Title: State of Amphibia 2020: Five years of amphibian research, diversity and resources

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Introduction

Amphibians are an ancient, diverse lineage of vertebrates that have been studied in research fields from evolution and ecology to engineering and medicine. Although amphibians are often considered sensitive species, they have survived the last four global mass extinction events and have a nearly worldwide distribution (Wake and Vredenburg 2008, Barnosky et al. 2011, Alroy 2015). Most have biphasic lifestyles, serving as a vital link for energy and nutrient flows between terrestrial and aquatic systems (Finlay and Vredenburg 2007). Many species have large populations and fast growth rates, occupying key roles in food webs as abundant food sources whilst simultaneously shaping the functional diversity of their own prey communities (Colón-Gaud et al. 2009, Zipkin et al. 2020). Despite the ecological importance of amphibians and their diverse evolutionary histories, we lack even basic natural history and location data for a large proportion of species, with 16.4% (1185 species) classified as Data Deficient by the IUCN – the highest proportion of data deficiency for any vertebrate class (IUCN 2021).

Amphibian research has grown rapidly over the last few decades, expanding from a focus on the early model species to an exploration and description of the evolution, ecology, and diversity of amphibians found globally. Decades of concentrated research on three species – *Xenopus laevis*, *Xenopus tropicalis*, and *Ambystoma mexicanum* – have developed amphibian model systems that are associated with sophisticated molecular and genomic tools (Getwan and Lienkamp 2017). Although these species scarcely capture the diversity of Amphibia (over 8,400 species; (University of California, Berkeley, CA, USA.), they have served important roles during the last half century, providing insight into tetrapod evolution (Edholm et al. 2013, Rozenblit and Gollisch 2020), developmental biology, molecular biology, neurobiology (Dascal 1987, Yakushiji et al. 2009, Harland and Grainger 2011), and tissue regeneration (Nye et al. 2003, Freitas et al. 2019). New tools have since promoted the emergence of more model systems from classically “non-model” species, such as: dendrobatid poison frogs for the neurobiology of parental care (Roland and O’Connell 2015, O’Connell 2020) and the molecular evolution of chemical defense (Tarvin et al. 2017), *Physalaemus* for sexual selection (Ryan et al. 1990), and *Nanorana parkeri* for adaptation to high elevation (Sun et al. 2015, 2018, Wang et al. 2018). As we will highlight here, the growing availability of amphibian genomes and other molecular resources is poised to promote the further development of other amphibians as new “model” species.

New genetic tools and increasing availability of amphibian sequence data are also reshaping and expanding our knowledge of amphibian phylogeny and evolution (Blackburn et al. 2019). Until recently, many deeper phylogenetic relationships remained unresolved, resulting in frequent taxonomic changes. Moreover, new species continue to be described, two or three each week on average. Since 2000, there has been an annual average of 150 new species described every year with no sign of slowing down (University of California, Berkeley, CA, USA.).

Nevertheless, understanding current amphibian biodiversity is imperative as amphibians are undergoing severe global population declines. The ancient amphibian lineage (~300 million years old; Wake and Koo 2018) is now the most endangered vertebrate class in the ongoing Holocene Extinction (Wake and Vredenburg 2008, Barnosky et al. 2011). Roughly 3% of anuran and caudatan diversity are believed to have declined to the point of extinction since the 1970s (Alroy 2015), and an estimated 40% of extant species are threatened with extinction (IUCN 2021). Continued research on amphibian biology, as well as efforts to share the fruits of this research through public databases, can guide efforts to buffer amphibians from the threats of habitat loss, climate change, and infectious diseases– particularly in light of opportunities presented by broad global initiatives to protect biodiversity, such as the proposal to protect 30% of the earth's surface by 2030 (Kubiak 2020, HAC 2021).

Given the ever increasing accumulation of biological information, the expanding scale at which research is undertaken, and the urgent need for knowledge to combat amphibian declines, we aim to summarize the state of amphibian research to both improve awareness of existing resources and highlight gaps in knowledge. Focusing on the past five years (2016–2020), we assess the following: 1) trends in publishing, 2) advances in amphibian conservation research, 3) trends and updates in systematics and amphibian diversity, and 4) a review of existing community resources.

Materials and Methods

1. Trends in publishing

To assess changes in the focal topics of amphibian research from 2016 to 2020, we performed a standardized literature search in Academic Search Ultimate (EBSCO Industries, Inc., Ipswich, MA). First, we quantified the total number of amphibian scholarly articles published from 2016 to 2020, as well as the total number within each individual year, that had the following search term in their abstract: "amphibian" OR "amphibians" OR “Caudata” OR “salamander” OR “salamanders” OR “newt” OR “newts” OR “Anura” OR "anuran" OR "frog" OR "frogs" OR “toad” OR “toads” OR “Gymnophiona” OR “caecilian” OR “caecilians”. Next, we quantified the total number of amphibian scholarly articles published in those years (and within each year) in specific subfields of biology by adding an additional search term to the one above. The full list of added subfield search terms was: “behavior”, “development”, “diet”, “cell” AND “molecular”, “climate”, “conservation”, “ecology”, “eDNA”, “fossil” OR “fossils”, "genetic" OR "genetics", "genomic" OR "genomics", “genetic” OR “genetics” OR “genomic” OR “genomics”, “phylogenetic” OR “phylogenetics”, “phylogenomic” OR “phylogenomics”, “microbiome”, “morphology”, “physiology” and “trait” OR “traits”. In addition to reporting the absolute numbers of amphibian publications from 2016 to 2020, we report the percent change in amphibian publications (overall and within each subfield) over that five year period (number of articles published in 2020/number of articles published in 2016). We searched the total number of scholarly articles published (all publications, no search terms) in 2016 and in 2020 to determine the background percent change in publication rate to serve as a reference point for the percent change in amphibian publications from 2016 to 2020. We documented which journals published the amphibian papers recovered in our 2016–2020 literature search and how many languages were represented in these publications. In an effort to examine how many publications focused on model amphibian species, we determined how many amphibian publications in each research field also mentioned *Xenopus laevis, Xenopus tropicalis,* OR *Ambystoma mexicanum* in their abstracts. We also reviewed and discussed the recent literature on trends in publishing in herpetology as it relates to gender and country. Plots and data formatting were performed in R v4.1.0 (R Core Team 2021) with the following packages for figures and data analysis: cowplot v1.1.1 (Wilke 2020), ggplot2 v3.3.3 (Wickham 2016), reshape2 v1.4.4 (Wickham 2007), and tidyverse v1.3.1.9 (Wickham et al. 2019).

2. *Advances in amphibian conservation research*

To understand the major contributors to amphibian declines, for each species we obtained IUCN Red List status (or recommended IUCN Red List status) and associated drivers of decline from AmphibiaWeb species accounts (see supplemental data files; IUCN data were updated as of early 2021). The twenty-five AmphibiaWeb drivers of decline were ordered into ten broader categories as follows: a ‘habitat modification and loss’ category includes general habitat alteration and loss, secondary succession, subtle changes to necessary specialized habitat, habitat fragmentation; a ‘resource exploitation’ category includes habitat modification from deforestation or logging related activities, mining, and intensified agriculture or grazing; a ‘roads and urban development’ category includes urbanization, disturbance or death from vehicular traffic, barriers to movement, and accidental traps; a ‘pollutants’ category includes local and long-distance pesticides, toxins, fertilizers, and pollutants; a ‘climatic factors’ category includes climate change, prolonged drought, floods, increased UVB, or increased sensitivity to it; a ‘disease and immune functioning’ category includes disease, parasitism, and weakened immune capacity; an ‘intentional changes to hydrology’ category includes drainage of habitat and dams changing river flow and/or covering habitat; a ‘predators and competitors’ category includes changing dynamics with both introduced and native species; an ‘intentional mortality’ category includes over-harvesting, the pet trade, and collecting; a ‘genetic degradation’ category includes loss of genetic diversity from small population phenomena and loss of distinctiveness through hybridization. We visualized these data in R v4.1.0 (R Core Team 2021) by order and IUCN status for each category using ggplot2 v3.3.3 (Wickham 2016), tidyr v1.1.3 (Wickham 2017), stringr v1.4.0 (Wickham 2010), dplyr v1.0.7 (Wickham and Francois 2016), and cowplot v1.1.1 (Wilke 2020), and discussed in the context of major new findings on habitat loss and disease as drivers of amphibian declines between 2016 and 2020.

3. Trends and updates in systematics and amphibian diversity

To visualize the accumulation of new species over time, we used the AmphibiaWeb database of new species between 2007 and 2020 (see supplemental data files). We joined the type localities of these new species to country and biogeographic realm using Quantum GIS (vers. 3.2, QGIS Development Team 2021). We made a heatmap of the type localities of the new species (2016–2020) using the heatmap option in QGIS and calculated the number of new species per region using the QGIS point cluster option with radius distance set to 800 km for both the heatmap and clusters. We summarized the cumulative number of new species graphically in R (R Core Team 2021) using ggplot2 v3.3.5 (Wickham 2016), cowplot v1.1.1 (Wilke 2020), lubridate v1.80 (Grolemund and Wickham 2011), rentrez v1.2.3 (Winter 2017), tidyverse v1.3.1 (Wickham et al. 2019), XML v3.99-0.8 (Lang 2021), and included data in the phylogenetic matrix as described in Section 4. We also review higher level taxonomic changes in modern amphibians, largely based on recent phylogenomic studies.

4. A review of community resources

We compiled a list of published amphibian genomes by searching the NCBI Genome database with the “Organism” field set to “Amphibia” and reviewing Google Scholar results for “amphibian genome”. We obtained a list of all available amphibian genetic sequences in the NCBI Sequence Read Archive (SRA; on 21 June 2021) by setting the “Organism” search field to “Amphibia” and downloading metadata files from Run Selector. To obtain metadata on the available sequences in the NCBI GenBank Nucleotide database, we used the Entrez retrieval tool (Clark et al. 2016, NCBI Resource Coordinators 2016). GenBank data were downloaded on 27 June 2021 in 1-month batches from January 1982 to December 2020 using esearch (-db nuccore -query "amphibia [ORGN]" -mindate "$yr/$month" -maxdate "$yr/$month"), extracting the following elements from the document summary: Caption, Title, CreateDate, TaxId. We used the CreateDate information as the deposit date for each sequence. Using regular expressions and lists of keywords in R, we categorized each sequence as mitochondrial DNA (title containing one or more of the words "cytochrome oxidase", "COX", "tRNA", "ND", "ribosomal RNA", "rRNA", "NADH dehydro", "mitochondri", "cyt[.]b","cytochrome b", "ATP8", "ATP6", "control region", "d-loop", "cytb"), as mRNA (title containing one or more of the words "mRNA", "transcript, or "TSA:"), or genomic DNA (all other sequences). To assign a taxonomic order to each sequence in the SRA and GenBank datasets, we merged sequence metadata with the NCBI taxonomy database (https://ftp.ncbi.nlm.nih.gov/pub/taxonomy/new_taxdump/) using tools from the R package 'dplyr' v1.0.6 (Wickham, Hadley, Romain François, Lionel Henry, and Kirill Müller 2021). See supplemental data files for raw data.

To count the cumulative number of species represented in the SRA database over time, we summed the number of unique species names in SRA metadata across years. We note, however, that these numbers are artificially inflated because of unspecified (e.g., " *Hyloxalus* sp. 1 WG-2019"), subspecies (e.g., "*Cryptobranchus alleganiensis bishopi*"), and hybrid (e.g., "*Hyla intermedia* x *Hyla* sp. n. DJ-2018") samples that are included in the data. To more accurately count the number of species added to NCBI databases each year, we used the *entrez_search* function from the R package 'rentrez' v1.2.3 (Winter 2017) to query the ncbi taxonomy database by year and by Order, with additional search terms to filter out ambiguous or unspecified sequences (query = "<Order> and [SubTree] AND <year> AND species[Rank] NOT uncultured[prop] NOT unspecified[prop]"). Finally, we summarized and plotted data using the dplyr v1.0.6 (Wickham, Hadley, Romain François, Lionel Henry, and Kirill Müller 2021), cowplot v1.1.1 (Wilke 2020), and ggplot2 v3.3.5 (Wickham 2016) packages in R v3.6.1 (R Core Team 2021).

To quantify the representation of amphibian species in other public databases, we collated metadata from several databases that contain information about amphibians. We identified all major bioacoustic repositories by surveying relevant literature and asked leading experts in bioacoustics. For each repository, we used website searches to obtain the number of available recordings and the number of species represented (see supplemental data files). If those data were not available, we contacted the person in charge of the website to obtain the database of the recordings. For microCT data, we identified all amphibian scans available on MorphoSource (https://www.morphosource.org; (Boyer et al. 2016), DigiMorph (http://digimorph.org), and Phenome10K (https://www.phenome10k.org) (see supplemental data files for MorphoSource and Phenome10K results). We downloaded Amphibian Disease Portal data on *Batrachochytrium dendrobatidis* (Bd) swabs taken and swabs testing positive for Bd, and summarized by amphibian family, by year, and by geography in R v4.1.0 (R Core Team 2021) tidyr v1.1.3 (Wickham 2017), stringr v1.4.0 (Wickham 2010), and dplyr v1.0.7 (Wickham and Francois 2016). We used ggplot2 v3.3.3 (Wickham 2016) and cowplot v1.1.1 (Wilke 2020) to plot geographic representation of the database over time (see supplemental data files). Finally, in addition to these trait- or data type-specific databases, we also review recent publications of large databases that provide information on amphibian morphological, ecological, and life-history traits.

We summarized the phenotypic, genetic, and disease data available for each anuran family in a phylogenetic matrix plot using a trimmed version of the phylogeny from (Hime et al. 2021). We added four families to match the AmphibiaWeb taxonomy, Allophrynidae, Micrixalidae, Ranixalidae, and Chikilidae, that were not in the original tree by either using a species within a sister family to represent the missing family (in the cases of Allophrynidae and Chikilidae) or artificially adding branches to the tree using the bind.tree function (in the cases of Micrixalidae and Ranixalidae). For data formatting and plotting we used R v4.1.0 (R Core Team 2021) with the following packages for figures and data analysis: ape v5.5 (Paradis and Schliep 2019), geiger v2.0.7 (Pennell et al. 2014), phytools v0.7.8, (Revell 2012), and tidyverse v1.3.1.9, (Wickham et al. 2019).

Results

1. Trends in publishing

1.1 Trends in research topics

We identified 8,164 articles published from 2016 through 2020 that included at least one of our amphibian-specific search terms in their abstracts. Overall, amphibian publications increased by 15% from 2016 to 2020, which exceeds the 11% increase in total publications (no search filters) during that time period (figure 1a; table S1). The majority of amphibian publications were in five subfields: development (1,042), conservation (1,030), genetics OR genomics (887), behavior (701), and phylogenetics (606). Relatively few amphibian publications mentioned phylogenomics (23), microbiome (46), or eDNA (59) (figure 1b; table S1). Almost all subject areas increased in amphibian publications, with the exception of fossil publications, which had 30 amphibian publications in 2016 and 29 amphibian publications in 2020. The fastest growing subject areas, phylogenomics, eDNA, physiology, diet, and ecology, all showed a greater than 50% increase in amphibian publications from 2016 through 2020 (figure 1a; table S1). The peer-reviewed journals with the largest number of amphibian publications from 2016 through 2020 were *Herpetological Review* (497), *PLOS One*

(311), and *Ecology and Evolution* (156; table S2). Although our literature search recovered amphibian publications in 24 languages, the vast majority (97%) of amphibian publications recognized in our search were written in English (table S3).

Of the 8,164 total amphibian publications from 2016 through 2020, 429 (4%) mentioned *Xenopus laevis, Xenopus tropicalis,* OR *Ambystoma mexicanum* in their abstracts. These model amphibian publications were not evenly distributed among research areas, making up a substantial proportion of cell AND molecular (24%), development (12%), genomic(s) (10%), and physiology (8%) publications, but only 5% or less of all other research areas (figure S1).

1.2 Trends in authorship

Numerous studies published between 2016 and 2020 have shown that, as in other STEM (science, technology, engineering, and mathematics) disciplines (Huang et al. 2020, Urbina-Blanco et al. 2020, Maas et al. 2021), female authors are still under-represented in peer-reviewed publications of amphibian biology (Rock et al. 2021). The proportion of female authors in herpetological research has increased over time, from 8% in 1973–1982, 15% in 1983–1993 (Wilson 1998) to 31% in 2010–2015 and 33% in 2016–2019 (Rock et al. 2021), at a remarkably constant rate (although these two studies considered different datasets and journals). However, the increase in female authorship should be considered in the context of a concomitant increase in the proportion of female PhD graduates in the biological sciences. Thus, the gap between the proportion of total female authorships and female PhD graduates may not be narrowing (Frances et al. 2020).

Several factors likely underlie the persistent gender gap in amphibian biology publications. We have learned that within herpetology, papers with female first or last authors are often more likely to have female co-authors than papers with male first or last authors (Salerno, et al. 2019, Grosso et al. 2021, Rock et al. 2021). The gradual attrition of under-represented groups in academic career trajectories might partially explain changes in the proportion of female first authors, which have been growing much faster than the proportion of female last authors in the recent amphibian biology literature (Rock et al. 2021). The repercussions of the leaky pipeline are evident in many aspects of publishing, including gender inequity of editorial boards (Liévano-Latorre et al. 2020, Chuliver et al. 2021, Grosso et al. 2021), as well as the broader herpetological community, such as gender inequity in leadership positions, boards and committees of professional societies, and senior academic positions (Chuliver et al. 2021). Biased or low quality peer review may disproportionately harm scholars from groups that are already under-represented in the literature (Silbiger and Stubler 2019). Finally, geographic patterns of authorship have not been examined in detail for publications in amphibian biology, but country-level trends in authorship in ecology and evolution point towards cultural differences affecting authorship inequality (e.g., (Fox et al. 2018, Huang et al. 2020, Maas et al. 2021). Fox and colleagues (Fox et al. 2018) found female first authors were less likely to be the corresponding author and that this effect was more pronounced when authors were from countries with greater gender equality in rights and opportunities. For example, first authors were more likely to be corresponding authors when they come from home institutions in Australia, New Zealand and North America, but less likely in Africa, Europe, Asia, and Latin America.

In terms of publishing outlets, two herpetological journals acquired new names: *Revista Latinoamericana de Herpetología* in 2017 (formerly *Revista Mexicana de Herpetología*), and *Ichthyology and Herpetology* (formerly *Copeia*) in 2021.The latter is published by the American Society of Ichthyologists and Herpetologists, which acknowledged the racist views of eponymous herpetologist Edward Drinker Cope and whose Board of Governors approved the name change in July 2020. Thus, the title change reflects the wider movement towards making the discipline more inclusive.

2. Advances in amphibian conservation research

The principal driver of amphibian declines is habitat alteration and loss. The drivers subsumed in our habitat alteration and loss category threaten at least 46.6% of amphibians that are analyzed on AmphibiaWeb (figure 2). Furthermore, pooling the habitat alteration and loss category with resource exploitation, roads and urban development, and intentional changes to hydrology categories– which encompass the repercussions of specific classes of habitat alteration and loss– the percentage of affected species increases to 51.2%. The role of habitat loss and modification as principal drivers of amphibian declines is not a new finding (IUCN 2021), yet relative to their importance, these drivers have been neglected in amphibian biology (Green et al. 2020). Even still, large-scale meta analyses have confirmed several basic expectations of the repercussions of habitat degradation for amphibians over the last five years: (i) land use change decreases amphibian species richness (Cordier et al. 2021), (ii) amphibian abundance declines towards the edge of fragmented habitat (Schneider-Maunoury et al. 2016), and (iii) habitat conversion tends to hurt specialist amphibians, driving the phylogenetic homogenization of communities (Thompson et al. 2016, Nowakowski et al. 2018a). Lamentably, the most amphibian-rich communities undergo the most species loss and turnover after habitat modification, and communities fail to recover completely over time (Thompson and Donnelly 2018, Goldspiel et al. 2019, Cordier et al. 2021). Models of the impact of habitat loss and a 'middle of the road' climate and development scenario predict that 10% of known amphibians will be lost by

2070 (Powers and Jetz 2019). We cannot prevent the loss of amphibian species to climate change altogether, but protecting areas from further land use change will be critical to mitigating further losses (See Discussion; (Chen et al. 2017).

Though habitat loss and degradation are undebatable drivers of amphibian declines, it is important that we interpret these data (figure 2) with the caveat that certain drivers are easier to measure than others, and that some drivers have only recently been studied. For example, habitat loss can be described based on observational data alone. However, we also know that climate change and disease threaten a large proportion of extant amphibian diversity (Warren et al. 2013, Olson et al. 2021), but these drivers have only been focal points in amphibian conservation over the past two to three decades. In turn, disease and climate factors are less extensively documented than pollutants, which have been a focus for at least sixty years (225 amphibian species being documented as declining due to pollutants versus 170 species for climatic factors and 149 for disease and immune functioning; figure 2). Likewise, the low percentage of amphibian species for which genetic degradation is a documented driver of decline (50 species) can partly be attributed to the requirement of molecular work and knowledge of the species' evolutionary history for its ascertainment.

When prioritizing which drivers of amphibian decline should receive limited conservation attention and resources, we should consider not only the raw count of amphibian species affected by a driver, but also which threats drive the most severe declines or tend to impact already vulnerable species. For example, while habitat alteration and loss may be the most common threat, the threat categories most closely associated with endangered or extinct species are disease and immune functioning (59.11% of EN, CR, EX/EW species) and genetic degradation (56%). Thus, disease and genetic degradation may tend to drive sudden and dramatic declines, particularly for endangered species that are also facing other stressors (Knapp et al. 2016, Fisher and Garner 2020). The overrepresentation of highly endangered or extinct species in certain threat categories makes them clear strategic targets for conservation programs.

Among diseases driving amphibian declines, the primary concern over the past five years has continued to be chytridiomycosis, the disease caused by the fungal pathogens *Batrachochytrium dendrobatidis* (Bd) and *B. salamandrivorans* (Bsal). Some long-term monitoring projects of Bd-exposed amphibian species or communities are reaching their tenth or twentieth year, making large-scale meta-analyses possible. Bd has now been detected in 55% of amphibian species and 69% of countries sampled (Olson et al. 2021), contributing to declines across many families (Scheele et al. 2019)—though disentangling the extent of its impact is still challenging (Lambert et al. 2020). In some sites, populations declined or were extirpated synchronously with Bd epizootics, and have not recovered under the burden of Bd and additional stressors

(Adams et al. 2017b, Bosch et al. 2021). Other populations may be recovering, despite the continued presence of Bd (Knapp et al. 2016, Seimon et al. 2017, Voyles et al. 2018). The broader impacts of amphibian declines on ecosystems are largely unknown, though steep amphibian declines in Panama appear to have induced a trophic cascade, driving declines in snake diversity and body condition (Zipkin et al. 2020).

Species recovering after Bd-associated declines appear to have altered their response to Bd (Knapp et al. 2016, Palomar et al. 2016, Kosch et al. 2019), with instances of positive directional selection documented in the major histocompatibility complex (MHC) and other immunogenes (Kosch et al. 2016, Savage and Zamudio 2016, Voyles et al. 2018), while species continuing to decline in the wild remain susceptible to Bd despite prolonged exposure (Catenazzi et al. 2017). Such continued declines might be particularly common in systems with additional stressors like climate change, pollution, and habitat fragmentation, which synergistically impair amphibians' capacity to respond to any individual stressor (Nowakowski et al. 2016, Scheele et al. 2016, Adams et al. 2017a, Cohen et al. 2017, 2019, Greenspan et al. 2017, Rollins-Smith 2017, McCoy and Peralta 2018).

Unlike Bd, which is no longer causing mass amphibian die offs in most regions, Bsal continues to drive steep local declines and extirpations (Schmeller et al. 2020, Thein et al. 2020, Vences and Lötters 2020). It has spread across Northern Europe, even in areas with low host densities, causing collapses in susceptible species (Spitzen-van der Sluijs et al. 2016, Schmidt et al. 2017, Stegen et al. 2017). Alarmingly, we do not yet have evidence for acquired immunity to Bsal across multiple exposures, and Bsal pathogenicity has not attenuated over time (Stegen et al. 2017). Herpetologists continue to monitor for Bsal elsewhere in the world, as it could drive devastating biodiversity decline in places like North America, which contains half of global salamander diversity (Richgels et al. 2016, Iwanowicz et al. 2017, Parrott et al. 2017, Yap et al. 2017, Waddle et al. 2020). Continued widespread surveillance for Bd and Bsal, and platforms promoting the accessibility of these data (see section 4.2.2), will help us improve our capacity to mitigate the impacts of these pathogens through monitoring, policy, and management (see Discussion).

3. Trends and updates in systematics and amphibian diversity

3.1 Trends in amphibian diversity

Between 2016 and 2020, 780 new species of amphibians were described (figure 3), a higher number than in the previous five years (732 species between 2011 and 2015). Most (705) of the new species described in the last five years were from the largest amphibian order, Anura (salamanders gained 66 species and caecilians gained 9). Six genera of frogs were described based entirely on newly discovered species: *Astrobatrachus* (Vijayakumar et al. 2019) (also representing the new subfamily Astrobatrachinae); *Blythophryne* (Chandramouli et al. 2016); *Mini* (Scherz et al. 2019) (figure 3f); *Siamophryne* (Suwannapoom et al. 2018); *Sigalegalephrynus* (Smart et al. 2017); and *Vietnamophryne* (Poyarkov et al. 2018).

At a regional level, most new species added between 2016 and 2020 are from Latin America (40.8%), Asia (37.2%) and Africa (12.0%) (figure 4a). Less than 10% of the new species were from the other regions: Oceania-Australia, North America and Europe. All regions had more described species between 2016–2020 than during 2011–2015, except for Oceania-Australia (22 fewer species). The countries with the most new species added between 2016 and 2020 were China (100 species), Brazil (95 species), Ecuador (67 species), Madagascar (56 species), and Peru (56 species). Regions with a high density of new species described are Ecuador, northern Madagascar, and southern China (figure 4a). If the global trend continues as in the last decade (10–11% species increase every five years), we can expect to reach 9,000 amphibian species by the end of 2024.

Remarkably, the yearly rates of increase in the numbers of anurans, caudatans, and gymnophionans are quite consistent (figure 4bc). The steeper increase in anuran species indicates that we are still very much in the age of discovery for amphibian primary diversity. It remains unclear how much of this pattern is tied to the recognition of cryptic species based on molecular studies. We suggest that much of the substantial cryptic diversity remains unaccounted for taxonomically as many taxa are given informal identifiers such as “Hyla species 1” in published papers and on GenBank, but many GenBank accessions are not updated when the species is formally named. This phenomenon is captured by figure 4d, which illustrates the growing number of GenBank sequences representing unspecified amphibian species. New species were described in the majority of amphibian families, and Strabomantidae and Microhylidae had the absolute greatest number of new species (figure 5).

3.2 Review of significant advances in systematics

In contrast with the first 15 years of the new millennium, during which dramatic changes occurred in both our understanding of the higher-level phylogeny of amphibians and in the corresponding taxonomy, the past five years have seen much less flux. This stability has been maintained despite the transition from Sanger-sequencing-based multilocus phylogenetic approaches and mitogenomic analyses to phylogenomic analyses based on new datasets of hundreds to thousands of sequenced loci (e.g., Lemmon and Lemmon 2012, Portik et al. 2016, Hutter et al. 2021). There is complete agreement among recent phylogenomic studies regarding the family-level relationships of salamanders (Shen et al. 2013, Hime et al. 2021) and caecilians; only Hime et al. (Hime et al. 2021) among the recent major studies included caecilians, but their findings are in agreement with prior understanding of caecilian relationships based on Sanger data, such as Kamei et al. (Kamei et al. 2012). Even among the anurans, the various major studies have found nearly complete agreement except within Hyloidea, where some weakly supported arrangements are resolved differently across studies (e.g., (Feng et al. 2017, Streicher et al. 2018, Hime et al. 2021). Even the major relationships among the 19 families that comprise Ranoidea have been almost entirely stable in recent treatments. There is now remarkable agreement in terms of the higher order phylogenetic relationships among and within all three amphibian orders and this has resulted in corresponding taxonomic stability.

The most significant changes in our understanding of the deep relationships of amphibians comes from phylogenomic analyses of neobatrachians. Within ranoid frogs, phylogenomic analyses support a sister relationship between the Afrobatrachia (Arthroleptidae, Brevicipitidae, Hemisotidae, Hyperoliidae) and Natatanura (Feng et al. 2017, Hime et al. 2021) in contrast to previous analyses that found a sister relationship between Microhylidae and Afrobatrachia. Within the Natatanura, these same analyses resolve a clade of the six families endemic to continental Africa (Conrauidae, Odontobatrachidae, Petropedetidae, Phrynobatrachidae, Ptychadenidae, Pyxicephalidae). This is the sister-group of all other nataturans (Feng et al. 2017, Yuan et al. 2018, Hime et al. 2021). Yuan et al. (Yuan et al. 2018) provided strong support for Ranixalidae + Nyctibatrachidae; this clade is the sister-group of other natatanurans excluding the clade of six endemic African families. No phylogenomic analyses have simultaneously included the Micrixalidae, Nyctibatrachidae, and Ranixalidae—all endemic to India. However, other analyses that combine available loci with phylogenomic datasets found a close relationship between Micrixalidae and Ranixalidae (Feng et al. 2017), suggesting that these three families might together form a clade.

Phylogenomic analyses also are beginning to make sense of the diverse hyloid radiation. Rhinodermatidae is strongly supported as the sister to all other South American hyloids, followed by a clade of four families (Alsodidae, Batrachylidae, Cycloramphidae, Hylodidae) referred to as the Neoaustrana (Feng et al. 2017, Streicher et al. 2018, Hime et al. 2021). This is followed by the Telmatobiidae and then by a strongly supported clade of three families (Ceratophryidae, Hemiphractidae, Hylidae) referred to as the Amazorana (Feng et al. 2017, Streicher et al. 2018). All remaining hyloids form a well supported clade, though recent studies differ in the relationships among these taxa.

4. A review of community resources

4.1 Genomic data.

4.1.1 Genomes.

A total of 28 amphibian genomes with representatives from 14 different families have been sequenced as of July 2021 (figures 5 and 6). Of these, 13 are assembled to chromosome-level (scaffold N50 = 0.42 ± 0.29 Gb; mean ± standard deviation), eight are scaffolded (scaffold N50 = 0.24 ± 0.24 Mb), and six are contigs (contig N50 = 880 ± 610 bp) (table S4). The first genome sequenced was that of *Xenopus tropicalis* in 2010 (Hellsten et al. 2010), and it remained the sole amphibian genome until *Nanorana parkeri* became available in 2015 (Sun et al. 2015). Since then, sequencing of amphibian (mostly anuran) genomes has slowly but steadily increased (figure 6). The largest amphibian genome sequenced to date is *Ambystoma maculatum*, with an estimated diploid genome size of ~34 Gb (Nowoshilow et al. 2018). Not surprisingly, all but one (*Nanorana parkeri*) of the chromosome-scale genomes used a combination of sequencing technologies, while those that remain as scaffolds or contigs were built using only the Illumina system short-read technologies (table S4).

4.1.2 NCBI Sequence Read Archive.

Similarly, the amount of next generation sequencing data deposited into the NCBI Sequence Read Archive (SRA) since its origin in 2008 (Leinonen et al. 2011) has been steadily increasing for both model and non-model amphibian species (figure 7a). In 2019, the amount of data available for non-model anurans surpassed that of model anurans (i.e., *Xenopus laevis, X. tropicalis*). The cumulative number of SRA studies (figure 7b) and cumulative number of species (figure 7c) increased in parallel over time. By the end of 2020, nearly 1000 species of amphibians (815 of which are anurans) had sequences deposited in the SRA (figure 5; figure 7c; note that these numbers are inflated because they include unspecified, subspecies, and hybrid samples; see Fig 4d).

4.1.3 NCBI GenBank Nucleotide database.

Although the NCBI GenBank database was established in 1982 (Choudhuri 2014), very few amphibian species were represented in the database until 2000 (figure 8). Early amphibian data were almost exclusively from *Xenopus* (figure 8, solid line, green circles). Since then, the number of represented species in NCBI databases has increased dramatically, to 6203 (of a total of 8,268 known species) in 2020 (figure 8). However, despite this linear increase in representation, non-model species were not represented by large numbers of sequences until 2016; even today, most existing amphibian sequences in GenBank are from *Xenopus* (figure 8).

While the number of mtDNA sequences for anurans has risen gradually over time, the number for salamanders and caecilians has remained relatively flat (figure 8 mtDNA panel). In contrast, the number of nDNA and mRNA sequences added to GenBank has been stochastic and likely reflects specific large-scale sequencing projects (figure 8). For example, in 2012, >100,000 nDNA sequences of *Xenopus tropicalis* and *Xenopus laevis* were deposited as part of new genome data that were beginning to be published at that time (Hellsten et al. 2010); many of these sequences were generated from Bacterial Artificial Chromosomes (BAC). Earlier BAC-generated sequences from *Xenopus tropicalis* are responsible for the 2003 nDNA peak (Wells et al. 2011). The notable increase in model anuran mRNA from 2000 to 2007 is largely from the NCBI full-length cDNA project, which added *Xenopus* to its list of focal species in 2002 (Klein et al. 2002, Gerhard et al. 2004). Additional notable contributors to increases in nDNA include whole-genome shotgun sequences from *X. laevis (Session et al. 2016)* and *Nanorana parkeri* (Sun et al. 2015), as well as other large-scale sequencing projects (e.g., Ultra Conserved Element sequences from *Kaloula;* (Alexander et al. 2017)) (figure 8). In addition, several notable increases in non-model mRNA and nDNA sequence deposition are likely related to other new genomes (e.g., *Rana catesbeiana* in 2017 (Hammond et al. 2017) , *Microcaecilia unicolor* in 2019, *Geotrypetes seraphini* in 2020) and transcriptomes (e.g., *Bombina variegata variegata* in 2016, *R. catesbeiana* in 2017, both in Transcriptome Shotgun Assembly [TSA] formats, which are primarily built from short-read technology) (Nürnberger et al. 2016, Suzuki et al. 2016).

4.2 Phenotypic data

4.2.1 Trait databases

Acoustic data.— We identified eight major repositories that collectively contain 156,514 amphibian recordings (table 1): Macaulay Library, Fonozoo, La Sonothèque, AmphibiaWeb, Fonoteca Neotropical Jacques Vielliard, Anfibios del Ecuador BIOWEB, Australian Museum FrogID Project, and Chinese National Specimen Resource Sharing Platform. Collectively, these call repositories contain calls for 1,985 unique species from 45 anuran families and four salamander families. The anuran families Pipidae (41 species), Mantellidae (232 species), Myobatrachidae (133 species), Scaphiopodidae (seven species), and Rhinophrynidae (one species) each have calls recorded for more than 50% of the family's species (figure 5). Fonozoo contains the highest number of species represented, although FrogID contains the greatest number of recordings (table 1). Of note among these databases are the Fonoteca Neotropical Jacques Vielliard

(FNJV), which is the largest public and institutional online audiovisual repository in Latin America, and the Australian Museum FrogID Project, which is Australia's first national citizen science frog identification initiative.

CT scan data.—Since 2016, CT-scanning datasets for 1,947 amphibian specimens, including image stacks and 3D mesh files, have been shared via MorphoSource (www.morphosource.org). These include 1,530 anuran specimens representing 976 species (in 402 genera; 88% of genera), 362 caudate specimens representing 184 species (in 66 genera; 97%), and 55 gymnophionan specimens representing 40 species (in 32 genera; 97%) (figure 5). Many of these data were generated as part of the NSF openVertebrate (oVert) Thematic Collections Network. In addition, there are a small handful of CT-scans of extinct crown-group amphibians, such as 26 fossils of *Beelzebufo* deposited in 2015. Morphosource.org also houses most, if not all, of the CT-scan media from the Digital Morphology project (DigiMorph; www.digimorph.org). DigiMorph began in the early 2000s and still has CT-scan media available from 25 anuran species (in 21 genera), 28 caudate species (in 16 genera; plus one extinct salamander), and seven caecilian species (in seven genera).

Phenome10K also hosts 3D mesh files of amphibian skulls associated with several recent publications (Marshall et al. 2019, Fabre et al. 2020, Bardua et al. 2021)e.g., (Marshall et al. 2019, Fabre et al. 2020, Bardua et al. 2021). As of October 2021, the website (www.phenome10k.org) makes available 3D mesh files of skulls for 105 anuran species (in 94 genera), 104 caudate species (in 51 genera), and seven gymnophionan species (in seven genera). In many cases, the image stacks for these specimens are also available on MorphoSource.

Other trait databases.— From 2016 through 2020, two large amphibian trait databases were published: AmphiBIO (Oliveira et al. 2017) and a Colombian anuran database (Mendoza-Henao et al. 2019). AmphiBIO (Oliveira et al. 2017), the largest species-level amphibian trait database that can be readily downloaded, contains 6,776 species and a broad range of ecological and life-history traits (e.g. microhabitat, diet, activity time, clutch size), but the matrix completeness is only 21%. Although the Colombian anuran database is much more complete, it contains morphological data from fewer species (239), which represent 38% of Colombian anuran diversity. Of note, the Colombian anuran database includes individual-level data for 4,623 museum specimens, with a range of 1 to 118 individuals (median = 8) measured per species. Two other databases were identified: one includes conservation, ecological, and life-history traits of 86 European species (Trochet et al. 2014); another, the Anuran Traits of the United States (ATraiU) (Moore et al. 2021), contains ecological, morphological, and life history data of 106 anuran species, representing 91% of frog species in the USA (University of

California, Berkeley, CA, USA.). Finally, more than 500 papers on conservation efforts with amphibians are collated in a Conservation Evidence database (https://www.conservationevidence.com).

4.2.2 Online portals for amphibians

Anfibios del Ecuador-BIOWEB—With 656 amphibian species (as of November 2021), Ecuador is the third most species rich country in the world. In 2018 the Zoology museum of the Catholic University of Ecuador (QCAZ) launched the website Anfibios del Ecuador (https://bioweb.bio/faunaweb/amphibiaweb) to give access to comprehensive information about all amphibian species of Ecuador, which represent nearly 8% of the amphibian species worldwide. Anfibios del Ecuador was inspired by AmphibiaWeb and has a similar scope but at a country level. Anfibios del Ecuador replaced the previous portal "AmphibiaWebEcuador," which operated between 2010 and 2017. The website is currently part of a larger Ecuadorian biodiversity database called BIOWEB.

Anfibios del Ecuador provides detailed species accounts, which include an extensive photo gallery with 206,785 images. Species phenotypic variation is well documented with an average number of photographs per species of 323 (maximum 8746 for *Pristimantis achatinus*) and a median of 144. Species distribution is documented with a database of over 50,000 geographic records from the literature and the specimen database of the QCAZ museum. Those records are used to build species distribution models under current and future environmental conditions using the MAXENT algorithm (Phillips et al. 2017).

The website also presents overviews of the biogeography, species richness, and the conservation status of the Ecuadorian amphibians. Overviews of the Natural Regions, geography and climate of Ecuador are also provided. Anfibios del Ecuador gives access to: (1) the database of the amphibian QCAZ collection, the largest for Ecuadorian amphibians (76,500 specimens), and (2) the QCAZ sound collection with 1297 recordings for 222 species (table 1).

Crucially, Anfibios del Ecuador is in Spanish and helps to provide scientific data in languages other than English. For most species, Anfibios del Ecuador presents the only comprehensive species accounts available online, in Spanish. Since 2018, Anfibios del Ecuador has been connected with AmphibiaWeb through a web API that allows visualizing the Spanish species accounts and photographs of Anfibios del Ecuador within AmphibiaWeb.

Anfibios del Ecuador has high visitor traffic (data from Google Analytics). Between June and November 2021, for example, it received approximately 16,000 monthly visitors from 106 countries. 51% of visitors shared demographic data, of which 72% were women and 28% men. Younger age groups are the most frequent visitors: 18–24 years old represented 37% of the visits, followed by 25–34 years (23%).

AmphibiaChina.—In November of 2015, the Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ, CAS) launched the website AmphibiaChina (www.amphibiachina.org) as an online database for Chinese Amphibians (Jing and Wang 2016). China currently hosts 587 amphibian species (2021-12-12) and many new species are being described each year. AmphibiaChina aims to provide a platform for sharing research progress and promoting accessibility to people and institutions (e.g., scientists, governmental agencies, and the public) who are interested in Chinese amphibians. Visitors to AmphibiaChina from 2016–2020 come from over 100 countries each year.

During the past five years, AmphibiaChina has undergone some structural changes, including a comprehensive update to version 2. AmphibiaChina has the following major sections: Classification, Species Identifications, Chinese Amphibian Tree of Life, News, and Photo Gallery. Users can navigate the Classification section using the hierarchical system of formal taxonomy or by geographic region (province). An up-to-date phylogeny of Chinese amphibians is provided. Comprehensive information on each species is available, and multiple species can be compared in a single page. The photograph gallery is extensive, with 9042 images representing 433 species. AmphibiaChina also offers two online species identification tools: an amphibian image recognition module that uses deep learning and image processing techniques to automatically identify the species in user images, and a search engine which compares user-uploaded mtDNA sequences to a sequence database using BLAST. Since 2016, AmphibiaChina has been connected with AmphibiaWeb through a web API that allows visualizing the Chinese species accounts within AmphibiaWeb.

AmphibiaWeb.— In 2020, AmphibiaWeb celebrated its 20th anniversary, marking its commitment to the original vision of AmphibiaWeb—that “a healthy future for all life on Earth must include thriving amphibians, and the means to conserving amphibians is to enable and facilitate better research and education with an accessible, consolidated, and curated information system for all amphibian species” (University of California, Berkeley, CA, USA.): https://amphibiaweb.org/about/index.html). Many of the core activities of AmphibiaWeb have not changed in the last two decades – a web page for every amphibian species with literature-based accounts and spatial data. Much of the data we track (e.g., species accounts, type localities, range maps and traits) have been used in research studies (reviewed in (Uetz et al. 2021)), including in this article.

Usage of AmphibiaWeb (tracked by Google Analytics) continues to be strong, averaging 28,000 users per month (between June and November 2021) from 215 countries or sovereignties. Of the over 35% of users who shared demographic data, users trended female (54.5%) and young (33% 18–24 years old, 27% 25–34 years old). The site averaged 1.74 M page views per year in the last five years, with a high of 2.5 M page views during the pandemic of 2020 (page views are a measure of the number of times a page has been visited even in a single session of a single user).

Over the last five years, the AmphibiaWeb team has added 277 species accounts, a set of family-richness maps, and improved methods to access data and materials including a searchable repository (https://github.com/AmphibiaWeb/aw-assets). A new registration, authoring, and training system is poised to increase the number of new species accounts in the immediate future. New educational materials range from a primer on why phylogeny, taxonomy, and nomenclature are useful in the study of amphibians to Spanish and English educational materials aimed for K-12 students. Recent outreach initiatives have been the art contest with original AmphibiaWeb designs (“#ArtYourAmphibian”) and a quarterly newsletter.

Amphibian Disease Portal.— Following the discovery of the pathogen Bsal in Europe (Martel et al. 2013), biologists in the USA, Mexico, and Canada formed the North American Bsal Task Force to address the potential for Bsal-caused chytridiomycosis outbreak in North America. AmphibiaWeb became the co-lead for the Data Management effort with the USDA Forest Service and launched an effort to to establish a new open-access repository and archive for both Bd and Bsal data (Koo et al. 2021) called the Amphibian Disease Portal (https://amphibiandisease.org). The archive addressed two urgent needs: 1) to create a sustainable, modernized repository to aggregate and rapidly share global data on the fungal pathogens of amphibians *Bd* and *Bsal*; and 2) to upgrade and migrate the discontinued *Bd*-Maps database (Olson et al. 2013) to a new repository. While the Amphibian Disease Portal is an independent database platform, it reciprocally links with AmphibiaWeb species pages to display species-specific Bd and Bsal data. Since its introduction in 2017, it now encompasses a broad global and temporal coverage of Bd (figure 9) and Bsal data (see (Koo et al. 2021, Olson et al. 2021) for details). The amphibian disease portal contains Bd samples from all but five amphibian families (two anuran, two gymnophionan, one caudatan) and positive Bd samples from all but sixteen amphibian families (figure 5). The next phase of development will focus on enhancing access and online dynamic data visualizations enabled by its application programming interface (API). Currently, the Disease Portal dashboard displays dynamic counts of sample data by country, species and diseases tested and provides species-specific pie charts and links to original and downloadable datasets.

Discussion

Current picture and future projections for amphibian biodiversity —
The pace of amphibian species descriptions continues unabated, with over 150 new species being described each year. However, our picture of amphibian diversity is changing in some predictable ways. The majority of new species are being described in Latin America (Vasconcelos et al. 2019) and Asia and specifically concentrated in diverse families such as the Strabomantidae and Megophryidae. For example, the number of new species listed on AmphibiaChina increased from just four new species in 2015 (Murphy 2016), to 41 new species reported in 2020 (Chen et al. 2021). Furthermore, our understanding of the relationships among amphibian families remains largely stable, however there remain several diverse lineages, including both subfamilies and genera, for which thorough and synoptic revisionary phylogenetic studies are needed.

Challenges and opportunities in amphibian research —
Large amphibian genome sizes remain one of the greatest challenges in amphibian research. The size and repetitive content of amphibian genomes has hindered whole-genome sequencing efforts (Sun et al. 2020). For comparison, >500 fish genomes (Randhawa and Pawar 2021, average size of 808 Mb) and >300 bird genomes have been sequenced (Feng et al. 2020; average size of 1.13 Gb (Randhawa and Pawar 2021)), yet only 27 amphibian genomes are available. The average sizes of sequenced amphibian genomes (excluding contig-level assemblies: 4.03 Gb for Anura [N = 18], 33.99 Gb for Caudata [N = 1], 4.75 Gb for Gymnophiona [N = 3]) are below the average amphibian genome sizes (4.28 Gb for Anura, 35.95 Gb for Caudata, 6.44 Gb for Gymnophiona, based on values reported in (Liedtke et al. 2018)). Nevertheless, the number of species represented in NCBI sequence databases continues to increase, as does the use of high-throughput technologies for non-model species. We expect to see exponential growth in genomic data for amphibians in the coming years, especially as more reference genomes are made available. Moreover, we expect growth in the development of new tools for other amphibian model species, such as *Notophthalamus viridescens* (Joven et al. 2019) and *Rana sylvatica* (Joanisse and Storey 1996, Gerber et al. 2016, Costanzo 2019), and even more innovative advances in existing model systems like the self-replicating biological robots created from *Xenopus* tissue (Xenobots; (Kriegman et al. 2021)). These advances in genetic tools paired with more accessible and inexpensive sequencing technologies will accelerate research in areas

currently underrepresented in amphibian publications, such as research focused on phylogenomics, microbiomes, and eDNA.

Although amphibians are well-represented in some of the databases we examined (e.g., Morphosource, figure 5), we still lack basic natural history and phenotypic data for a large portion of amphibian genera and families. For example, although most anuran families have calls recorded, certain families that contain species thought or known to call (Ceuthomantidae, Ranixalidae, Odontobatrachidae, Conrauidae, Petropedetidae, Brevicipitidae, and Heleophrynidae) have no call records in the databases examined here and many other families (Arthroleptidae, Craugastoridae, Megophryidae, Micrixalidae, Phrynobatrachidae, Pyxicephalidae, and Telmatobiidae) have calls recorded for fewer than 10% of species in their family. Interviews conducted at two herpetology conferences found that nearly 80% of herpetologists did not catalog collected sound data because they did not have the time or expertise, or felt that the efforts were unnecessary (Dena et al. 2020). Additionally, although all amphibian families (except Chikilidae) have microCT scans for at least one species, most families (41 of 74 total) have microCT scans available for fewer than one quarter of their family's species. Ecological and natural history databases often lack information for many genera and families (e.g., ~80% missing data in AmphiBIO, Oliveira et al. 2017) and Paluh et al. (2021) recently found that 161 of 456 total frog genera lacked any records of dietary data. Furthermore, while data exist for Bd and Bsal for many amphibian families, much of those data are not yet in a centralized database like Amphibian Disease Portal. These data deficits and the lack of integration among databases make comparative work and synthetic studies difficult. Increasing natural history studies, and storing natural history data in publicly accessible, easy-to-download databases are necessary aids to amphibian research and conservation. In addition, it is critically important to link data and specimens across repositories so that researchers and policy-makers can integrate and track different data types (e.g., DNA sequences, microCT scans, audio recordings, pathogen data) for the same individual or population.

Inequality in the demography of amphibian research hinders diverse viewpoints that would aid in tackling amphibian research challenges. Rock et al. (2021) showed that female authors were underrepresented on amphibian publications. Although we lack a concrete understanding of the primary barriers to authorship inequality in amphibian research specifically, many are likely consistent with barriers and bias found in other STEM disciplines, such as male homophily (Helmer et al. 2017, Salerno et al. 2019, Grosso et al. 2021, Rock et al. 2021), attrition of women and underrepresented groups (Chuliver et al. 2021, Rock et al. 2021), bias in peer review (Silbiger and Stubler 2019), and the culture of the geographic location of the authors (Fox et al. 2018, Huang et al. 2020, Maas et al. 2021). Double-blind reviews are a potential solution to minimize bias during the reviewing process (Tomkins et al. 2017) and some herpetological journals are currently transitioning to double-blind reviews: *Revista Latinoamericana de Herpetología* and *Herpetological Conservation and Biology*. Amphibian research would benefit from further analysis of amphibian-specific publishing inequalities for identities beyond gender and assessments of whether changing publishing practices can affect change.

Using centralized portals for amphibian biology to translate research into policy and management

Amphibian conservation biology is a crisis discipline: the urgency of amphibian declines means that difficult decisions must be made even in cases with deep uncertainty. We no longer speculate on the prospect of a sixth mass extinction but rather document its progress (Wake and Vredenburg 2008, Ceballos et al. 2015). One of the motivations for this review is to help consolidate major findings, trends, and public databases that can have immediate impact on policy and management. We urge for increased adoption of adaptive management practices by relevant agencies, NGOs, and research units, where decisions are made under best current information, closely monitored, and then actions are updated accordingly (Berger et al. 2016, Grant et al. 2016, Meredith et al. 2016; Adams et al. 2018). Here, we highlight public databases for molecular (NCBI), acoustic (table 1), phenotypic and natural history data (Trochet et al. 2014, Oliveira et al. 2017, Mendoza-Henao et al. 2019, Moore et al. 2021), as well as expert-curated reference databases (AmphibiaWeb, AmphibiaWebEcuador, AmphibiaChina, IUCN Red List, and Conservation Evidence), that can be vital tools in designing and updating adaptive management strategies by centralizing and collating information relevant to conservation-oriented policy and management from a diffuse literature.

An example of an exciting new opportunity to deploy these public databases in the interests of more effective, scientifically-informed conservation is provided by global 30x30 initiatives– commitments by governments to protect 30% of the Earth's land and oceans by 2030 (Kubiak 2020, HAC 2021). If new 30x30 protected areas are to serve amphibian conservation needs, sites with coverage of amphibian functional, phylogenetic, and taxonomic diversity should be selected, a process greatly facilitated by centralized databases. Additionally, sites that alleviate cataloged decline drivers (e.g., selecting sites that create climate corridors to protect species threatened by climate change) could be a focus (Gonçalves et al. 2016, Subba et al. 2018, Zellmer et al. 2020). In cases where Bd has been detected, *in situ* mitigation has had such limited success that the most robust strategy for improving amphibian outcomes may be to address other synchronous stressors (Knapp et al. 2016, Fisher and Garner 2020). For example, restoring or creating water features, promoting the development of microhabitat to buffer amphibians against climate change, removing invasive species, managing pollution from activities like mining, and addressing barriers to amphibian movement are all methods that can promote amphibian population health (Hamer 2016, Nowakowski et al. 2016, 2018b, Reeves et al. 2016, Arntzen et al. 2017, Laufer and Gobel 2017, Goldspiel et al. 2019, Magnus and Rannap 2019, Mayani-Parás et al. 2019, Simpkins et al. 2021).

Conclusion

The wealth of amphibian data offers both opportunities and challenges in the coming years. New species continue to accumulate at a steady rate and genomic data is exponentially increasing. Conservation continues to be a major focus in amphibian research and the most recent findings highlight both the role of adaptive management and the importance of managing multiple stressors. To facilitate research and conservation, we urge scientists to continue building and contributing to centralized public databases capable of informing conservation decision-making. Although our perspectives may not be representative of all amphibian biologists, we aimed to provide a timely overview of research trends and major databases with the idea that the resources and gaps highlighted here will spark and facilitate basic and applied amphibian research. Finally, the overview of literature and data resources presented herein provides a framework that can be adapted for other organism clades and revisited over time to highlight major advances and identify opportunities for research growth.

Data accessibility

Data summarized within this manuscript along with R scripts for all figures (except figures 3 and 4) can be found within supplemental materials.

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Conflict of interest statement

The authors declare no conflict of interest.

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Table 1. The most comprehensive amphibian call databases available online. For geographic regions, Af = African, Au = Australians, Ne = Nearctic, Nt=neotropical, Or = Oriental, Pa= Paleartic. Unless otherwise noted, all recordings are available for download online.

Database	**Maintained by**	**No. species**	**No. calls**	**Regions represented (% of calls)**	**Accessibility for researchers**
Fonozoo	Museo Nacional de Ciencias Naturales de Madrid, Spain	886	9,794	Nt (49%), Af (29%), Pa (16%), Or (4%), Ne (1%); 63 countries	1098 can be played online. Other recordings require an online form and in some cases author permission.
Macaulay Library	Cornell Lab of Ornithology	788	11,460	Nt (38%), Or (6%), Ne (52%); 73 countries	Recordings are available for download online through a request form.
Fonoteca Neotropical Jacques Vielliard	Audiovisual Collection,Museu de Diversidade Biológica	568	5,959	Nt (>99%), Pa (<1%), Af (<1%); 19 countries	89% can be downloaded after curator authorization; 11% are available with author permission.
AmphibiaWeb	Museum of Vertebrate Zoology, UC Berkeley	557	813	Af (34%), Nt (31%), Au (14%), Ne (11%), Or (8%), Pa (3%); 59 countries	Recordings are available for download online.
Anfibios del Ecuador BIOWEB	QCAZ Museum of Pontificia Universidad Católica del Ecuador	222	1297	Nt (100%); nearly all from Ecuador	Recordings are available for direct download online.
FrogID	Australian Museum	182	126,169	Au (100%); all from Australia	Recordings are available for direct download online.
La Sonothèque	Muséum National d’Histoire Naturelle	61	953	Pa (75%), Nt (21%), Ne (2%), Af (1%); 14 countries	Recordings are available for direct download online.
Chinese National Specimen Resource Sharing Platform	Chinese National Specimen Information Infrastructure	35	69	Or (100%); all from China	Recordings are not available for download.

Figure Legends

Figure 1. Trends in amphibian research from 2016 through 2020 by (a) proportion change in publication number and (b) absolute number of publications in each biological subfield. The additional categories of “amphibian” and “background” in panel A refer to the proportional change of all amphibian publications and all publications (not amphibian-specific) from 2016 to 2020.

Figure 2. The number of species in each Order threatened by different drivers of amphibian decline, where each species can be represented by multiple drivers. IUCN conservation status categories are: extinct or extinct in the wild (EX/EW), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC), and data deficient (DD). Of species with accounts on AmphibiaWeb, 53.3% (1261 of 2364 species) have data on at least one factor driving their decline

Figure 3. Images of new species described in the last five years. (a) *Ichthyophis benjii* from Mizoram, India (Lalremsanga et al. 2021), photo by Hmar Tlawmte Lalremsanga; (b) *Hydromantes samweli* (Bingham et al. 2018), holotype from Shasta County, CA, USA, photo by Robert Hansen; (c) *Nasutixalus medogensis (Jiang et al. 2016)*, holotype from Medog, Tibet, China, photo by Ke Jiang ; (d) *Rhinella lilyrodriguezae* (Cusi et al. 2017), holotype from Cordillera Azul National Park, Perú, photo by Anton Sorokin; (e) *Pristimantis verrucolatus* (Páez and Ron 2019), holotype from Azuay Province, Ecuador, photo by Santiago Ron; (f) *Mini mum* (Scherz et al. 2019), holotype from Manombo Special Reserve, Madagascar, photo by Mark Scherz.

Figure 4. Additions of amphibian species over time. (a) Geographic heat map and point cluster of new species described between 2016 and 2020. Inset graphs indicate the cumulative number of new species described by region between 2007 and 2020; years 2016–2020 are highlighted with the blue rectangle; y-axis scale indicated for Latin America is the same for all insets. Total cumulative number of (b) species and (c) genera in AmphibiaWeb taxonomy database, split by order. (d) Cumulative numbers of formal and unspecified (informal) species names in the GenBank Taxonomy database. Examples of unspecified names are "*Hyla* cf *arenicolor*" or "*Hyla* sp. B". See supplemental data files for data used to generate this figure.

Figure 5. Phylogenetic heat map showing the number and proportion of species within each family that were described in 2016–2020 and the proportion of species within each family that have accessible phenotypic, genetic, and disease data. Lighter to darker colored matrix cells represent lower to higher species-level representation for each family and white cells indicate that no species from the corresponding family have those data types available. From left to right in the matrix: 1) the proportion of new species

added in 2016–2020, 2) the proportion of species with call data available in one of the seven databases listed in table 1, 3) the proportion of species with microCT data available on morphosource.org or Phenome10K, 4) the proportion of species with sequenced genomes, 5) the proportion of species with sequences in NCBI GenBank 6) the proportion of species with sequences in the NCBI Sequence Read Archive 7) the proportion of species in the Amphibian Disease Portal that have been tested for Bd, 8) the proportion of species in that have positive tests for Bd documented in the Amphibian Disease Portal. Data used to generate this figure can be found in table S5.

Figure 6. a) Cumulative number and b) size of sequenced amphibian genomes by year. The blue box highlights years 2016–2020.

Figure 7. The (a) cumulative amount of data and (b) number of studies in the Sequence Read Archive, separated by model (Ambystoma mexicanum, Xenopus laevis, Xenopus tropicalis) and non-model (all other) species (c) total number of species represented in the Sequence Read Archive. Years missing data points indicate that no data were submitted that year for that order.

Figure 8. The cumulative number of mitochondrial DNA (mtDNA), nuclear DNA (nDNA), and messenger RNA (mRNA) sequences, as well as species, added to the GenBank Nucleotide database from 1982 to 2020, highlighting the last five years, 2016–2020, in blue. Some of the projects that contributed substantially to increase sequence numbers are highlighted on the figure; see text for references. Years missing data points indicate that no data were submitted that year for that order.

Figure 9. *Batrachochytrium dendrobatidis* samples in the Amphibian Disease Portal. (a) A log-scale histogram of Bd swab counts, binned by the five-year time span in which the amphibian swabbed was captured. (b) A stacked histogram showing the proportional representation of swabs taken from different continents, binned by the same five-year blocks. Bsal data archived in the portal only includes sample data in the US (Waddle et al. 2020) and from the Bsal Consortium Germany (Vences and Lötters 2020).

Supplementary File information

Figure S1. Number and proportion of amphibian publications within each research area that mention model organisms (*Xenopus laevis, Xenopus tropicalis,* OR *Ambystoma mexicanum*) in their abstract.

Table S1. Literature search results
Table S2. Number of publications by journal

Table S3. Number of amphibian publications by language
Table S4. Amphibian-Genomes - *metadata for the 28 amphibian species with genomes published when this manuscript was prepared, including the 7 released as of July 2021*
Table S5. Family-level_PhylogeneticHeatMapData - *data used to generate figure 5*

Supplementary Data files uploaded "not for review"

Data files

1. ncbi_nuccore-data.csv - *metadata for all sequences deposited into the NCBI Nucleotide Core between 1982 and 2020, downloaded on 27 June 2021*

    * this file is too large and will be uploaded to a repository on AmphibiaWeb and linked in the paper upon acceptance
2. ncbi_taxonomy-database.csv - *NCBI taxonomy database, downloaded on 21 June 2021*
3. sra_metadata-20210621.txt - *metadata for all sequences deposited into the NCBI SRA between 2008 and 2020, downloaded on 21 June 2021*
4. GenBank-Amphib.tsv - *raw and cumulative counts of specified and unspecified amphibian taxa represented by sequences in GenBank, downloaded on 28 October 2021*
5. AWeb-taxonomy-archive-master_2012-2020.zip - *monthly lists of amphibian species represented in AmphibiaWeb, spanning November 2012 until December 2020, downloaded on 14 May 2021*

    *this file is too large and will be uploaded to a repository on AmphibiaWeb and linked in the paper upon acceptance
6. AmphibiaWeb_newspecies.csv - *list of new species described by year of description, obtained from AmphibiaWeb*
7. orders_accounts.csv - *data on AmphibiaWeb species accounts available*
8. Aweb-threats_2021-09-21.csv - *data on factors driving amphibian declines as logged in AmphibiaWeb species accounts, downloaded on 21 September 2021*
9. Amphibian_disease_data_processed.csv - *data from the Amphibian Disease Portal*

    *this file is too large and will be uploaded to a repository on AmphibiaWeb and linked in the paper upon acceptance

10. DiseaseData_ForPhylogeneticHeatMap.csv - *count species sampled is the number of species sampled within each family, disease tested is always just "Bd", Bd tested is the number of Bd swabs taken for members of that family, Bd positive is the number of those tested Bd swabs that were Bd+ for that family*
11. SpeciesLevel_CallData.csv - *number of calls for each amphibian species contained in each of the call databases in Table 1*

12. Morphosource_TaxonomyCTscans_2021126.csv - *all Anura, Caudata, and Gymnophiona CT scans on morphosource.org*
13. Phenome10k_CTscans.csv - *all Anura, Caudata, and Gymnophiona CT scans on Phenome10k.org*

R scripts

1. Figs1andS1_LiteratureSearchSummary.R *R script to generate Figures 1 and S1*
2. Fig2_ConservationScripts.R *Scripts in R to create figures for conservation and disease segments of manuscript*
3. Fig5_PhylogeneticHeatMapData.R *R script to generate Figure 5*
4. Figs6-8_genetic-data.R *R script to generate Figures 6-8*

FIGURE 1

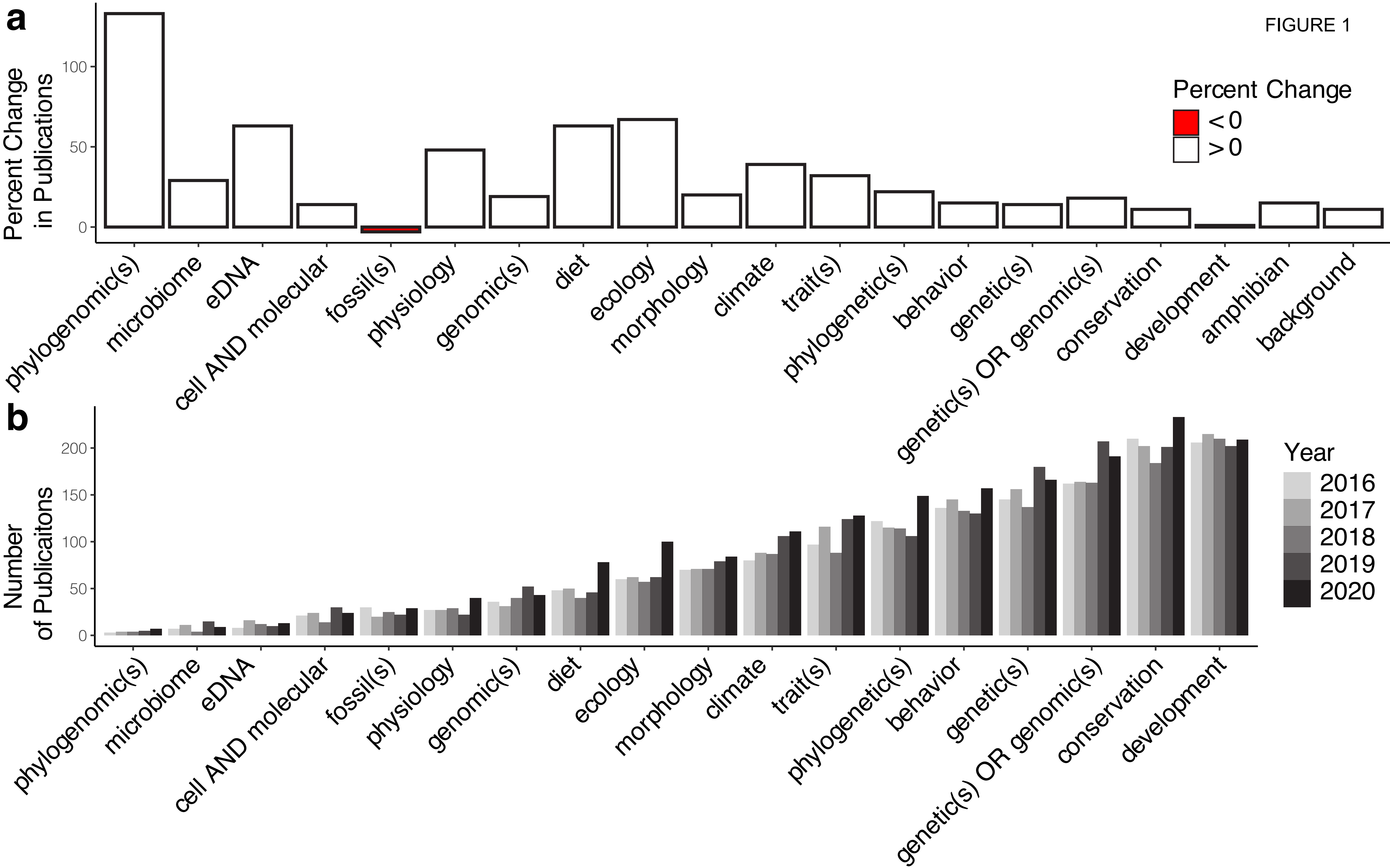
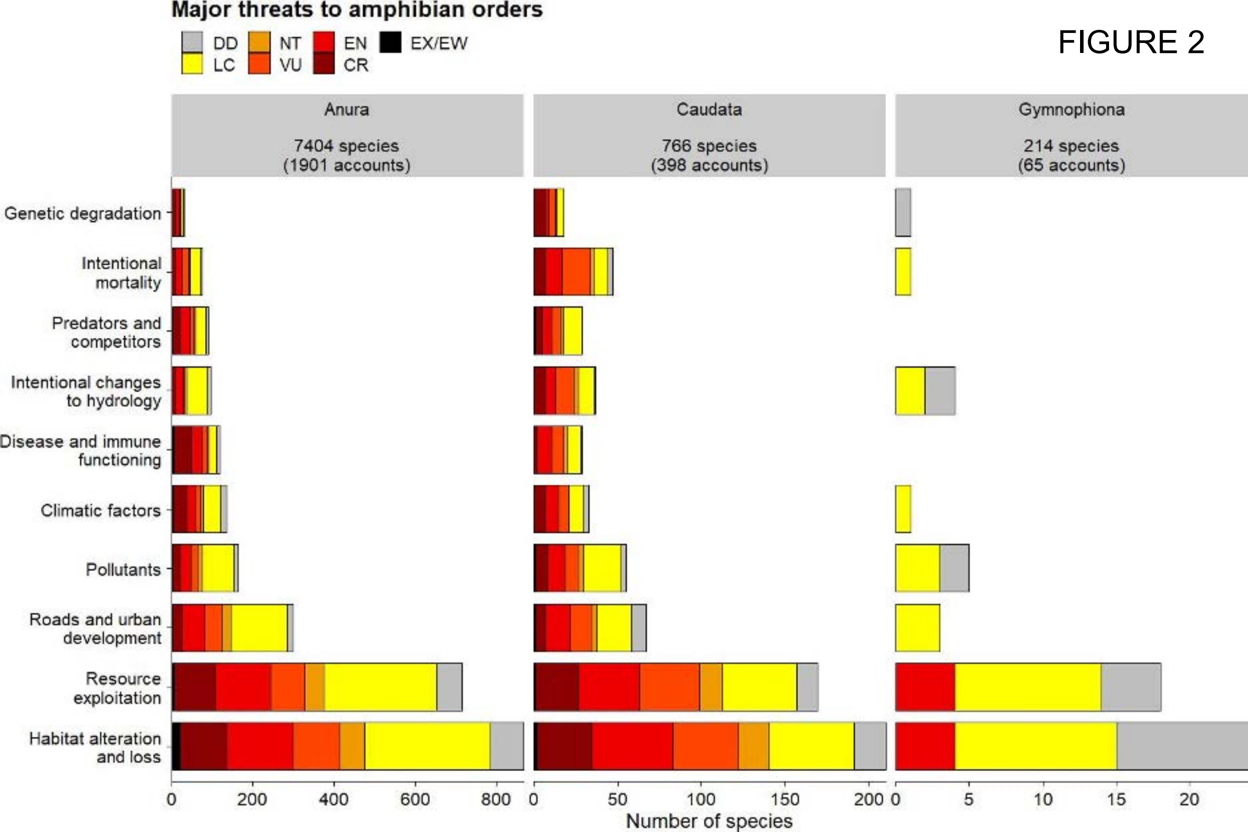

a
Percent Change in Publications
0
50
100
Percent Change
🟥 < 0
☐ > 0
phylogenomic(s)
microbiome
eDNA
cell AND molecular
fossil(s)
physiology
genomic(s)
diet
ecology
morphology
climate
trait(s)
phylogenetic(s)
behavior
genetic(s)
genetic(s) OR genomic(s)
conservation
development
amphibian
background
b
Number of Publicaitons
0
50
100
150
200
Year
2016
2017
2018
2019
2020
phylogenomic(s)
microbiome
eDNA
cell AND molecular
fossil(s)
physiology
genomic(s)
diet
ecology
morphology
climate
trait(s)
phylogenetic(s)
behavior
genetic(s)
genetic(s) OR genomic(s)
conservation
development

FIGURE 2


Major threats to amphibian orders
DD
LC
NT
VU
EN
CR
EX/EW
Anura
7404 species
(1901 accounts)
Caudata
766 species
(398 accounts)
Gymnophiona
214 species
(65 accounts)
Genetic degradation
Intentional mortality
Predators and competitors
Intentional changes to hydrology
Disease and immune functioning
Climatic factors
Pollutants
Roads and urban development
Resource exploitation
Habitat alteration and loss
0
200
400
600
800
0
50
100
150
200
0
5
10
15
20
Number of species

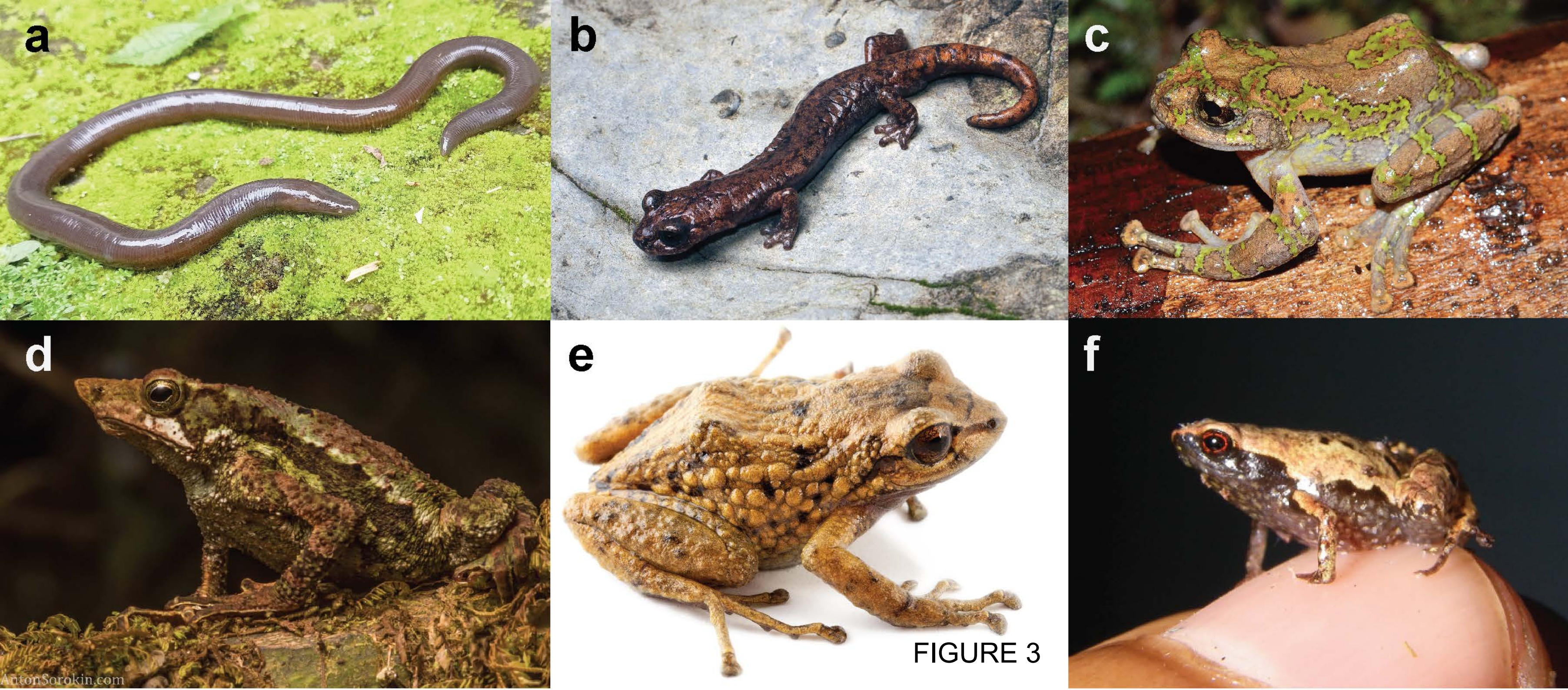


FIGURE 3

FIGURE 4

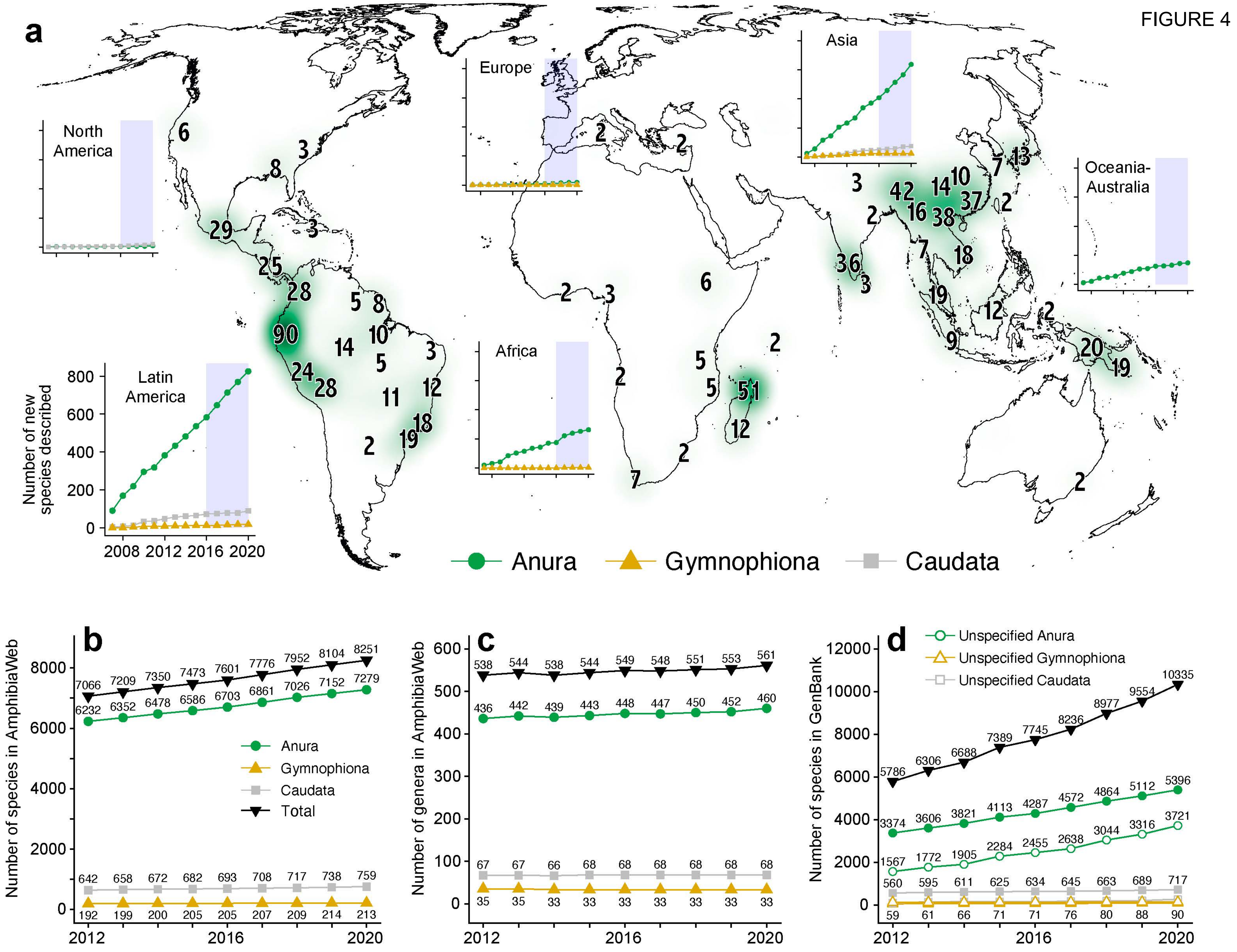
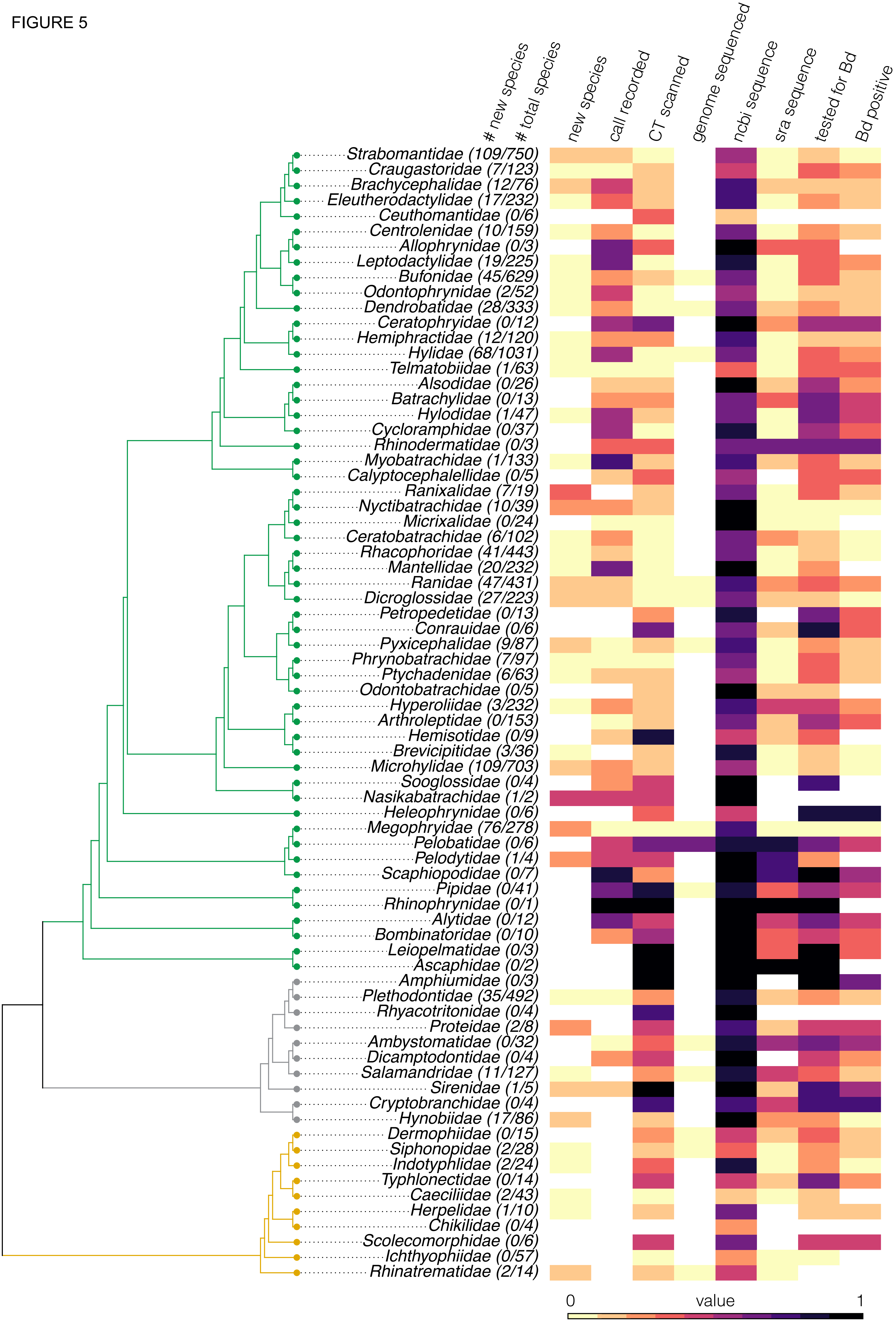

a
North America
Europe
Asia
Oceania-Australia
Africa
Latin America
Number of new species described
800
600
400
200
0
2008
2012
2016
2020
6
3
8
29
3
25
28
90
5
8
10
14
5
3
24
28
11
12
18
19
2
2
2
2
3
6
2
5
5
51
12
2
2
7
3
42
14
10
7
13
2
16
38
37
2
7
18
36
3
19
12
2
9
20
19
2
Anura
Gymnophiona
Caudata
b
Number of species in AmphibiaWeb
8000
6000
4000
2000
0
2012
2016
2020
7066
7209
7350
7473
7601
7776
7952
8104
8251
6232
6352
6478
6586
6703
6861
7026
7152
7279
642
658
672
682
693
708
717
738
759
192
199
200
205
205
207
209
214
213
Anura
Gymnophiona
Caudata
Total
c
Number of genera in AmphibiaWeb
600
500
400
300
200
100
0
2012
2016
2020
538
544
538
544
549
548
551
553
561
436
442
439
443
448
447
450
452
460
67
67
66
68
68
68
68
68
68
35
35
33
33
33
33
33
33
33
d
Number of species in GenBank
12000
10000
8000
6000
4000
2000
0
2012
2016
2020
Unspecified Anura
Unspecified Gymnophiona
Unspecified Caudata
5786
6306
6688
7389
7745
8236
8977
9554
10335
3374
3606
3821
4113
4287
4572
4864
5112
5396
1567
1772
1905
2284
2455
2638
3044
3316
3721
560
595
611
625
634
645
663
689
717
59
61
66
71
71
76
80
88
90

FIGURE 5



new species
total species
new species
call recorded
CT scanned
genome sequenced
ncbi sequence
sra sequence
tested for Bd
Bd positive
Strabomantidae (109/750)
Craugastoridae (7/123)
Brachycephalidae (12/76)
Eleutherodactylidae (17/232)
Ceuthomantidae (0/6)
Centrolenidae (10/159)
Allophrynidae (0/3)
Leptodactylidae (19/225)
Bufonidae (45/629)
Odontophrynidae (2/52)
Dendrobatidae (28/333)
Ceratophryidae (0/12)
Hemiphractidae (12/120)
Hylidae (68/1031)
Telmatobiidae (1/63)
Alsodidae (0/26)
Batrachylidae (0/13)
Hylodidae (1/47)
Cycloramphidae (0/37)
Rhinodermatidae (0/3)
Myobatrachidae (1/133)
Calyptocephalellidae (0/5)
Ranixalidae (7/19)
Nyctibatrachidae (10/39)
Micrixalidae (0/24)
Ceratobatrachidae (6/102)
Rhacophoridae (41/443)
Mantellidae (20/232)
Ranidae (47/431)
Dicroglossidae (27/223)
Petropedetidae (0/13)
Conrauidae (0/6)
Pyxicephalidae (9/87)
Phrynobatrachidae (7/97)
Ptychadenidae (6/63)
Odontobatrachidae (0/5)
Hyperoliidae (3/232)
Arthroleptidae (0/153)
Hemisotidae (0/9)
Brevicipitidae (3/36)
Microhylidae (109/703)
Sooglossidae (0/4)
Nasikabatrachidae (1/2)
Heleophrynidae (0/6)
Megophryidae (76/278)
Pelobatidae (0/6)
Pelodytidae (1/4)
Scaphiopodidae (0/7)
Pipidae (0/41)
Rhinophrynidae (0/1)
Alytidae (0/12)
Bombinatoridae (0/10)
Leiopelmatidae (0/3)
Ascaphidae (0/2)
Amphiumidae (0/3)
Plethodontidae (35/492)
Rhyacotritonidae (0/4)
Proteidae (2/8)
Ambystomatidae (0/32)
Dicamptodontidae (0/4)
Salamandridae (11/127)
Sirenidae (1/5)
Cryptobranchidae (0/4)
Hynobiidae (17/86)
Dermophiidae (0/15)
Siphonopidae (2/28)
Indotyphlidae (2/24)
Typhlonectidae (0/14)
Caeciliidae (2/43)
Herpelidae (1/10)
Chikilidae (0/4)
Scolecomorphidae (0/6)
Ichthyophiidae (0/57)
Rhinatrematidae (2/14)
0
value
1

FIGURE 6

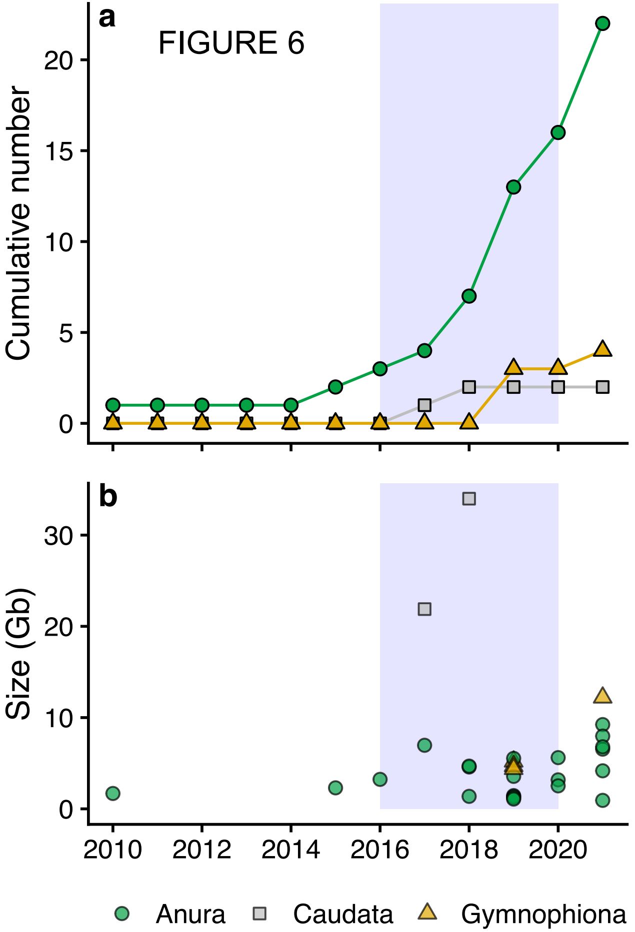

a
Cumulative number
0
5
10
15
20
b
Size (Gb)
0
10
20
30
2010
2012
2014
2016
2018
2020
Anura
Caudata
Gymnophiona

FIGURE 7

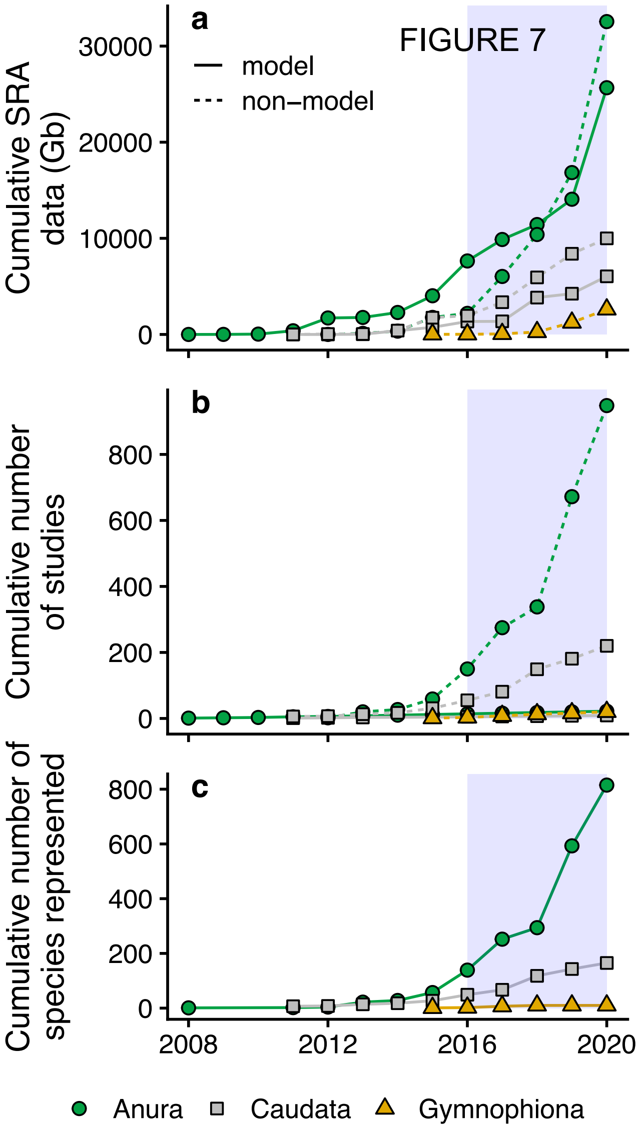

a
model
non–model
Cumulative SRA data (Gb)
30000
20000
10000
0
b
Cumulative number of studies
800
600
400
200
0
c
Cumulative number of species represented
800
600
400
200
0
2008
2012
2016
2020
Anura
Caudata
Gymnophiona

FIGURE 8

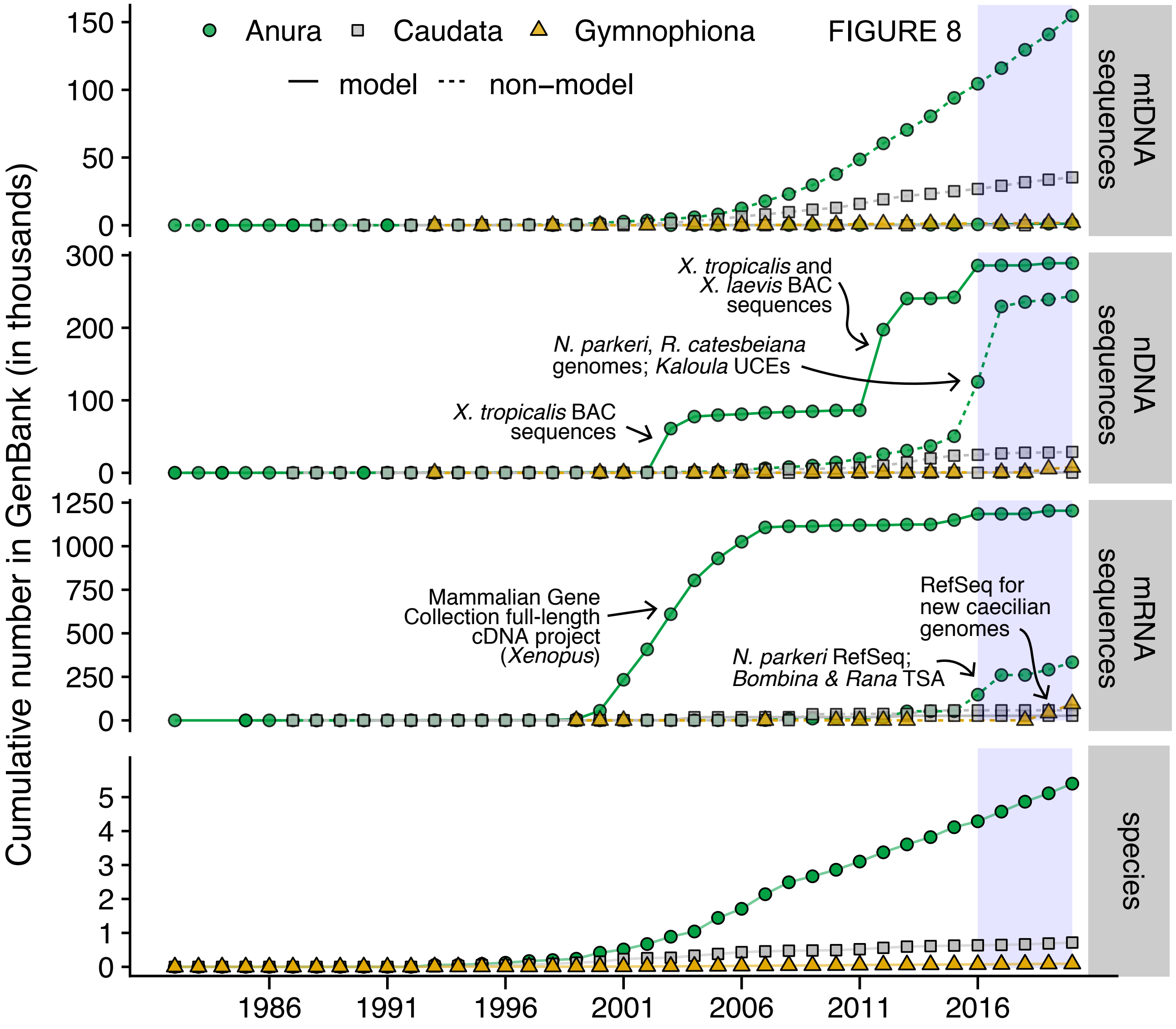
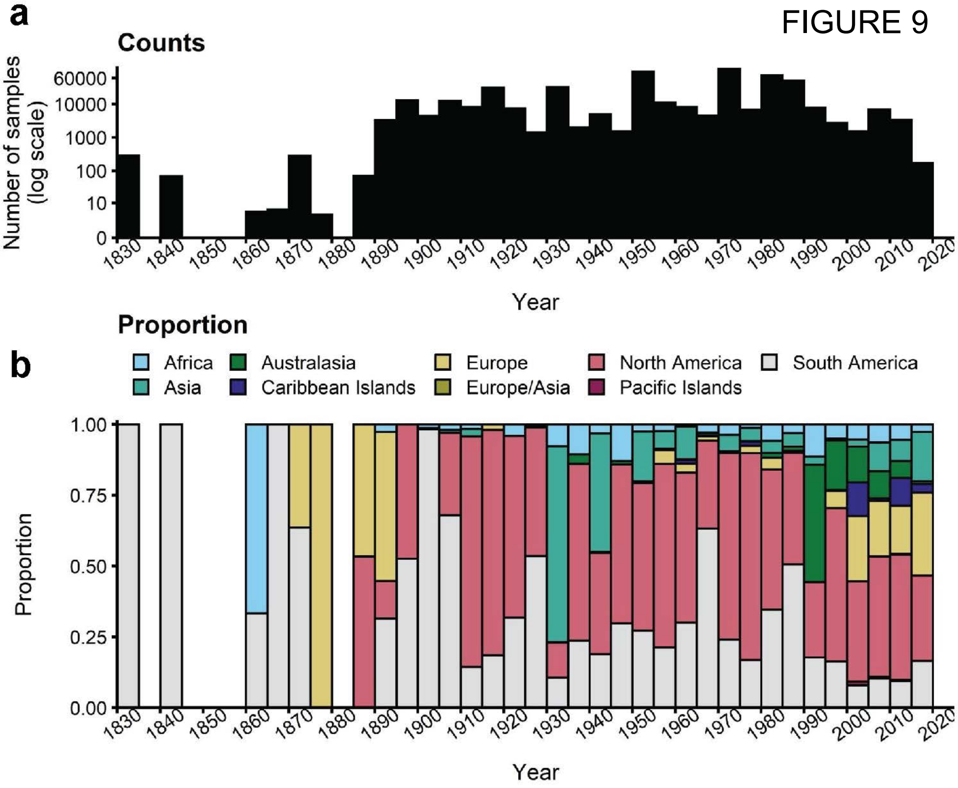

Anura
Caudata
Gymnophiona
model
non–model
mtDNA sequences
nDNA sequences
mRNA sequences
species
Cumulative number in GenBank (in thousands)
150
100
50
0
300
200
100
0
1250
1000
750
500
250
0
5
4
3
2
1
0
1986
1991
1996
2001
2006
2011
2016
X. tropicalis and *X. laevis* BAC sequences
N. parkeri, *R. catesbeiana* genomes; *Kaloula* UCEs
X. tropicalis BAC sequences
Mammalian Gene Collection full-length cDNA project (*Xenopus*)
RefSeq for new caecilian genomes
N. parkeri RefSeq; *Bombina* & *Rana* TSA

FIGURE 9


a
Counts
Number of samples (log scale)
60000
10000
1000
100
10
0
1830
1840
1850
1860
1870
1880
1890
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010
2020
Year
Proportion
b
Africa
Asia
Australasia
Caribbean Islands
Europe
Europe/Asia
North America
Pacific Islands
South America
Proportion
1.00
0.75
0.50
0.25
0.00
1830
1840
1850
1860
1870
1880
1890
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010
2020
Year