more detectable and more distinct) are already known and the current challenge is to identify small, cryptic, and endemic species, presumably with low detectability.

4.3. Brazilian amphibian species estimation

Our models to estimate the total richness of Brazilian amphibian species showed that there are still many species to be described. However, the exponential pattern of the species accumulation curve also reflects an increase in effort of taxonomic studies. Therefore, according to the species/taxonomist ratio curve, species description is stabilizing. For instance, considering the total estimated richness of our first analytical approach (1473 species) and the current average rate of 25 species discovered per year, it would take about 15 years to discover all the amphibian species in Brazil. Nonetheless, that stabilization should be viewed with caution, as research investments have been, as said above, geographically biased, indicating that regions that historically prioritized research may have made their anuran diversity better known in a short period of time, and thus investments should be diversified to cover unsampled regions. Our second analytical approach

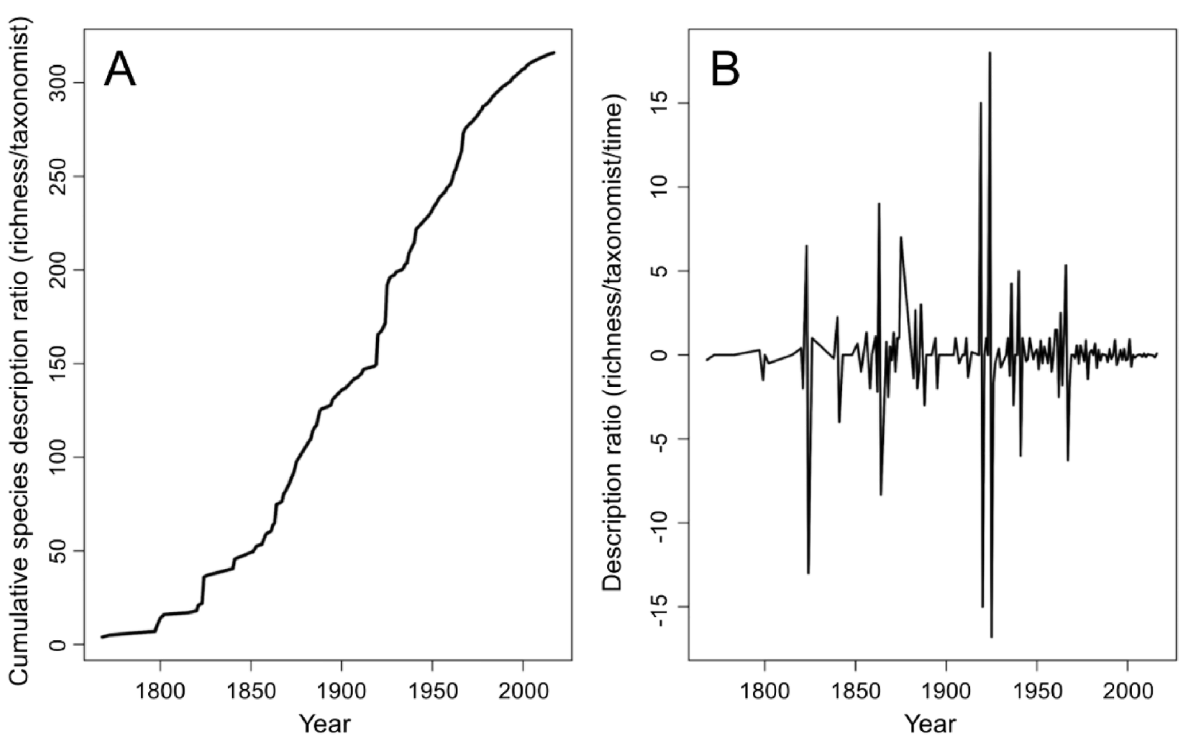

Fig. 5. Cumulative description ratio of Brazilian amphibian species per taxonomist over time (A) and variation in the rate of species descriptions over taxonomists over time (B).

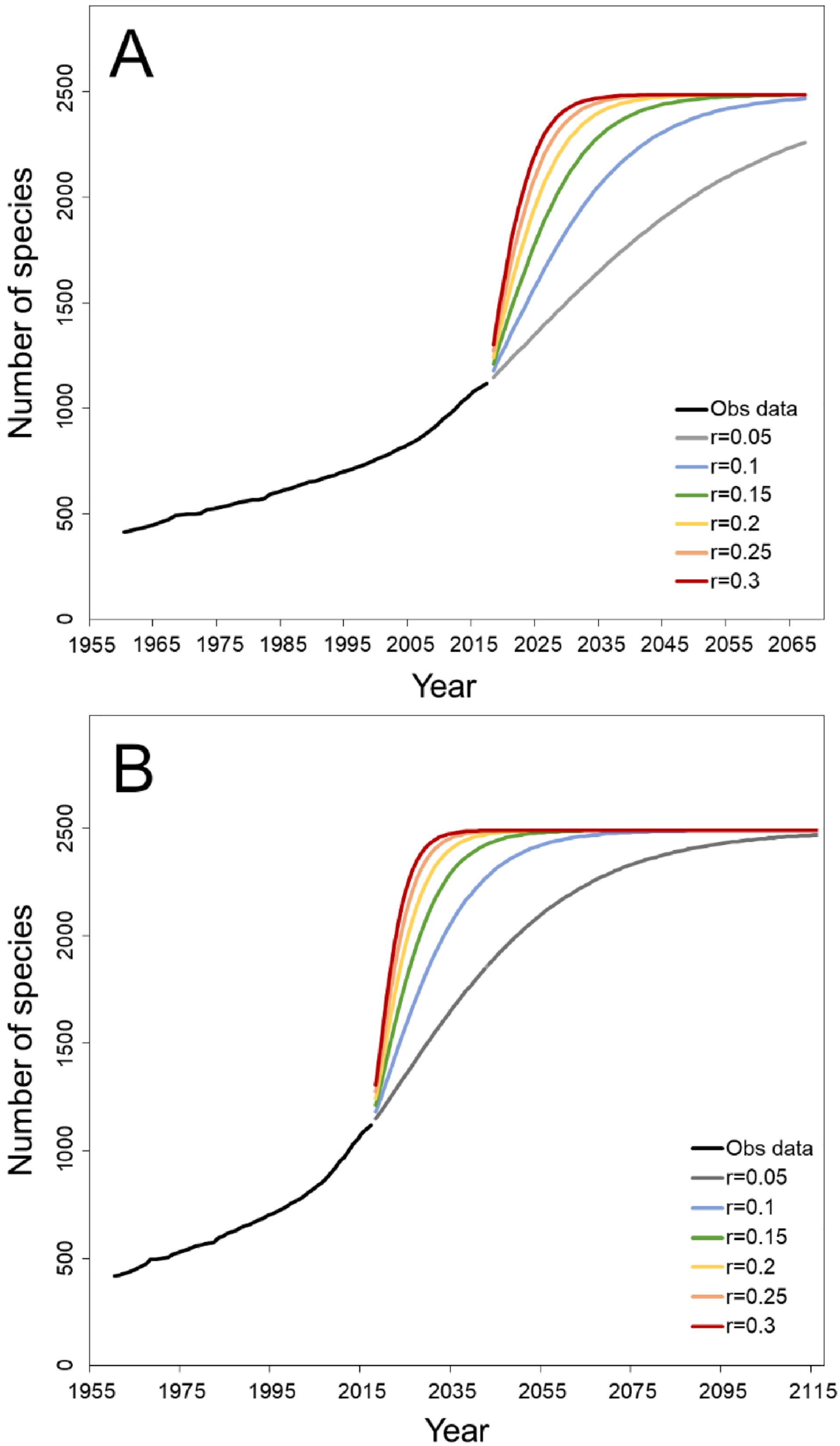

Fig. 6. Observed and predicted annual number of descriptions of new Brazilian amphibian species for two simulated periods: (A) 50 years and (B) 100 years. Observed data are indicated by the continuous line (1960–2017). Predicted data were estimated by logistic models using different growth rates (r). Extrapolation of the accumulation curves stabilized when reaching the value of 2487 species obtained by the estimator Jackknife 2.

was less conservative because it did not consider the taxonomic effort, estimating a much higher species richness for Brazil. Thus, at least 40 years of studies would be necessary to describe all species.

While it is challenging to describe all Brazilian amphibian species in the coming years, historical events may influence the number of researchers and their efficiency in describing species, such as changes in public research investment, economic crises and deceleration in technological advances (Gaston et al., 1995b; Essl et al., 2013; Randhawa et al., 2015; Lu and He, 2017; Vasconcelos et al., 2019a). The steep rise in species discoveries since the 1950 s was due to the increase in the number of taxonomists (e.g. A. Lutz, B. Lutzi, A. de Miranda-Ribeiro, D. M. Cochran, W. R. Heyer, W. C. A. Bokermann), investment in science and the advent of molecular techniques (Vasconcelos et al., 2019a). In fact, Brazil is currently freezing the budget of the Ministry of Science, Technology, Innovation and Communication as well as that of the Ministry of Education, severely impacting funding of research projects, undergraduate and graduate grants and consequently decreasing the training of new researchers (Fernandes et al., 2015; Magnusson et al., 2018; de Area Leão Pereirae et al., 2019; Escobar, 2019). All these measures will likely slow down the current rates of species description.

Knowing the actual richness of a taxon group has been a major challenge for researchers, but it is also crucial for setting conservation priorities and analyzing biogeographic patterns (Joppa et al., 2011a,b; Scheffers et al., 2012; Tedesco et al., 2014; Vasconcelos et al., 2019c). Among vertebrate groups, birds (Bebber et al., 2007) and large marine animals (Solow and Smith, 2005; Appeltans et al., 2012) present accumulation curves of described species as reaching an asymptote, with the number of species currently described being close to the predictions.

The predictive models used in this study can be viewed in the context of pattern-oriented modeling (see Grimm, 2005). Overall, models used to predict the species number are criticized due the nature of the data, since it is difficult to formulate realistic predictions when the number of described species is still far from the real number (Bebber et al., 2007; Nabout et al., 2013). The best models are reached on local scales rather than on regional and global scales, but it depends also on the taxa of interest, with some taxa better estimated than others (Gaston et al., 1995b; Gaston, 2000; Wilson and Costello, 2005; Bebber et al., 2007; Joppa et al., 2011a,b; Appeltans et al., 2012; Lu and He, 2017). Although some problems may be associated with these models, and the main drawback is geographic sampling bias, they do allow us to understand that a wide number of species are waiting to be described.

5. Conclusion

There are significant Linnaean and Wallacean shortfalls in the knowledge of Brazilian amphibian species. These shortfalls have a direct effect on systematic conservation planning and may be particularly serious for poorly known regions of Brazil, characterized by recent and dense human occupation and, often, by very high biodiversity (Bini et al., 2006; Hortal et al., 2015). Initially, the best way to circumvent the Linnaean shortfall is to invest in biodiversity inventories (Balmford and Gaston, 1999; Bini et al., 2006; Costello et al., 2012). Many regions of Brazil are still poorly sampled, as is the case of the Amazon and Caatinga. The Caatinga, as well as the Cerrado, although initially considered biomes poor in amphibians due the dry environmental and climatic characteristics, both contain unique and endemic species and should be explored intensively by researchers. We would also like to encourage studies in the northern region of Brazil, and especially in the areas of transition between biomes, which is located between the Amazon and Cerrado, and presents areas of Ecological Tension and of Pioneer Formations. Special attention should be directed to small-sized species, which are more vulnerable to population fluctuations independent of density, so that the differential extinction (or contraction of the distribution area) of these species tends to be positively correlated with size of area of distribution and body size (Gaston and Lawton, 2006).

Knowledge about biodiversity and natural history of amphibian species is important to identify present trends as a basis for future studies (Toledo and Batista, 2012; Guerra et al., 2018). As knowledge about biodiversity is incomplete and evident, we emphasize the need to describe species, as well as to study the species composition of communities. Morphological and environmental factors, such as skin permeability, dependence on moist and relatively well-preserved environments, make amphibians the most endangered group of vertebrates in the world (Becker et al., 2007; Blaustein et al., 2011; do Amaral et al., 2019). In developing countries such as Brazil, the adoption of laws that provide amnesty for deforestation (Soares-Filho et al., 2014; Escobar, 2018; Freitas et al., 2018) and the reduction of investments in education and research (Alves et al., 2018; Abessa et al., 2019) may slow down the gathering of knowledge about biodiversity. Increasing our knowledge of biodiversity will allow scientists to establish research networks, and will encourage society to invest in science, technology, and education, and therefore in the preservation of natural habitats.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106754.

References

Abessa, D., Famá, A., Buruaem, L., 2019. The systematic dismantling of Brazilian environmental laws risks losses on all fronts. Nature Ecol. Evol. https://doi.org/10.1038/s41559-019-0855-9.

Adams, M.J., Muths, E., 2019. Conservation research across scales in a national program: How to be relevant to local management yet general at the same time. Biolog. Conserv. https://doi.org/10.1016/j.biocon.2019.05.027.

Affonso I de, P., Oda, F.H., Gambale, P.G., Batista, V.G.V.G., Gomes, L.C., Bastos, R.P., 2015. Publicações científicas em Herpetologia na região Sul do Brasil. Boletim do Museu de Biologia Mello Leitão 37:409–425.

Agosta, S.J., Bernardo, J., 2013. New macroecological insights into functional constraints on mammalian geographical range size. Proc. R. Soc. B: Biol. Sci. doi:10.1098/rspb.2013.0140.

Alves, R.J.V., Weksler, M., Oliveira, J.A., Buckup, P.A., Pombal Jr., J.P., Santana, H.R.G., Peracchi, A.L., Kellner, A.W.A., Aleixo, A., Langguth, A., et al., 2018. Brazilian legislation on genetic heritage harms Biodiversity Convention goals and threatens basic biology research and education. Anais da Academia Brasileira de Ciências 90, 1279–1284. https://doi.org/10.1590/0001-3765201820180460.

do Amaral, D.F., Guerra, V., Motta, A.G.C., de Melo e Silva, D., Rocha, T.L., 2019. Ecotoxicity of nanomaterials in amphibians: a critical review. Sci. Total Environ. 686:332–344. doi:10.1016/j.scitotenv.2019.05.487.

Appeltans, W., Ahyong, S.T., Anderson, G., Angel, M.V., Artois, T., Bailly, N., Bamber, R., Barber, A., Bartsch, I., Berta, A., et al., 2012. The magnitude of global marine species diversity. Curr. Biol. 22, 2189–2202. https://doi.org/10.1016/j.cub.2012.09.036.

de Area Leão Pereira, E.J,, Silveira Ferreira, P.J,, de Santana Ribeiro, L.C., Sabadini Carvalho, T., de Barros Pereira, H.B., 2019. Policy in Brazil (2016–2019) threaten conservation of the Amazon rainforest. Environ. Sci. Policy. doi:10.1016/j.envsci.2019.06.001.

Balmford, A., Gaston, K.J., 1999. Why biodiversity surveys are good value. Nature. https://doi.org/10.1038/18339.

Bebber, D.P., Marriott, F.H.C., Gaston, K.J., Harris, S.A., Scotland, R.W., 2007. Predicting unknown species numbers using discovery curves. Proc. R. Soc. B: Biolog. Sci. 274, 1651–1658. https://doi.org/10.1098/rspb.2007.0464.

Becker, C.G., Fonseca, C.R., Haddad, C.F.B., Batista, R.F., Prado, P.I., 2007. Habitat split and the global decline of amphibians. Science 318, 1775–1777. https://doi.org/10.1126/science.1149374.

Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Bastos, R.P., Pinto, M.P., 2006. Challenging Wallacean and Linnean shortfalls: Knowledge gradients and conservation planning in a biodiversity hotspot. Divers. Distrib. 12, 475–482. https://doi.org/10.1111/j.1366-9516.2006.00286.x.

Blaustein, A.R., Han, B.A., Relyea, R.A., Johnson, P.T.J., Buck, J.C., Gervasi, S.S., Kats, L.B., 2011. The complexity of amphibian population declines: understanding the role of cofactors in driving amphibian losses. Ann. New York Acad. Sci. 1223, 108–119. https://doi.org/10.1111/j.1749-6632.2010.05909.x.

Brown, J.H., Maurer, B.A., 1989. Macroecology: the division of food and space among species on continents. Science 243, 1145–1150. https://doi.org/10.1126/science.243.4895.1145.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach, second ed. Springer-Verlag, New York.

Cardoso, M.N., Shimano, Y., Nabout, J.C., Juen, L., 2015. An estimate of the potential number of mayfly species (Ephemeroptera, Insecta) still to be described in Brazil. Revista Brasileira de Entomologia. https://doi.org/10.1016/j.rbe.2015.03.014.

Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T., Moritz, C., 2009. Stability predicts genetic diversity in the Brazilian atlantic forest hotspot. Science 323, 785–789. https://doi.org/10.1126/science.1166955.

de Carvalho, M.R., 2005. Revisiting the taxonomic impediment. Science. https://doi.org/10.1126/science.307.5708.353b.

De Clerck, O., Guiry, M.D., Leliaert, F., Samyn, Y., Verbruggen, H., 2013. Algal taxonomy: a road to nowhere? J. Phycol. 49, 215–225. https://doi.org/10.1111/jpy.12020.

Costello, M.J., May, R.M., Stork, N.E., 2013. Can we name earth's species before they go extinct? Science 339, 413–416. https://doi.org/10.1126/science.1230318.

Costello, M.J., Wilson, S.P., 2011. Predicting the number of known and unknown species in European seas using rates of description. Global Ecol. Biogeogr. https://doi.org/10.1111/j.1466-8238.2010.00603.x.

Costello, M.J., Wilson, S., Houlding, B., 2012. Predicting total global species richness using rates of species description and estimates of taxonomic effort. System. Biol. 61, 871. https://doi.org/10.1093/sysbio/syr080.

Diniz-Filho, J.A.F., Carvalho, P., Bini, L.M., Tôrres, N.M., 2005. Macroecology, geographic range size–body size relationship and minimum viable population analysis for new world carnivora. Acta Oecologica 27, 25–30. https://doi.org/10.1016/j.actao.2004.08.006.

Dormann, C.F., Calabrese, J.M., Guillera-Arroita, G., Matechou, E., Bahn, V., Bartoń, K., Beale, C.M., Ciuti, S., Elith, J., Gerstner, K., et al., 2018. Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference. Ecolog. Monogr. 88, 485–504. https://doi.org/10.1002/ecm.1309.

Dubois, A., 2017. The nomenclatural status of Hysaplesia, Hylaplesia, Dendrobates and related nomina (Amphibia, Anura), with general comments on zoological nomenclature and its governance, as well as on taxonomic databases and websites. Bionomina 11, 1. https://doi.org/10.11646/bionomina.11.1.1.

Duellman, W.E., 1978. In: The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication, Museum of Natural History, Kansas. https://doi.org/10.1017/CBO9781107415324.004.

Duellman, W.E., 2005. Cusco Amazónico: The Lives of Amphibians and Reptiles in an Amazonian Rainforest. Comstock Publishing Associates, Kansas.

Duellman, W.E., Marion, A.B., Hedges, S.B., 2016. Phylogenetics, classification, and biogeography of the treefrogs (Amphibia: Anura: Arboranae). Zootaxa 4104, 1. https://doi.org/10.11646/zootaxa.4104.1.1.

Ebach, M.C., Valdecasas, A.G., Wheeler, Q.D., 2011. Impediments to taxonomy and users of taxonomy: accessibility and impact evaluation. Cladistics. https://doi.org/10.1111/j.1096-0031.2011.00348.x.

Escobar, H., 2018. Scientists, environmentalists brace for Brazil's right turn. Science 362, 273–274. https://doi.org/10.1126/science.362.6412.273.

Escobar, H., 2019. Brazilian scientists lament 'freeze' on research budget. Science 364, 111. https://doi.org/10.1126/science.364.6436.111.

Essl, F., Rabitsch, W., Dullinger, S., Moser, D., Milasowszky, N., 2013. How well do we know species richness in a well-known continent? Temporal patterns of endemic and widespread species descriptions in the European fauna. Glob. Ecol. Biogeogr. https://doi.org/10.1111/j.1466-8238.2012.00787.x.

Fernandes, G.W., Vale, M.M., Overbeck, G.E., Bustamante, M.M.C., Grelle, C.E.V., Bergallo, H.G., Magnusson, W.E., Akama, A., Alves, S.S., Amorim, A., et al., 2015. Dismantling Brazil's science threatens global biodiversity heritage. Perspect. Ecol. Conserv. 3, 239–243. https://doi.org/10.1016/j.pecon.2017.07.004.

Ferrão, M., Colatreli, O., De Fraga, R., Kaefer, I.L., Moravec, J., Lima, A.P., 2016. High species richness of *Scinax* treefrogs (hylidae) in a threatened Amazonian landscape revealed by an integrative approach. PLoS ONE. https://doi.org/10.1371/journal.pone.0165679.

Field, A., 2005. Discovering statistics using SPSS, second ed. Sage Publications, London.

Fouquet, A., Loebmann, D., Castroviejo-Fisher, S., Padial, J.M., Orrico, V.G.D., Lyra, M.L., Roberto, I.J., Kok, P.J.R., Haddad, C.F.B., Rodrigues, M.T., 2012. From Amazonia to the Atlantic forest: Molecular phylogeny of Phyzelaphryninae frogs reveals unexpected diversity and a striking biogeographic pattern emphasizing conservation challenges. Mol. Phylogenet. Evol. 65, 547–561. https://doi.org/10.1016/j.ympev.2012.07.012.

Freckleton, R.P., Harvey, P.H., Pagel, M., 2002. Phylogenetic analysis and comparative data: a test and review of evidence. Am. Natural. 160, 712–726. https://doi.org/10.1086/343873.

Freitas, F.L.M., Sparovek, G., Berndes, G., Persson, U.M., Englund, O., Barretto, A., Mörtberg, U., 2018. Potential increase of legal deforestation in Brazilian Amazon after Forest Act revision. Nat. Sustain. 1, 665–670. https://doi.org/10.1038/s41893-018-0171-4.

Frost, D.R., 2019. Amphibian Species of the World: an Online Reference. Version 6.0 Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA. Accessed 14 May 2019.

Gaston, K.J., 2000. Global patterns in biodiversity. Nature. https://doi.org/10.1038/35012228.

Gaston, K.J., Blackburn, T.M., 1996. Range size-body size relationships: evidence of scale dependence. Oikos 75, 479. https://doi.org/10.2307/3545889.

Gaston, K.J., Lawton, J.H., 2006. Effects of scale and habitat on the relationship between regional distribution and local abundance. Oikos. https://doi.org/10.2307/3545224.

Gaston, K.J., Blackburn, T.M., Loder, N., 1995a. Which species are described first? The case of North American butterflies. Biodiv. Conserv. 4, 119–127. https://doi.org/10.1007/BF00137780.

Gaston, K.J., Scoble, M.J., Crook, A., 1995b. Patterns in species description: a case study using the Geometridae (Lepidoptera). Biol. J. Linnean Soc. https://doi.org/10.1111/j.1095-8312.1995.tb01061.x.

Gehara, M., Crawford, A.J., Orrico, V.G.D., Rodríguez, A., Lötters, S., Fouquet, A., Barrientos, L.S., Brusquetti, F., De la Riva, I., Ernst, R., et al., 2014. High levels of diversity uncovered in a widespread nominal taxon: continental phylogeography of the neotropical tree frog *Dendropsophus minutus*. PLoS ONE 9, e103958. https://doi.org/10.1371/journal.pone.0103958.

Gotelli, N.J., 2008. A primer of ecology. Sinauer Associates, Vermont.

Grafen, A., 1989. The phylogenetic regression. Philos. Trans. R. Soc. London. Ser. B, Biol. Sci. https://doi.org/10.1098/rstb.1989.0106.

Grimm, V., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310, 987–991. https://doi.org/10.1126/science.1116681.

Guerra, V., Llusia, D., Gambale, P.G., de Morais, A.R., Márquez, R., Bastos, R.P., 2018. The advertisement calls of Brazilian anurans: Historical review, current knowledge and future directions. PLoS ONE 13. https://doi.org/10.1371/journal.pone.0191691.

Guiry, M.D., 2012. How many species of algae are there? J. Phycol. https://doi.org/10.1111/j.1529-8817.2012.01222.x.

Haddad, C.F.B., Toledo, L.F., Prado, C.P.A., Loebmann, D., Gasparini, J.L., Sazima, I., 2013. Guia dos anfíbios da Mata Atlântica – diversidade e biologia. Anolis Books Editora, São Paulo.

Higgs, N.D., Attrill, M.J., 2015. Biases in biodiversity: wide-ranging species are discovered first in the deep sea. Front. Mar. Sci. 2, 61. https://doi.org/10.3389/fmars.2015.00061.

Heyer, W.R., Rand, A.S., Cruz, C.A.G., Peixoto, O.L., Nelson, C.E., 1990. Frogs of Boracéia. Arquivos de Zoologia 31, 231–410 11154/62782.

Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., Ladle, R.J., 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. Ann. Rev. Ecol., Evolut., System. 46, 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400.

Hsu, J., Huang, D., 2011. Correlation between impact and collaboration. Scientometrics 86, 317–324. https://doi.org/10.1007/s11192-010-0265-x.

IUCN, 2017. The IUCN Red List of Threatened Species. Version 2016-3. Available at http://www.iucnredlist.org/ (accessed July 25, 2017).

Joppa, L.N., Roberts, D.L., Myers, N., Pimm, S.L., 2011a. Biodiversity hotspots house most undiscovered plant species. Proc. Natl. Acad. Sci. https://doi.org/10.1073/pnas.1109389108.

Joppa, L.N., Roberts, D.L., Pimm, S.L., 2011b. How many species of flowering plants are

there? Proc. R. Soc. B: Biolog. Sci. https://doi.org/10.1098/rspb.2010.1004.
Kemppinen, K.M.S., Collins, P.M., Hole, D.G., Wolf, C., Ripple, W.J., Gerber, L.R., 2020. Global reforestation and biodiversity conservation. Conserv. Biol. https://doi.org/10.1111/cobi.13478.
Komarek, J., 2006. Cyanobacterial taxonomy: current problems and prospects for the integration of traditional and molecular approaches. ALGAE 21, 349–375. https://doi.org/10.4490/ALGAE.2006.21.4.349.
Kwet, A., 2001. Frösche im brasilianischen Araukarienwald. Münster: NTV Natur und Tier-Verlag.
Lescure, J., Marty, C., 2000. Atlas des Amphibiens de Guyane. Paris: Muséum national d'Histoire naturelle.
Linnaeus, C., 1753. Species Plantarum. Stockholm: Laurentii Salvii.
Llusia, D., Márquez, R., Beltrán, J.F., Benítez, M., do Amaral, J.P., 2013. Calling behaviour under climate change: geographical and seasonal variation of calling temperatures in ectotherms. Glob. Change Biol. 19, 2655–2674. https://doi.org/10.1111/gcb.12267.
Lomolino, M.V., Heaney, L.R., 2004. Frontiers of Biogeography: New Directions in the Geography of Nature. Sinauer Associates Inc.
Lu, M., He, F., 2017. Estimating regional species richness: The case of China's vascular plant species. Global Ecol. Biogeogr. https://doi.org/10.1111/geb.12589.
Magnusson, W.E., Grelle, C.E.V., Marques, M.C.M., Rocha, C.F.D., Dias, B., Fontana, C.S., Bergallo, H., Overbeck, G.E., Vale, M.M., Tomas, W.M., et al., 2018. Effects of Brazil's political crisis on the science needed for biodiversity conservation. Frontiers in Ecology and Evolution 6. https://doi.org/10.3389/fevo.2018.00163.
May, R.M., 1988. How many species are there on earth? Science. https://doi.org/10.1126/science.241.4872.1441.
McCullagh, P., Nelder, J.A., 1989. In: Generalized Linear Models. Springer US, Boston, MA. https://doi.org/10.1007/978-1-4899-3242-6.
Nabout, J., Carneiro, F., Borges, P., Machado, K., Huszar, V., 2015. Brazilian scientific production on phytoplankton studies: national determinants and international comparisons. Braz. J. Biol. 75, 216–223. https://doi.org/10.1590/1519-6984.11713.
Nabout, J.C., da Silva, Rocha B., Carneiro, F.M., Sant'Anna, C.L., 2013. How many species of Cyanobacteria are there? Using a discovery curve to predict the species number. Biodiver. Conserv. https://doi.org/10.1007/s10531-013-0561-x.
Oliveira, U., Paglia, A.P., Brescovit, A.D., de Carvalho, C.J.B., Silva, D.P., Rezende, D.T., Leite, F.S.F., Batista, J.A.N., Barbosa, J.P.P.P., Stehmann, J.R., et al., 2016. The strong influence of collection bias on biodiversity knowledge shortfalls of Brazilian terrestrial biodiversity. Divers. Distrib. 22, 1232–1244. https://doi.org/10.1111/ddi.12489.
Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., Pearse, W., 2014. Caper: Comparative analyses of phylogenetics and evolution in R. R package version 0.5.2/ r121. DOI: 10.1016/j.meatsci.2006.10.019.
Ortega-Andrade, H.M., Rojas-Soto, O.R., Valencia, J.H., De Los, Espinosa, Monteros, A., Morrone, J.J., Ron, S.R., Cannatella, D.C., 2015. Insights from integrative systematics reveal cryptic diversity in *Pristimantis* frogs (Anura: Craugastoridae) from the upper Amazon Basin. PLoS ONE 10. https://doi.org/10.1371/journal.pone.0143392.
Ota, R.R., Message, H.J., da Graça, W.J., Pavanelli, C.S., 2015. Neotropical Siluriformes as a Model for Insights on Determining Biodiversity of Animal Groups. PLoS ONE 10, e0132913. https://doi.org/10.1371/journal.pone.0132913.
Pagel, M., 1999. Inferring the historical patterns of biological evolution. Nature. https://doi.org/10.1038/44766.
Pimenta, B.V.S., da Cruz, C.A.G., Caramaschi, U., 2014. Taxonomic Review of the species complex of Crossodactylus dispar A. Lutz, 1925 (Anura, Hylodidae). Arquivos de zoologia 45, 1–33. https://doi.org/10.11606/2176-7793.2014.45.01.
Provete, D.B., Garey, M.V., Da Silva, F.R., Jordani, M.X., 2012. Knowledge gaps and bibliographical revision about descriptions of free-swimming anuran larvae from Brazil. *North-Western*. J. Zool.
Pyron, R.A., Wiens, J.J., 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. Mol. Phylogenet. Evol. 61, 543–583. https://doi.org/10.1016/j.ympev.2011.06.012.
QGIS Development Team, 2011. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Software accessible at http://www.qgis.org/.
Quinn, G., Keogh, M., 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.
R Core Team (2019). 2019. R: A language and environment for statistical computing. Accessed 1st April 2019.
Randhawa, H.S., Poulin, R., Krkošek, M., 2015. Increasing rate of species discovery in sharks coincides with sharp population declines: Implications for biodiversity. Ecography. https://doi.org/10.1111/ecog.00793.
Revell, L.J., 2010. Phylogenetic signal and linear regression on species data. Methods Ecol. Evol. 1, 319–329. https://doi.org/10.1111/j.2041-210X.2010.00044.x.
Ribeiro, L.F., Bornschein, M.R., Belmonte-Lopes, R., Firkowski, C.R., Morato, S.A.A., Pie, M.R., 2015. Seven new microendemic species of *Brachycephalus* (Anura: Brachycephalidae) from southern Brazil. PeerJ 3, e1011. https://doi.org/10.7717/peerj.1011.
Rojas, R.R., Chaparro, J., Carvalho, V., Avila, R., Farias, I., Hrbek, T., Gordo, M., 2016. Uncovering the diversity in the *Amazophrynella minuta* complex: integrative taxonomy reveals a new species of *Amazophrynella* (Anura, Bufonidae) from southern Peru. ZooKeys 563, 43–71. https://doi.org/10.3897/zookeys.563.6084.
Roskov Y, Abucay L, Orrel T, Nicholson D, Flann C, Bailly N, Kirk P, Burgoin T, DeWalt RE, Decock W, De Wever A. 2019. Species 2000 & ITIS Catalogue of Life, 2019 Annual Checklist. Digital resource at www.catalogueoflife.org/annual-checklist/2016. Species 2000: Naturalis, Leiden, the Netherlands.
Scheffers, B.R., Joppa, L.N., Pimm, S.L., Laurance, W.F., 2012. What we know and don't know about Earth's missing biodiversity. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2012.05.008.
Scheffers, B.R., Paszkowski, C.A., 2012. The effects of urbanization on North American amphibian species: Identifying new directions for urban conservation. Urban Ecosyst. https://doi.org/10.1007/s11252-011-0199-y.
Segalla, M.V., Caramaschi, U., Cruz, C.A.G., Garcia, P.C.A., Grant, T., Haddad, C.F.B., Santana, D.J., Toledo, L.F., Langone, J.A., 2019. Brazilian amphibians: list of species. Herpetologia Brasileira 8, 65–96.
Soares-Filho, B., Rajão, R., Macedo, M., Carneiro, A., Costa, W., Coe, M., Rodrigues, H., Alencar, A., 2014. Cracking Brazil's forest code. Science. https://doi.org/10.1126/science.1246663.
Solow, A.R., Smith, W.K., 2005. On estimating the number of species from the discovery record. Proc. R. Soc. B: Biol. Sci. 272, 285–287. https://doi.org/10.1098/rspb.2004.2955.
Tedesco, P.A., Bigorne, R., Bogan, A.E., Giam, X., Jézéquel, C., Hugueny, B., 2014. Estimating how many undescribed species have gone extinct. Conserv. Biol. 28, 1360–1370. https://doi.org/10.1111/cobi.12285.
Thomé, M.T.C., Zamudio, K.R., Haddad, C.F.B., Alexandrino, J., 2012. Delimiting genetic units in Neotropical toads under incomplete lineage sorting and hybridization. BMC Evolut. Biol. 12, 1–13. https://doi.org/10.1186/1471-2148-12-242.
Toledo, L.F., Batista, R.F., 2012. Integrative study of Brazilian anurans: geographic distribution, size, environment, taxonomy, and conservation. Biotropica 44, 785–792. https://doi.org/10.1111/j.1744-7429.2012.00866.x.
Vacher, J.P., Kok, P.J.R., Rodrigues, M.T., Lima, J.D., Lorenzini, A., Martinez, Q., Fallet, M., Courtois, E.A., Blanc, M., Gaucher, P., et al., 2017. Cryptic diversity in Amazonian frogs: Integrative taxonomy of the genus *Anomaloglossus* (Amphibia: Anura: Aromobatidae) reveals a unique case of diversification within the Guiana Shield. Molecular Phylogenetics Evolution 112, 158–173. https://doi.org/10.1016/j.ympev.2017.04.017.
Van Bocxlaer, I., Loader, S.P., Roelants, K., Biju, S.D., Menegon, M., Bossuyt, F., 2010. Gradual adaptation toward a range-expansion phenotype initiated the global radiation of toads. Science 327, 679–682. https://doi.org/10.1126/science.1181707.
Vasconcelos, T.S., da Silva, F.R., dos Santos, T.G., Prado, V.H.M., Provete, D.B., 2019a. South American Anurans: Species Diversity and Description Trends Through Time and Space. In: Biogeographic Patterns of South American Anurans. Springer International Publishing, Cham, pp. 9–84. https://doi.org/10.1007/978-3-030-26296-9_2.
Vasconcelos, T.S., da Silva, F.R., dos Santos, T.G., Prado, V.H.M., Provete, D.B., Vasconcelos, T.S., da Silva, F.R., dos Santos, T.G., Prado, V.H.M., Provete, D.B., 2019b. Patterns of Species Richness, Range Size, and Their Environmental Correlates for South American Anurans. In: Biogeographic Patterns of South American Anurans, https://doi.org/10.1007/978-3-030-26296-9_3.
Vasconcelos, T.S., Silva, F.R. da, Santos T.G. dos, Prado, V.H.M., Provete, D.B., 2019. Biogeographic Patterns of South American Anurans. New York: Springer.
Vermeulen, N., Parker, J.N., Penders, B., 2013. Understanding life together: a brief history of collaboration in biology. Endeavour 37, 162–171. https://doi.org/10.1016/j.endeavour.2013.03.001.
Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M., Willis, K.J., 2005. Conservation biogeography: Assessment and prospect. Divers. Distrib. https://doi.org/10.1111/j.1366-9516.2005.00143.x.
Wilson, S.P., Costello, M.J., 2005. Predicting future discoveries of European marine species by using a non-homogeneous renewal process. J. R. Stat. Soc.. Ser. C: Appl. Stat. https://doi.org/10.1111/j.1467-9876.2005.00513.x.
Wollenberg, K.C., Vieites, D.R., Glaw, F., Vences, M., 2011. Speciation in little: the role of range and body size in the diversification of Malagasy mantellid frogs. BMC Evol. Biol. https://doi.org/10.1186/1471-2148-11-217.
Yang, W., Ma, K., Kreft, H., 2013. Geographical sampling bias in a large distributional database and its effects on species richness-environment models. J. Biogeogr. 40, 1415–1426. https://doi.org/10.1111/jbi.12108.
Young, B., Stuart, S.N., Chanson, J.S., Cox, N.A., Boucher, M.T., 2004. Disappearing jewels: The status of New World amphibians. NatureServe, Arlington.
Zar, J.H., 1999. Biostatistical Analysis. Prentice Hall, Michigan.