State of the Amphibia 2020: A Review of Five Years of Amphibian Research and Existing Resources

Authors: Womack, Molly C., Steigerwald, Emma, Blackburn, David C., Cannatella, David C., Catenazzi, Alessandro, et al.

Source: Ichthyology & Herpetology, 110(4) : 638-661

Published By: The American Society of Ichthyologists and Herpetologists

URL: https://doi.org/10.1643/h2022005

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Ichthyology-&-Herpetology on 06 Jul 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Ichthyology & Herpetology 110, No. 4, 2022, 638–661

REVIEWS

State of the Amphibia 2020: A Review of Five Years of Amphibian Research and Existing Resources

Molly C. Womack[1,¶], Emma Steigerwald[2,3,¶], David C. Blackburn[4], David C. Cannatella[5], Alessandro Catenazzi[6,7], Jing Che[8], Michelle S. Koo[2], Jimmy A. McGuire[2,9], Santiago R. Ron[10], Carol L. Spencer[2], Vance T. Vredenburg[2,11], and Rebecca D. Tarvin[2,9]

Amphibians are a clade of over 8,400 species that provide unique research opportunities and challenges. With amphibians undergoing severe global declines, we posit that assessing our current understanding of amphibians is imperative. Focusing on the past five years (2016–2020), we examine trends in amphibian research, data, and systematics. New species of amphibians continue to be described at a pace of ∼150 per year. Phylogenomic studies are increasing, fueling a growing consensus in the amphibian tree of life. Over 3,000 species of amphibians are now represented by expert-curated accounts or data in AmphibiaWeb, AmphibiaChina, BIOWEB, or the Amphibian Disease Portal. Nevertheless, many species lack basic natural history data (e.g., diet records, morphological measurements, call recordings) and major gaps exist for entire amphibian clades. Genomic resources appear on the cusp of a rapid expansion, but large, repetitive amphibian genomes still pose significant challenges. Conservation continues to be a major focus for amphibian research, and threats cataloged on AmphibiaWeb for 1,261 species highlight the need to address land use change and disease using adaptive management strategies. To further promote amphibian research and conservation, we underscore the importance of database integration and suggest that other understudied or imperiled clades would benefit from similar assessments of existing data.

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 to be sensitive to perturbation, they have survived the last four global mass extinction events and have a nearly worldwide distribution (Wake and Vredenburg, 2008; Kerby et al., 2010; 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 while 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 basic natural history and geographic distribution data for a large proportion of species, with 16.4% (1,185 species) classified as Data Deficient by the International Union for Conservation of Nature (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 an early focus on several model species to an exploration and description of the evolution,

---

[1] Department of Biology, Utah State University, Logan, Utah 84322; Email: molly.womack@usu.edu. ORCID: 0000-0002-3346-021X.

[2] Museum of Vertebrate Zoology, University of California, Berkeley, Berkeley, California 94720; Email: (ES) emma_steigerwald@berkeley.edu; (MSK) mkoo@berkeley.edu; (JAM) mcguirej@berkeley.edu; (CS) atrox@berkeley.edu; (VTV) vancevredenburg@gmail.com; and (RDT) rdtarvin@berkeley.edu. ORCID: (ES) 0000-0003-1027-1421; (MSK) 0000-0003-0410-722X; (JAM) 0000-0002-9562-5585; (VTV) 0000-0002-9682-1190; and (RDT) 0000-0001-5387-7250. Send correspondence to RDT.

[3] Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, California 94720.

[4] Department of Natural History, Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611; Email: dblackburn@flmnh.ufl.edu. ORCID: 0000-0002-1810-9886.

[5] Department of Integrative Biology, University of Texas at Austin, Austin, Texas 78712; Email: catfish@utexas.edu. ORCID: 0000-0001-8675-0520.

[6] Centro de Ornitología y Biodiversidad, Lima, Peru; Email: acatenazzi@gmail.com. ORCID: 0000-0002-3650-4783.

[7] Department of Biological Sciences, Florida International University, Miami, Florida 33199.

[8] State Key Laboratory of Genetic Resources and Evolution & Yunnan Key Laboratory of Biodiversity and Ecological Security of Gaoligong Mountain, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China; Email: chej@mail.kiz.ac.cn. ORCID: 0000-0003-4246-6514.

[9] Department of Integrative Biology, University of California, Berkeley, Berkeley, California 94720.

[10] Museo de Zoología, Escuela de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; Email: santiago.r.ron@gmail.com. ORCID: 0000-0001-6300-9350.

[11] Department of Biology, San Francisco State University, San Francisco, California 94116.

[¶] These authors contributed equally.

Submitted: 10 January 2022. Accepted: 20 June 2022. Associate Editor: D. S. Siegel.

DOI: 10.1643/h2022005

ecology, and diversity of amphibians found globally. Researchers have developed amphibian model systems that are associated with sophisticated molecular and genomic tools based on decades of concentrated research into the molecular biology of three species—*Xenopus laevis*, *Xenopus tropicalis*, and *Ambystoma mexicanum* (Getwan and Lienkamp, 2017). Although these three model species scarcely capture the diversity of Amphibia (over 8,400 species; AmphibiaWeb, 2021), 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). Research on many other amphibian genera has made notable historical contributions to biology: e.g., *Plethodon cinereus* in behavioral ecology and development (Dent, 1942; Heatwole, 1962; Kleeberger and Werner, 1982; Wyman and Hawksley-Lescault, 1987; Kerney, 2011; Kerney et al., 2012); *Engystomops* in sexual selection (Ryan et al., 1990); *Rana* in cloning (Briggs and King, 1952); *Rana* (Lefcort et al., 1998; Bridges, 2000; Hopkins et al., 2000; Pollet and Bendell-Young, 2000) and *Acris* (Fleming et al., 1982; Clark et al., 1998; Reeder et al., 1998) in community ecology and toxicology. New tools have since promoted the emergence of more model systems from classically "non-model" species and systems, 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 (Saporito et al., 2012; Tarvin et al., 2017; Caty et al., 2019; Alvarez-Buylla et al., 2022), toxic salamanders and resistant garter snakes for coevolution (Geffeney et al., 2005; Bucciarelli et al., 2022), *Spea* for phenotypic plasticity and life-history evolution (Levis et al., 2015, 2020), 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 poises amphibian researchers to further develop 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 average of 150 new species described every year, with no sign of slowing down (AmphibiaWeb, 2021).

Nevertheless, understanding current amphibian biodiversity is imperative, as amphibians are undergoing severe global population declines. The modern amphibian lineage is ancient (~300 million years old; Wake and Koo, 2018) and is now the most endangered vertebrate class in the ongoing Holocene Extinction (Stuart et al., 2004; 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 mitigate 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 five years from 2016 to 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

Trends in publishing.—To assess changes in the focal topics of amphibian research from 2016 to 2020, we performed a standardized literature search in Web of Science (© Copyright Clarivate 2022). 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 additional search terms 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. We also review name changes of herpetology-focused journals. 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.

Advances in amphibian conservation research.—To understand the major contributors to amphibian declines, for each species we obtained IUCN Red List status (or provisional IUCN Red List statuses from the AmphibiaWeb database) and associated drivers of decline from AmphibiaWeb species accounts (see supplemental data files; see Data Accessibility;

AmphibiaWeb and IUCN data were downloaded as of September 2021). The 25 AmphibiaWeb drivers of decline were collapsed into ten broad categories, which, owing to the nature of these threats, do not form entirely discrete, non-overlapping units. For instance, the following categories all ultimately relate to habitat modification or loss, but were divided as follows to allow for more granular insight into important amphibian threats: a 'habitat alteration and loss' category includes general habitat alteration and loss, secondary succession, subtle changes to necessary specialized habitat, and 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; and an 'intentional changes to hydrology' category includes drainage of habitat and dams changing river flow and/or covering habitat. The remaining threat categories were as follows: 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; 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; and a 'genetic degradation' category includes loss of genetic diversity from small population phenomena and loss of distinctiveness through hybridization. We visualized these data by order and IUCN status for each decline category and discussed in the context of major new findings on habitat loss and disease as drivers of amphibian declines between 2016 and 2020.

Trends and updates in amphibian diversity and systematics.— To visualize the accumulation of new species over time, we used the complete AmphibiaWeb database of new species between 2007 and 2020 (see supplemental data files; see Data Accessibility) to provide a baseline comparison to identify any trend changes during 2016–2020. 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 the section below ("A review of community resources"). We also review higher-level taxonomic changes in modern amphibians, largely based on recent phylogenomic studies.

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 one-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", or "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 et al., 2021). See supplemental data files for raw data (see Data Accessibility).

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]").

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; see Data Accessibility). 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; see Data Accessibility). 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) and

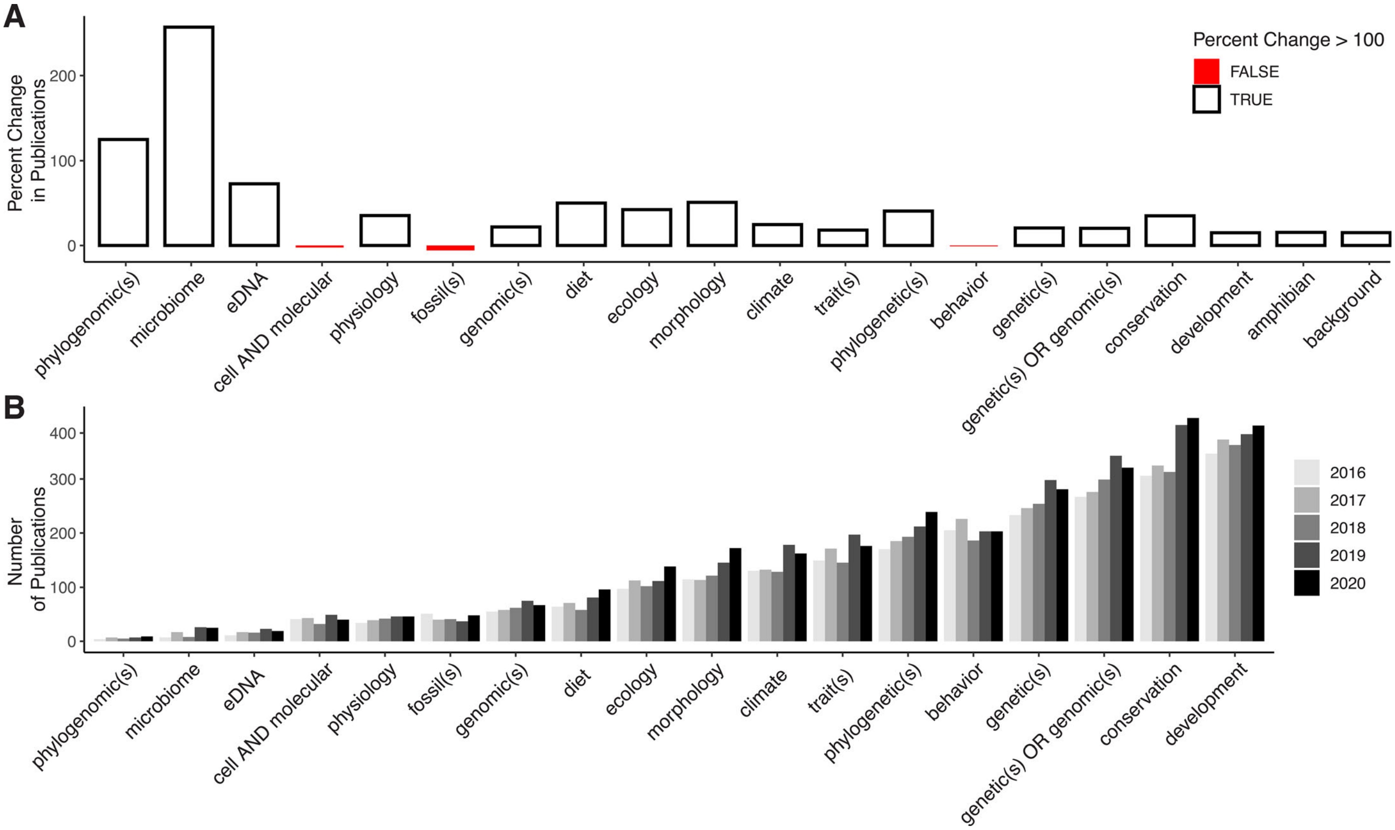

Fig. 1. Trends in amphibian research from 2016 through 2020 by (A) proportion change in publication number and (B) absolute number of publications in each biological subfield. The additional categories of "amphibian" and "background" in panel A refer to the proportional change of all amphibian publications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

plotted geographic representation of the database over time (see supplemental data files; see Data Accessibility). Finally, in addition to these trait- or data type-specific databases, we also review existing 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).

Data analysis and visualization.—Plots and data formatting were performed in R v4.1.0 (R Core Team, 2021) with the following packages: cowplot v1.1.1 (Wilke, 2020), dplyr v1.0.7 (Wickham et al., 2021), ggplot2 v3.3.5 (Wickham, 2016), reshape2 v1.4.4 (Wickham, 2007), stringr v1.4.0 (Wickham, 2010), tidyr v1.1.3 (Wickham, 2017), and tidyverse v1.3.1.9 (Wickham et al., 2019). For phylogenetic data formatting, analysis, and plotting, we used R v4.1.0 (R Core Team, 2021) with the following packages: 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

Trends in publishing

Research topics.—We identified 13,208 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 equals the 15% increase in total publications (no search filters) during that time period (Fig. 1A; Table S1; see Data Accessibility). The majority of amphibian publications were in five subfields: development (1,865), conservation (1,757), genetics OR genomics (1,506), behavior (1,023), and phylogenetics (999). Relatively few amphibian publications mentioned phylogenomics (32), microbiome (83), or eDNA (86; Fig. 1B; Table S1; see Data Accessibility). Almost all subject areas increased in amphibian publications, with the exception of fossil publications (30 in 2016 and 29 in 2020), cell and molecular publications (41 in 2016 and 40 in 2020), and behavior publications (205 in 2016 and 203 in 2020). The fastest growing subject areas, microbiome, phylogenomics, eDNA, morphology, and diet all showed a 50% or greater increase in amphibian publications from 2016 through 2020 (Fig. 1A; Table S1; see Data Accessibility).

Of the 13,208 total amphibian publications from 2016 through 2020, 629 (5%) 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 (23%), development (13%), genomic(s)

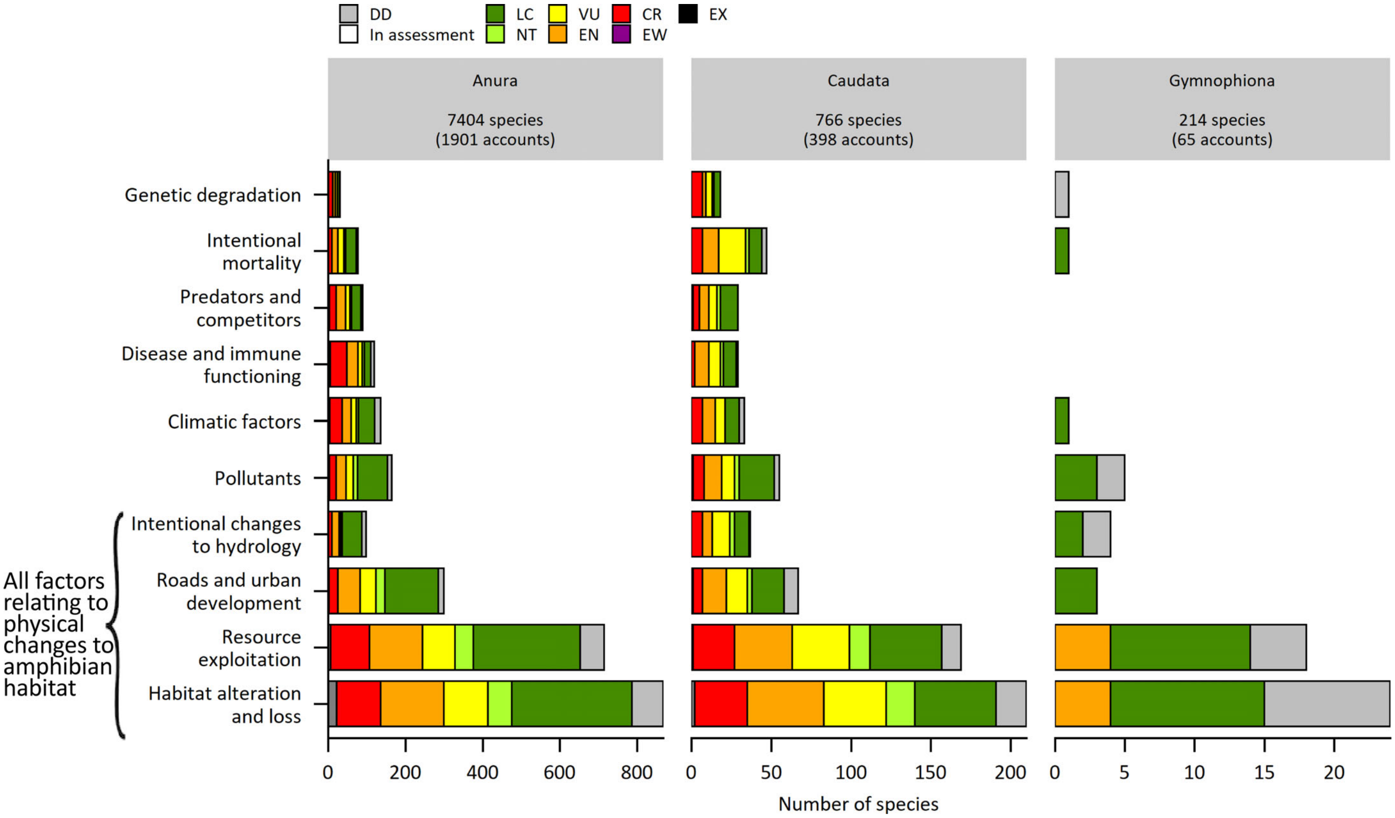

Fig. 2. The number of species in each order threatened by different drivers of amphibian decline, where each species can be represented by multiple drivers. IUCN conservation status categories are: extinct or extinct in the wild (EX/EW), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), least concern (LC), and data deficient (DD). Of species with accounts on AmphibiaWeb, 53.3% (1,261 of 2,364 species) have data on at least one factor driving their decline.

(10%), and physiology (9%) publications, but only 5% or less of all other research areas (Fig. S1; see Data Accessibility).

Journals.—The peer-reviewed journals with the largest number of amphibian publications from 2016 through 2020 were *PLoS ONE* (317), *Scientific Reports* (247), *Zootaxa* (186), *PeerJ* (174), and *Ecology and Evolution* (172; Table S2; see Data Accessibility). Although our literature search recovered amphibian publications in 23 languages, the vast majority (98%) of amphibian publications recognized in our search were written in English (Table S3; see Data Accessibility).

In the last five years, two herpetological journals acquired new names: *Revista Latinoamericana de Herpetología* in 2017 (formerly *Revista Mexicana de Herpetología*), and *Ichthyology & 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 toward making the discipline more inclusive (Cahan, 2020).

Advances in amphibian conservation research

Factors driving decline in the largest number of amphibian species.—Based on our review of AmphibiaWeb data, the principal driver of amphibian declines is habitat alteration and loss (Fig. 2). The drivers subsumed in our habitat alteration and loss category threaten at least 46.6% of amphibian species with accounts on AmphibiaWeb. Furthermore, pooling the habitat alteration and loss category with resource exploitation, roads and urban development, and intentional changes to hydrology categories—which all encompass the repercussions of physical changes to amphibian habitat—the percentage of affected species increases to 51.2%.

Though habitat loss and degradation are undebatable drivers of amphibian declines, it is important that we interpret these data (Fig. 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, while 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, which requires tools that have only recently been developed and democratized. Likewise, we 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. Meanwhile, pollutants are better documented as a driver of decline, but have been a focus for at least 60 years (225 amphibian species being documented as declining due to pollutants versus 170 species for climatic factors and 149 for disease and immune functioning; Fig. 2).

Factors largely associated with endangered or extinct amphibian species.—When prioritizing which drivers of amphibian

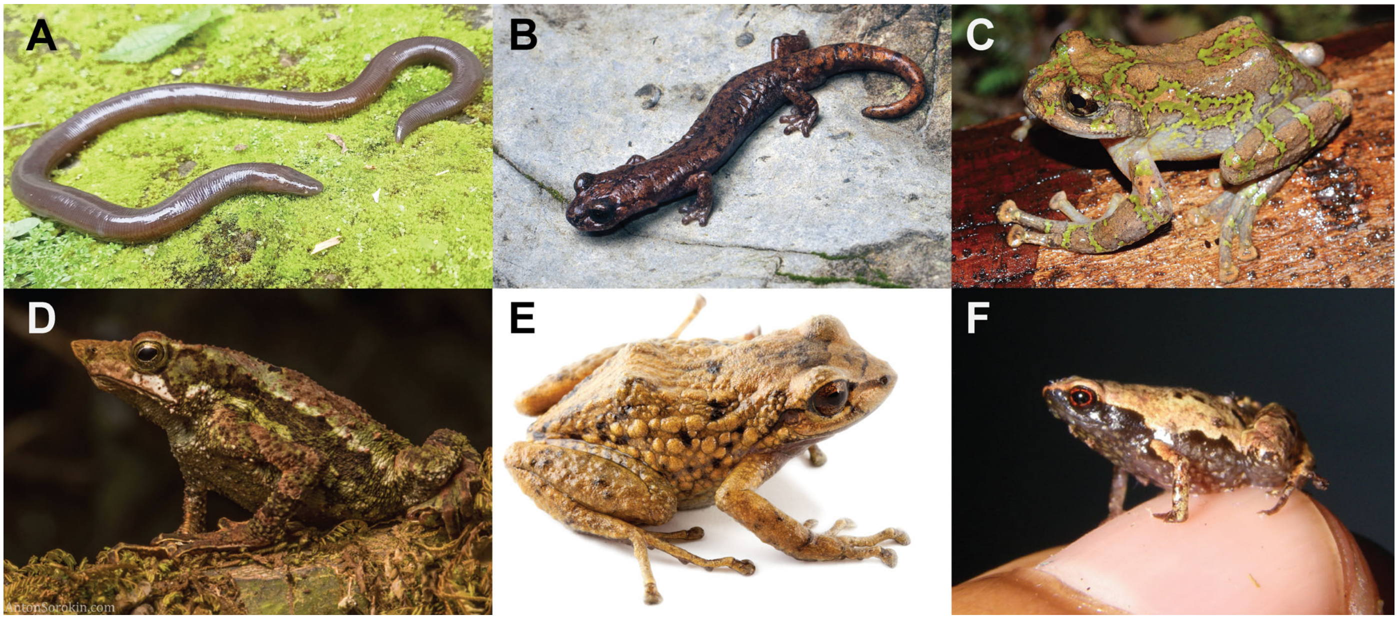

Fig. 3. Images of several new species described in the last five years. (A) *Ichthyophis benjii* from Mizoram, India (Lalremsanga et al., 2021), photo by Hmar Tlawmte Lalremsanga; (B) *Hydromantes samweli* (Bingham et al., 2018), holotype from Shasta County, CA, USA, photo copyright Robert Hansen; (C) *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 copyright 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.

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 weakened immune functioning (59.11% of EN, CR, EX/EW species) and genetic degradation (56%). Thus, these two types of threats 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.

Trends and updates in amphibian diversity and systematics

Amphibian diversity.—From 2016 to 2020, 780 new species of amphibians were described (Fig. 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 new 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; Fig. 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 from 2016 to 2020 are from Latin America (40.8%), Asia (37.2%), and Africa (12.0%; Fig. 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 from 2016 to 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 southern Andes of Ecuador, northern Madagascar, and southern China (Fig. 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 (Fig. 4B, C). The steeper increase in anuran species indicates that we are still very much in the age of discovery for amphibian 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 Fig. 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 (Fig. 5).

Amphibian 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

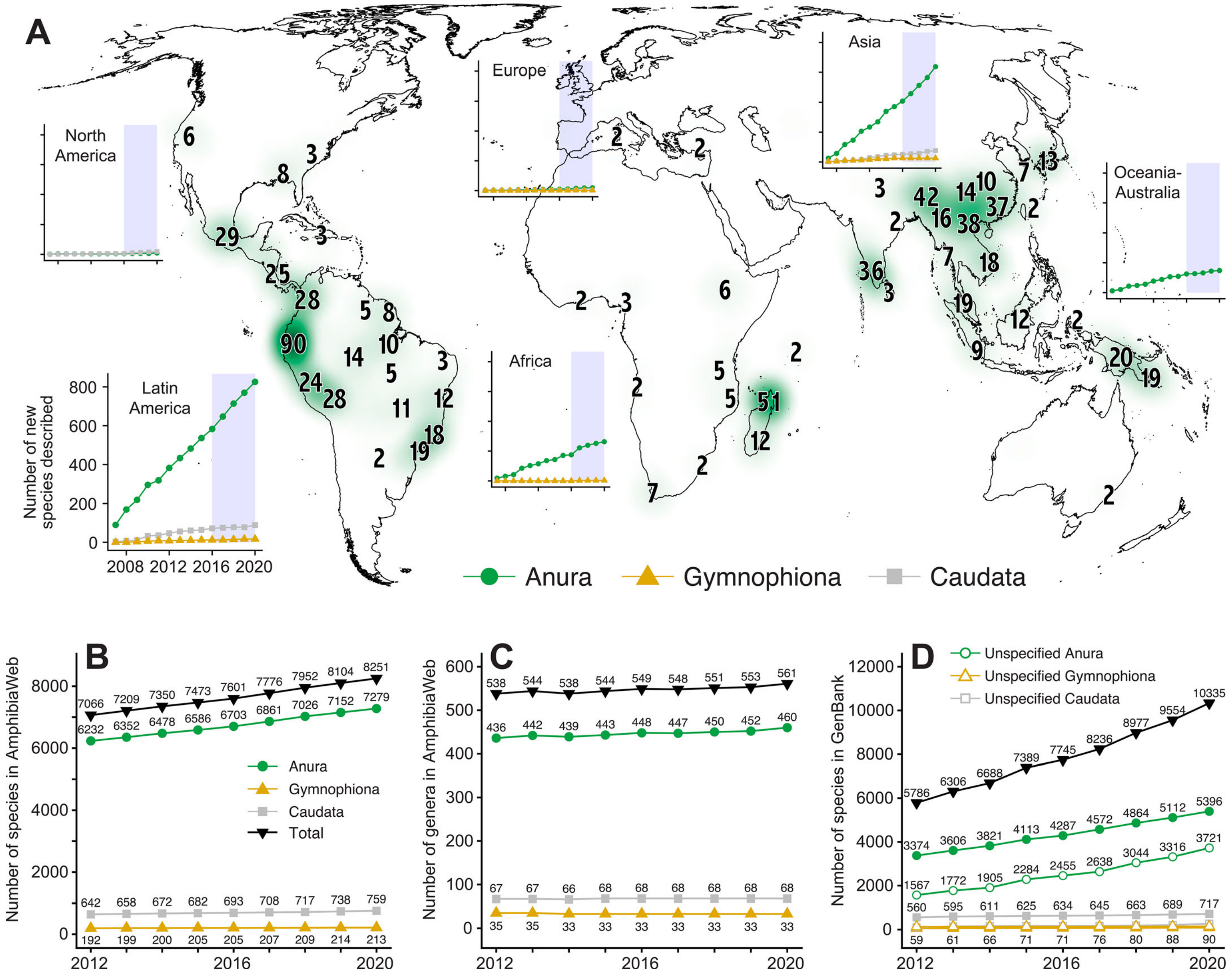

Fig. 4. Additions of amphibian species over time. (A) Geographic heat map and point cluster of new species described between 2016 and 2020. The countries with the highest numbers of new species in this time period are China (100 species), Brazil (95 species), Ecuador (67 species), Madagascar (56 species), and Peru (56 species). 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 (see Data Accessibility).

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; among the recent major studies, only Hime et al. (2021) included caecilians, but their findings are in agreement with prior understanding of caecilian relationships based on Sanger data, such as 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 largely stable in recent treatments. There is now remarkable agreement and taxonomic stability in terms of the higher-level phylogenetic relationships among and within all three amphibian orders.

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,

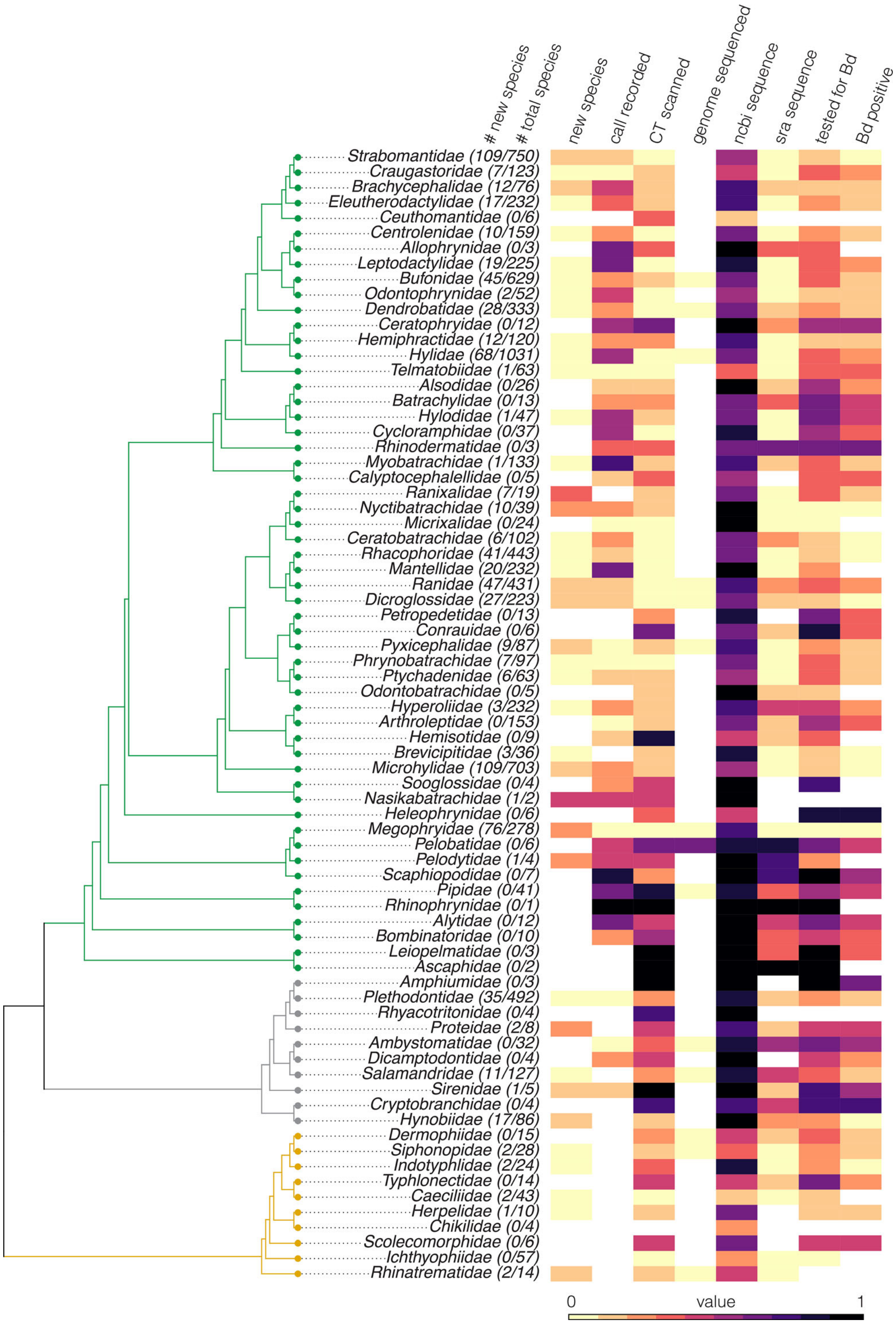

Fig. 5. Phylogenetic heat map showing the number and proportion of species within each family that were described in 2016–2020 and the proportion of species within each family that have accessible phenotypic, genetic, and disease data. Lighter to darker colored matrix cells represent lower to higher 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 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 (see Data Accessibility).

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. (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)

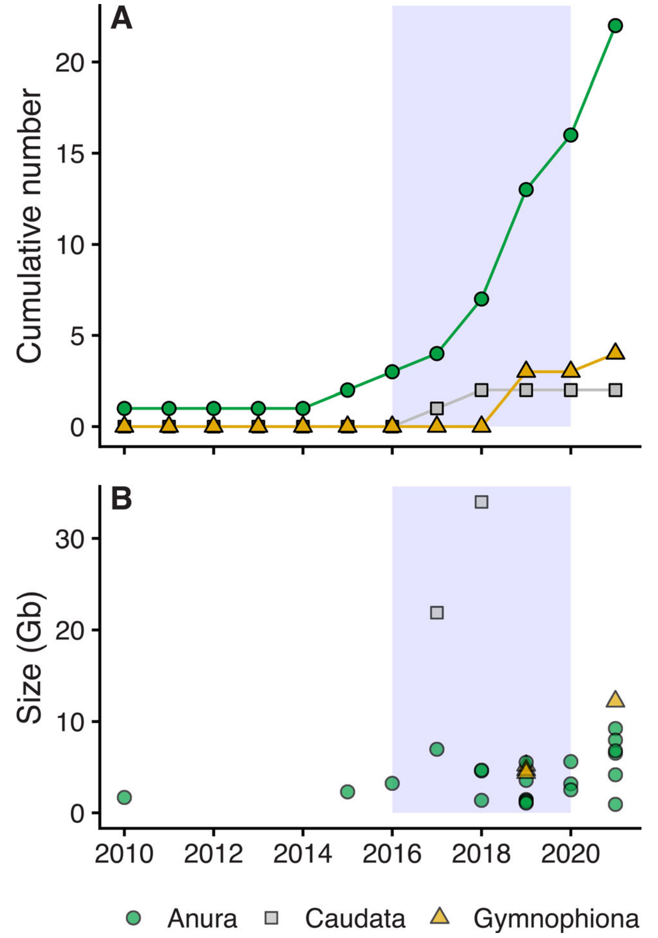

Fig. 6. (A) Cumulative number and (B) size of sequenced amphibian genomes by year. The blue box highlights the years 2016–2020.

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.

A review of community resources

Genomes.—A total of 28 amphibian genomes with representatives from 14 different families have been sequenced as of July 2021 (Figs. 5, 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; see Data Accessibility). 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 (Fig. 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; see Data Accessibility).

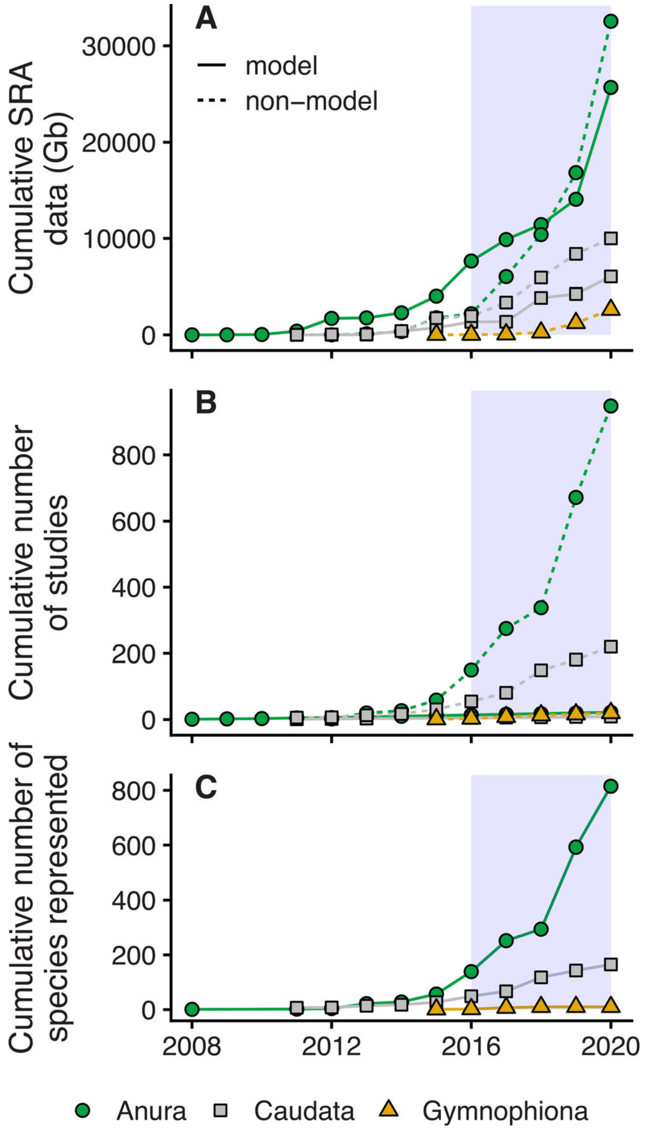

Fig. 7. The (A) cumulative amount of data and (B) number of studies in the Sequence Read Archive, separated by model (*Ambystoma mexicanum*, *Xenopus laevis*, *Xenopus tropicalis*) and non-model (all other) species. (C) Total number of species represented in the Sequence Read Archive. Years missing data points indicate that no data were submitted that year for that order.

NCBI Sequence Read Archive.—The amount of next-generation sequencing data deposited into the NCBI SRA since its origin in 2008 (Leinonen et al., 2011) has been steadily increasing for both model and non-model amphibian species (Fig. 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 (Fig. 7B) and cumulative number of species (Fig. 7C) increased in parallel over time. By the end of 2020, nearly 1,000 species of amphibians (815 of which are anurans) had sequences deposited in the SRA (Figs. 5, 7C; note that these numbers are inflated because they include unspecified, subspecies, and hybrid samples; see Fig. 4D).

NCBI GenBank nucleotide database.—Although the NCBI GenBank database was established in 1982 (Choudhuri, 2014), very few amphibian species were represented in the

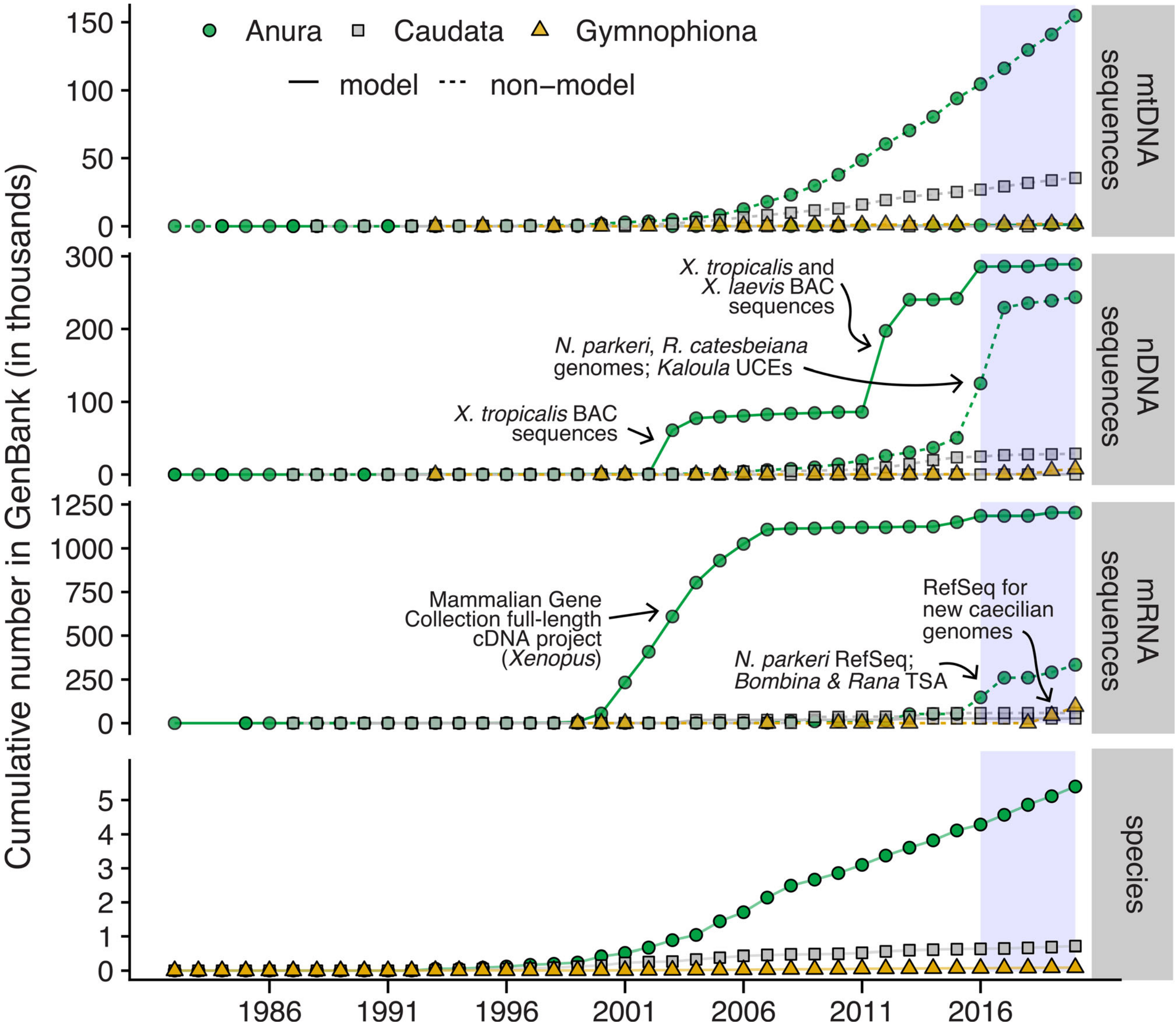

Fig. 8. The cumulative number of mitochondrial DNA (mtDNA), nuclear DNA (nDNA), and messenger RNA (mRNA) sequences, as well as species, added to the GenBank Nucleotide database from 1982 to 2020, highlighting the last five years, 2016–2020, in blue. Some of the projects that contributed substantially 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.

database until 2000 (Fig. 8). Early amphibian data were almost exclusively from *Xenopus* (Fig. 8, solid line, green circles). Since then, the number of represented species in NCBI databases has increased dramatically, to 6,203 (of a total of 8,268 known species) in 2020 (Fig. 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* (Fig. 8).

While the number of mtDNA sequences for anurans has risen gradually over time, the number for salamanders and caecilians has remained relatively flat (Fig. 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 (Fig. 8). For example, in 2012, >100,000 nDNA sequences of *Xenopus tropicalis* and *X. 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 *X. tropicalis* are responsible for the peak in 2003 of nDNA sequences (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; Fig. 8). In addition, several notable increases in non-model mRNA and nDNA sequence deposition likely are related to other new genomes (e.g., *Rana catesbeiana* in 2017 [Hammond et al., 2017]; *Microcaecilia unicolor* in 2019 and *Geotrypetes seraphini* in 2020, both from the Vertebrate Genomes Project, https://vertebrategenomesproject.org/; Koepfli et al., 2015) and transcriptomes (e.g., *Bombina*

Table 1. The most comprehensive amphibian call databases available online. For geographic regions, Af = African, Au = Australian, 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	1,098 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.

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]).

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 (Fig. 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 community-science frog identification initiative.

CT-scan data.—Since 2016, CT-scan datasets for 1,947 amphibian specimens, including image stacks and 3D mesh files, have been shared via MorphoSource. These include 1,530 anuran specimens representing 976 species (in 402 genera; 88% of genera), 362 caudatan specimens representing 184 species (in 66 genera; 97%), and 55 gymnophionan specimens representing 40 species (in 32 genera; 97%; Fig. 5). Many of these data were generated as part of the National Science Foundation (NSF) openVertebrate (oVert) Thematic Collections Network. In addition, there are a few CT scans of extinct crown-group amphibians, such as 26 fossils of *Beelzebufo* deposited in 2015. MorphoSource also now houses most, if not all, of the CT-scan media from the Digital Morphology project (DigiMorph). 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). As of October 2021, the website (https://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 also are 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. Three other existing 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 (AmphibiaWeb, 2021). Finally, NSF-funded VertNet (https://vertnet.org) aggregates individual-level amphibian trait data from records published by museum collections (e.g., body length, mass) that are tied to the location where individuals were collected and sometimes other traits (e.g., lifestage, sex). At the conclusion of 2020, VertNet had 1,261 individual records of amphibian body lengths (covering 897 species) and 455 individual records of amphibian body mass (covering 337 species).

Online portals for amphibians: AmphibiaWeb.—In 2020, AmphibiaWeb celebrated its twentieth anniversary, marking its commitment to its original vision—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" (AmphibiaWeb, 2021; https://amphibiaweb.org/about/index.html). Many of the core activities of AmphibiaWeb remain the same in the last two decades—a web page for every amphibian species with literature-based accounts and spatial data. Photos for species are provided through CalPhotos, a service also administered by UC Berkeley and used by other natural history projects (e.g., ReptileDatabase, etc.). Much of AmphibiaWeb's data (e.g., species accounts, type localities, range maps and traits) have been used in research studies (reviewed in Uetz et al., 2021), including 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 million page views per year in the last five years, with a high of 2.5 million 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 public repository (https://github.com/AmphibiaWeb/aw-assets). It now hosts over 3,500 species accounts with over 42,200 photos embedded from CalPhotos, representing 4,766 species. Newly added 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.

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 8,746 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 1,297 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-language species accounts and photographs from 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 or sovereignties. 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%).

Online portals for amphibians: AmphibiaChina.—In November of 2015, the Kunming Institute of Zoology, Chinese Academy of Sciences launched the website AmphibiaChina (https://www.amphibiachina.org) as an online database for Chinese amphibians (Che and Wang, 2016). China currently hosts

587 amphibian species (as of 12 December 2021) 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 9,042 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 linked reciprocally to accounts on AmphibiaWeb for species occurring in China.

Online portals for amphibians: Amphibian Species of the World.—An online resource launched around the same time as AmphibiaWeb in 2000 that extended work first presented by Frost (1985), the Amphibian Species of the World database provides a critical bibliography of all amphibian taxonomy and species with reciprocal links to several of the other listed online resources here (Frost, 2021).

Online portals for amphibians: IUCN Red List.—The IUCN (https://www.iucnredlist.org) sets the most comprehensive global ranking and listing of conservation status for animal, plant, and fungi species including amphibians based on expert assessments. The Red List, as the compilation of conservation statuses is called, includes categories from Extinct and Critically Endangered to Least Concern. Species which lack enough information for a conservation status are listed as Data Deficient. Details on threats, trends in population, conservation actions, basically any information that helped determine the status are available on their website as are spatial range data. Many of these data are linked or incorporated in other portals listed here.

Online portals for amphibians: Amphibian Ark, Conservation Needs, and Conservation Evidence.—The Amphibian Ark organization was borne from the need to implement the IUCN Amphibian Conservation Action Plan (Gascon et al., 2007), specifically charged to focus on *ex situ* conservation, hence Amphibian Ark maintains and provides valuable husbandry and *ex situ* conservation publications on many amphibian species (https://www.amphibianark.org/husbandry-documents). Amphibian Ark and their partners also develop, manage, and share Conservation Needs Assessments (CNA; https://www.conservationneeds.org), which integrate both *in situ* and *ex situ* conservation actions for species at either the regional or national level. Links to species-specific CNAs are incorporated into AmphibiaWeb species pages as part of the Conservation Status table.

Finally, more than 500 papers on conservation efforts with amphibians are collated in a Conservation Evidence database (https://www.conservationevidence.com), which has summary functions that allow users to review evidence for the most effective approaches to amphibian conservation.

Online portals for amphibians: 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 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 portal addresses 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. The Amphibian Disease Portal 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 (Fig. 9) and Bsal data (for details, see Koo et al., 2021; Olson et al., 2021). The Amphibian Disease Portal contains Bd samples from all but five amphibian families (missing are two frog, two caecilian, and one salamander family) and positive Bd samples from all but 16 amphibian families (Fig. 5). 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, downloadable datasets.

DISCUSSION

Current picture and future projections for amphibian biodiversity.—The pace of amphibian species descriptions continues unabated, with ~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 are 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.

On the other end of the spectrum from the description of previously unknown amphibian diversity, the study of amphibian declines has continued to be a central theme in amphibian biology. However, though the role of habitat loss and modification as principal drivers of amphibian declines is not a new finding (IUCN, 2021), relative to their importance these pivotal drivers have been de-emphasized in amphibian conservation research (Green et al., 2020).

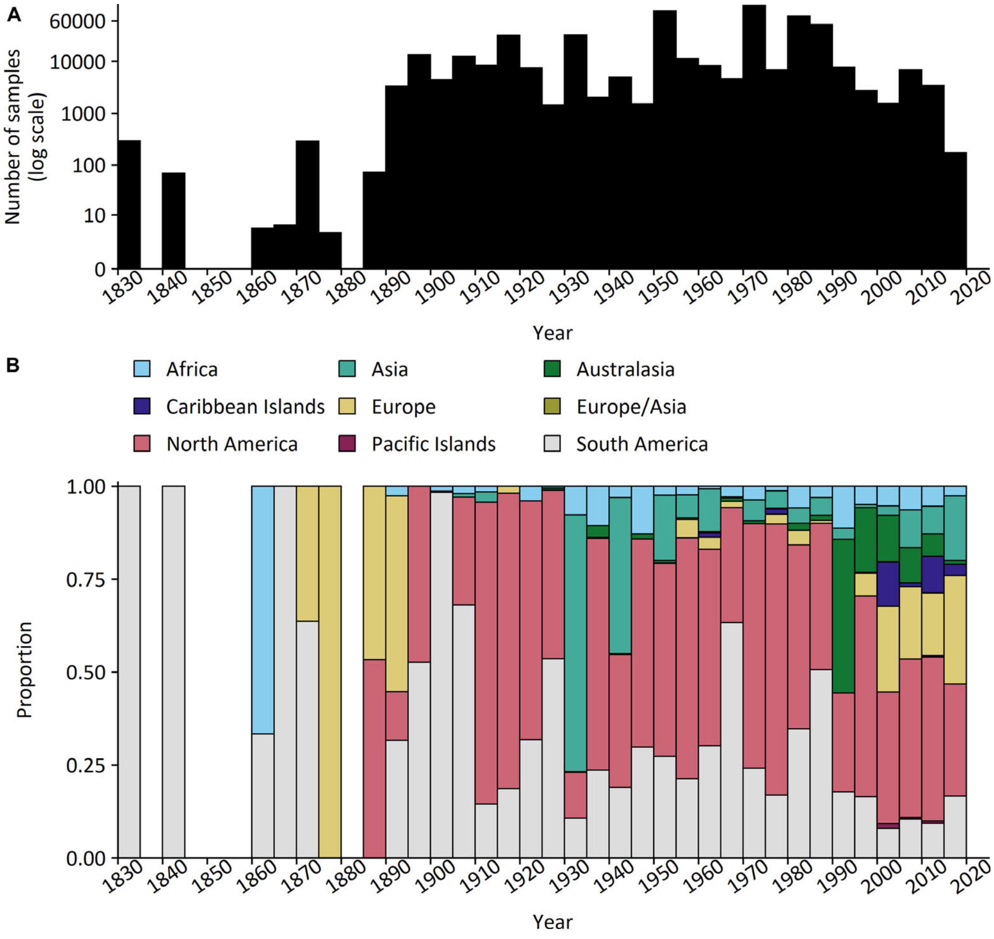

Fig. 9. Samples of *Batrachochytrium dendrobatidis* in the Amphibian Disease Portal. (A) A log-scale histogram of Bd swab counts, binned by the five-year time span in which the amphibian swabbed was captured. (B) A stacked histogram showing the proportional representation of swabs taken from different 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).

Even still, over the last five years large-scale meta-analyses have confirmed several basic expectations of the repercussions of habitat degradation for amphibians: (i) land use change decreases amphibian species richness (Cordier et al., 2021), (ii) amphibian abundance declines toward 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 (Chen et al., 2017).

Among diseases driving amphibian declines, a 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., 2017a; 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., 2017b; 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, 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 Community resources section), will help us improve our capacity to mitigate the impacts of these pathogens through monitoring, policy, and management.

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 28 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. A concerted effort to review and update the taxonomic identities of GenBank sequences will become more and more necessary as the database continues to grow.

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 emerging amphibian model species, such as medical applications arising from research on regeneration in *Notophthalmus viridescens* (Joven et al., 2019), freezing tolerance in *Rana sylvatica* (Joanisse and Storey, 1996; Gerber et al., 2016; Costanzo, 2019), and chytrid disease in *Atelopus zeteki* (McCaffery et al., 2015; Cohen et al., 2017; Byrne et al., 2021), along with 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 there is a wealth of accessible amphibian data online (Fig. 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. 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 publicly available CT scans for at least one species, most families (41 of 74 total) have CT 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 dietary records from the wild. Furthermore, while data exist for Bd and Bsal for many amphibian families, much of those data are not yet in a centralized database like the Amphibian Disease Portal. These data deficits and the lack of integration among databases make comparative work and synthetic studies difficult, putting amphibian research at a disadvantage compared to other tetrapod clades with more complete databases (e.g., EltonTraits for birds and mammals; Wilman et al., 2014). 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 crucially 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, CT scans, audio recordings, pathogen data) for the same individual or population.

Publication biases highlight obstacles to research progress.—Inequality in the demography of amphibian research can sideline diverse and locally relevant viewpoints that would otherwise aid in tackling amphibian research challenges. Numerous studies published from 2016 to 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 underrepresented in peer-reviewed publications of amphibian biology (Rock et al., 2021). Nevertheless, 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 we note that these two studies considered different datasets and journals).

Several factors likely underlie these patterns of underrepresentation of female authors. Within herpetology, papers with male first or last authors are less likely to have female coauthors than papers with female first or last authors (Salerno et al., 2019; Grosso et al., 2021; Rock et al., 2021). The trend of increasing numbers of women leaving academia as their career progresses (the "leaky pipeline") might partially explain the discrepancy in the relatively faster growing proportion of female first versus last authors found by Rock and colleagues (2021). A low proportion of senior female academics affects many aspects of publishing in herpetology through gender inequity of editorial boards, leadership positions, and committees of professional societies (Liévano-Latorre et al., 2020; Chuliver et al., 2021; Grosso et al., 2021). 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). In addition, region-specific gaps in amphibian data (e.g., trait data) indicate geographic bias in amphibian research, further accentuating the importance of increased support for amphibian research and equitable collaborations worldwide.

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: e.g., *Revista Latinoamericana de Herpetología*, *Herpetological Conservation and Biology*, *The Herpetological Journal (UK)*, and *Ichthyology & Herpetology*. Amphibian research would benefit from further analyses of amphibian-specific publishing inequalities for identities beyond gender and assessments of whether changing publishing practices can effect 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 increased adoption of adaptive management practices by relevant agencies, non-governmental organizations, 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 (Trochet et al., 2014; Oliveira et al., 2017; Mendoza-Henao et al., 2019; Moore et al., 2021) data, as well as expert-curated reference databases (AmphibiaWeb, Anfibios del Ecuador, 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 are 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. We aim 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 the R scripts to generate all figures (except Figs. 3 and 4) are available at a public repository: https://github.com/AmphibiaWeb/State-of-the-Amphibia. A Spanish-language translation of the manuscript and Chinese and French translations of the abstract are available in our supplemental material. Supplemental material is available at https://www.ichthyologyandherpetology.org/h2022005. The Spanish-language text was first machine-translated with DeepL and then human-verified by ES, SR, and AC; the Chinese translation was conducted by JC (车静) and Yunke Wu (吴耘珂); and the French-language text was first machine-translated with DeepL and then human-verified by AC. We hope that these translations make our work more accessible to a broad audience and that our open-access, human-verified translation can be used in training datasets to further improve machine translation technologies. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

ACKNOWLEDGMENTS

The authors declare no conflict of interest. We are grateful to current and past UC Berkeley AmphibiaWeb undergraduate apprentices who regularly compile amphibian species spatial data such as type localities and range maps for AmphibiaWeb and this study, especially Julia Chen, Julianne Oshiro, Alexandra Perkins, Elizabeth Pyle, Rigel Sison, and lead GIS assistant Zoe Yoo. We also thank AmphibiaWeb team members that read and provided comments on the manuscript, specifically Ann Chang. Rafael Márquez and Laura González Ortiz provided access to the database of recordings from Fonozoo; Mike Webster and Jay McGowan provided access to the database of the Macaulay Library. We thank Connor Tumelty for initial work compiling data on amphibian genomes. We thank NSF for funding several large-scale research initiatives that contributed much of the data cited herein, namely: openVertebrate (oVert) Thematic Collections Network (NSF DBI-1701714), MorphoSource (supported by NSF DBI-1902242), AmphibiaTree project (NSF DEB-0334952). We thank the USDA Forest Service for initial seed funding for the Amphibian Disease Portal (Cooperative Agreement #15-CR-11261953-098 to MSK, UC Berkeley). MCW was supported by the Utah Agricultural Experiment Station (UTA01574). ES was supported by an NSF GRFP and the Charles W. Woodworth Fellowship through the Rausser College of Natural Resources, UC Berkeley. RDT was supported by start-up funds from UC Berkeley. Finally, we dedicate this paper to David Wake, late founder of AmphibiaWeb and evolutionary biologist and herpetologist; discussions with David Wake often were as far-ranging, in-depth, and current on the state of the Amphibia as one could want.

LITERATURE CITED

Adams, A. J., S. J. Kupferberg, M. Q. Wilber, A. P. Pessier, M. Grefsrud, S. Bobzien, V. T. Vredenburg, and C. J. Briggs. 2017b. Extreme drought, host density, sex, and bullfrogs influence fungal pathogen infection in a declining lotic amphibian. Ecosphere 8:e01740.

Adams, A. J., A. P. Pessier, and C. J. Briggs. 2017a. Rapid extirpation of a North American frog coincides with an increase in fungal pathogen prevalence: historical analysis and implications for reintroduction. Ecology and Evolution 7:10216–10232.

Adams, M. J., R. N. Harris, E. H. C. Grant, M. J. Gray, M. C. Hopkins, S. A. Iverson, R. Likens, M. Mandica, D. H. Olson, A. Shepack, and H. Waddle. 2018. Prepublication communication of research results. EcoHealth 15:478–481.

Alexander, A. M., Y.-C. Su, C. H. Oliveros, K. V. Olson, S. L. Travers, and R. M. Brown. 2017. Genomic data reveals potential for hybridization, introgression, and incomplete lineage sorting to confound phylogenetic relationships in an adaptive radiation of narrow-mouth frogs. Evolution 71:475–488.

Alroy, J. 2015. Current extinction rates of reptiles and amphibians. Proceedings of the National Academy of Sciences of the United States of America 112:13003–13008.

Alvarez-Buylla, A., C. Y. Payne, C. Vidoudez, S. A. Trauger, and L. A. O'Connell. 2022. Molecular physiology of pumiliotoxin sequestration in a poison frog. PLoS ONE 17:e0264540.

AmphibiaWeb. 2021. University of California, Berkeley, California. https://amphibiaweb.org (accessed 1 December 2021).

Arntzen, J. W., C. Abrahams, W. R. M. Meilink, R. Iosif, and A. Zuiderwijk. 2017. Amphibian decline, pond loss and reduced population connectivity under agricultural intensification over a 38 year period. Biodiversity and Conservation 26:1411–1430.

Bardua, C., A.-C. Fabre, J. Clavel, M. Bon, K. Das, E. L. Stanley, D. C. Blackburn, and A. Goswami. 2021. Size, microhabitat, and loss of larval feeding drive cranial diversification in frogs. Nature Communications 12:2503.

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471:51–57.

Berger, L., A. A. Roberts, J. Voyles, J. E. Longcore, K. A. Murray, and L. F. Skerratt. 2016. History and recent progress on chytridiomycosis in amphibians. Fungal Ecology 19:89–99.

Bingham, R. E., T. J. Papenfuss, and L. Lindstrand. 2018. Phylogeography and species boundaries in the *Hydromantes shastae* complex, with description of two new species (Amphibia; Caudata; Plethodontidae). Bulletin of the Museum of Comparative Zoology 161:403–427.

Blackburn, D. C., G. Giribet, D. E. Soltis, and E. L. Stanley. 2019. Predicting the impact of describing new species on phylogenetic patterns. Integrative Organismal Biology 1: obz028.

Bosch, J., A. Mora-Cabello de Alba, S. Marquínez, S. J. Price, B. Thumsová, and J. Bielby. 2021. Long-term monitoring of amphibian populations of a National Park in northern Spain reveals negative persisting effects of *Ranavirus*, but not *Batrachochytrium dendrobatidis*. Frontiers in Veterinary Science 8:645491.

Boyer, D. M., G. F. Gunnell, S. Kaufman, and T. M. McGeary. 2016. Morphosource: archiving and sharing 3-D digital specimen data. The Paleontological Society Papers 22:157–181.

Bridges, C. M. 2000. Long-term effects of pesticide exposure at various life stages of the southern leopard frog (*Rana sphenocephala*). Archives of Environmental Contamination and Toxicology 39:91–96.

Briggs, R., and T. J. King. 1952. Transplantation of living nuclei from blastula cells into enucleated frogs' eggs. Proceedings of the National Academy of Sciences of the United States of America 38:455–463.

Bucciarelli, G. M., F. Alsalek, L. B. Kats, D. B. Green, and H. B. Shaffer. 2022. Toxic relationships and arms-race coevolution revisited. Annual Review of Animal Biosciences 10:63–80.

Byrne, A. Q., C. L. Richards-Zawacki, J. Voyles, K. Bi, R. Ibáñez, and E. B. Rosenblum. 2021. Whole exome sequencing identifies the potential for genetic rescue in iconic and critically endangered Panamanian harlequin frogs. Global Change Biology 27:50–70.

Cahan, E. 2020. Amid protests against racism, scientists move to strip offensive names from journals, prizes, and more. Science. DOI: 10.1126/science.abd6441.

Catenazzi, A., A. Swei, J. Finkle, E. Foreyt, L. Wyman, and V. T. Vredenburg. 2017. Epizootic to enzootic transition of a fungal disease in tropical Andean frogs: Are surviving species still susceptible? PLoS ONE 12:e0186478.

Caty, S. N., A. Alvarez-Buylla, G. D. Byrd, C. Vidoudez, A. B. Roland, E. E. Tapia, B. Budnik, S. A. Trauger, L. A. Coloma, and L. A. O'Connell. 2019. Molecular physiology of chemical defenses in a poison frog. Journal of Experimental Biology 222:jeb204149.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Science Advances 1:e1400253.

Chandramouli, S. R., K. Vasudevan, S. Harikrishnan, S. K. Dutta, S. J. Janani, R. Sharma, I. Das, and R. K. Aggarwal. 2016. A new genus and species of arboreal toad with phytotelmonous larvae, from the Andaman Islands, India (Lissamphibia, Anura, Bufonidae). ZooKeys 555:57–90.

Che, J., and K. Wang. 2016. AmphibiaChina: an online database of Chinese Amphibians. Zoological Research 37: 57–59.

Chen, J. M., Y. H. Wu, C. Q. Lu, S. B. Hou, and Z. T. Lyu. 2021. The taxonomic changes of Amphibians and Reptiles in China in 2020. http://www.amphibiachina.org/news (accessed 1 December 2021).

Chen, Y., J. Zhang, J. Jiang, S. E. Nielsen, and F. He. 2017. Assessing the effectiveness of China's protected areas to conserve current and future amphibian diversity. Diversity and Distributions 23:146–157.

Choudhuri, S. 2014. Bioinformatics for Beginners: Genes, Genomes, Molecular Evolution, Databases and Analytical Tools. Academic Press, London.

Chuliver, M., J. Grosso, G. Fontanarrosa, J. Fratani, D. Paola Ferraro, A. S. Duport-Bru, R. G. Schneider, M. D. Casagranda, L. Pereyra, N. Vicente, M. J. Salica, R. G. Medina, C. A. Bessa, R. Semhan, and M. C. Vera. 2021. Gender inequities in herpetology: the case of the Argentine community. Cuadernos de Herpetología 35:195–205.

Clark, D. R., Jr., R. Cantu, D. F. Cowman, and D. J. Maxson. 1998. Chronic exposure to pentavalent arsenic of larval leopard frogs (*Rana pipiens*): bioaccumulation and reduced swimming performance. Ecotoxicology 7:61–67.

Clark, K., I. Karsch-Mizrachi, D. J. Lipman, J. Ostell, and E. W. Sayers. 2016. GenBank. Nucleic Acids Research 44: D67–D72.

Cohen, J. M., T. A. McMahon, C. Ramsay, E. A. Roznik, E. L. Sauer, S. Bessler, D. J. Civitello, B. K. Delius, N. Halstead, S. A. Knutie, K. H. Nguyen, N. Ortega, B. Sears, M. D. Venesky . . . J. R. Rohr. 2019. Impacts of thermal mismatches on chytrid fungus *Batrachochytrium dendrobatidis* prevalence are moderated by life stage, body size, elevation and latitude. Ecology Letters 22:817–825.

Cohen, J. M., M. D. Venesky, E. L. Sauer, D. J. Civitello, T. A. McMahon, E. A. Roznik, and J. R. Rohr. 2017. The thermal mismatch hypothesis explains host susceptibility to an emerging infectious disease. Ecology Letters 20:184–193.

Colón-Gaud, C., M. R. Whiles, S. S. Kilham, K. R. Lips, C. M. Pringle, S. Connelly, and S. D. Peterson. 2009. Assessing ecological responses to catastrophic amphibian declines: patterns of macroinvertebrate production and food web structure in upland Panamanian streams. Limnology and Oceanography 54:331–343.

Cordier, J. M., R. Aguilar, J. N. Lescano, G. C. Leynaud, A. Bonino, D. Miloch, R. Loyola, and J. Nori. 2021. A global assessment of amphibian and reptile responses to land-use changes. Biological Conservation 253:108863.

Costanzo, J. P. 2019. Overwintering adaptations and extreme freeze tolerance in a subarctic population of the wood frog, *Rana sylvatica*. Journal of Comparative Physiology B 189:1–15.

Cusi, J. C., J. Moravec, E. Lehr, and V. Gvoždík. 2017. A new species of semiarboreal toad of the *Rhinella festae* group (Anura, Bufonidae) from the Cordillera Azul National Park, Peru. ZooKeys 673:21–47.

Dascal, N. 1987. The use of *Xenopus* oocytes for the study of ion channels. Critical Reviews in Biochemistry and Molecular Biology 22:317–387.

Dena, S., R. Rebouças, G. Augusto-Alves, C. Zornosa-Torres, M. R. Pontes, and L. F. Toledo. 2020. How much are we losing in not depositing anuran sound recordings in scientific collections? Bioacoustics 29:590–601.

Dent, J. N. 1942. The embryonic development of *Plethodon cinereus* as correlated with the differentiation and functioning of the thyroid gland. Journal of Morphology 71: 577–601.

Edholm, E.-S., L.-M. Albertorio Saez, A. L. Gill, S. R. Gill, L. Grayfer, N. Haynes, J. R. Myers, and J. Robert. 2013. Nonclassical MHC class I-dependent invariant T cells are evolutionarily conserved and prominent from early development in amphibians. Proceedings of the National Academy of Sciences of the United States of America 110: 14342–14347.

Fabre, A.-C., C. Bardua, M. Bon, J. Clavel, R. N. Felice, J. W. Streicher, J. Bonnel, E. L. Stanley, D. C. Blackburn, and A. Goswami. 2020. Metamorphosis shapes cranial diversity and rate of evolution in salamanders. Nature Ecology and Evolution 4:1129–1140.

Feng, S., J. Stiller, Y. Deng, J. Armstrong, Q. Fang, A. H. Reeve, D. Xie, G. Chen, C. Guo, B. C. Faircloth, B. Petersen, Z. Wang, Q. Zhou, M. Diekhans . . . G. Zhang. 2020. Dense sampling of bird diversity increases power of comparative genomics. Nature 587:252–257.

Feng, Y.-J., D. C. Blackburn, D. Liang, D. M. Hillis, D. B. Wake, D. C. Cannatella, and P. Zhang. 2017. Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous–Paleogene boundary. Proceedings of the National Academy of Sciences of the United States of America 114:E5864–E5870.

Finlay, J. C., and V. T. Vredenburg. 2007. Introduced trout sever trophic connections in watersheds: consequences for a declining amphibian. Ecology 88:2187–2198.

Fisher, M. C., and T. W. J. Garner. 2020. Chytrid fungi and global amphibian declines. Nature reviews. Microbiology 18:332–343.

Fleming, W. J., H. de Chacin, O. H. Pattee, and T. G. Lamont. 1982. Parathion accumulation in cricket frogs and its effect on American kestrels. Journal of Toxicology and Environmental Health 10:921–927.

Fox, C. W., J. P. Ritchey, and C. E. T. Paine. 2018. Patterns of authorship in ecology and evolution: first, last, and corresponding authorship vary with gender and geography. Ecology and Evolution 8:11492–11507.

Freitas, P. D., A. S. Yandulskaya, and J. R. Monaghan. 2019. Spinal cord regeneration in amphibians: a historical perspective. Developmental Neurobiology 79:437–452.

Frost, D. R. 1985. Amphibian Species of the World. Vol. 1. Allen Press, Lawrence, Kansas.

Frost, D. R. 2021. Amphibian Species of the World: an Online Reference. https://amphibiansoftheworld.amnh.org/index.php (accessed 1 December 2021).

Gascon, C., J. P. Collins, R. D. Moore, D. R. Church, J. E. McKay, and J. R. Mendelson III (Eds.). 2007. Amphibian Conservation Action Plan. IUCN/SSC Amphibian Specialist Group. Gland, Switzerland and Cambridge, UK.

Geffeney, S. L., E. Fujimoto, E. D. Brodie III, E. D. Brodie Jr., and P. C. Ruben. 2005. Evolutionary diversification of TTX-resistant sodium channels in a predator–prey interaction. Nature 434:759–763.

Gerber, V. E. M., S. Wijenayake, and K. B. Storey. 2016. Anti-apoptotic response during anoxia and recovery in a freeze-tolerant wood frog (*Rana sylvatica*). PeerJ 4:e1834.

Gerhard, D. S., L. Wagner, E. A. Feingold, C. M. Shenmen, L. H. Grouse, G. Schuler, S. L. Klein, S. Old, R. Rasooly, P. Good, M. Guyer, A. M. Peck, J. G. Derge, D. Lipman . . . J. Malek. 2004. The status, quality, and expansion of the NIH full-length cDNA project: the Mammalian Gene Collection (MGC). Genome Research 14:2121–2127.

Getwan, M., and S. S. Lienkamp. 2017. Toolbox in a tadpole: *Xenopus* for kidney research. Cell and Tissue Research 369:143–157.

Goldspiel, H. B., J. B. Cohen, G. G. McGee, and J. P. Gibbs. 2019. Forest land-use history affects outcomes of habitat augmentation for amphibian conservation. Global Ecology and Conservation 19:e00686.

Gonçalves, J., J. P. Honrado, J. R. Vicente, and E. Civantos. 2016. A model-based framework for assessing the vulnerability of low dispersal vertebrates to landscape fragmentation under environmental change. Ecological Complexity 28:174–186.

Grant, E. H. C., D. A. W. Miller, B. R. Schmidt, M. J. Adams, S. M. Amburgey, T. Chambert, S. S. Cruickshank, R. N. Fisher, D. M. Green, B. R. Hossack, P. T. J. Johnson, M. B. Joseph, T. A. G. Rittenhouse, M. E. Ryan . . . E. Muths. 2016. Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. Scientific Reports 6:25625.

Green, D. M., M. J. Lannoo, D. Lesbarrères, and E. Muths. 2020. Amphibian population declines: 30 years of progress in confronting a complex problem. Herpetologica 76:97–100.

Greenspan, S. E., D. S. Bower, E. A. Roznik, D. A. Pike, G. Marantelli, R. A. Alford, L. Schwarzkopf, and B. R. Scheffers. 2017. Infection increases vulnerability to climate change via effects on host thermal tolerance. Scientific Reports 7:9349.

Grolemund, G., and H. Wickham. 2011. Dates and times made easy with lubridate. Journal of Statistical Software 40:1–25.

Grosso, J., J. Fratani, G. Fontanarrosa, M. Chuliver, A. S. Duport-Bru, R. G. Schneider, M. D. Casagranda, D. P. Ferraro, N. Vicente, M. J. Salica, L. Pereyra, R. G. Medina, C. Bessa, R. Semhan, and M. C. Vera. 2021. Male homophily in South American herpetology: one of the major processes underlying the gender gap in publications. Amphibia-Reptilia 42:407–418.

HAC. 2021. High Ambition Coalition for Nature and People. https://www.hacfornatureandpeople.org/hac-members (accessed 1 December 2021).

Hamer, A. J. 2016. Accessible habitat delineated by a highway predicts landscape-scale effects of habitat loss in an amphibian community. Landscape Ecology 31:2259–2274.

Hammond, S. A., R. L. Warren, B. P. Vandervalk, E. Kucuk, H. Khan, E. A. Gibb, P. Pandoh, H. Kirk, Y. Zhao, M. Jones, A. J. Mungall, R. Coope, S. Pleasance, R. A. Moore . . . I. Birol. 2017. The North American bullfrog draft genome provides insight into hormonal regulation of long noncoding RNA. Nature Communications 8:1433.

Harland, R. M., and R. M. Grainger. 2011. *Xenopus* research: metamorphosed by genetics and genomics. Trends in Genetics 27:507–515.

Heatwole, H. 1962. Environmental factors influencing local distribution and activity of the salamander, *Plethodon cinereus*. Ecology 43:460–472.

Hellsten, U., R. M. Harland, M. J. Gilchrist, D. Hendrix, J. Jurka, V. Kapitonov, I. Ovcharenko, N. H. Putnam, S. Shu, L. Taher, I. L. Blitz, B. Blumberg, D. S. Dichmann, I. Dubchak . . . D. S. Rokhsar. 2010. The genome of the Western clawed frog *Xenopus tropicalis*. Science 328:633–636.

Helmer, M., M. Schottdorf, A. Neef, and D. Battaglia. 2017. Gender bias in scholarly peer review. eLife 6:e21718.

Hime, P. M., A. R. Lemmon, E. C. M. Lemmon, E. Prendini, J. M. Brown, R. C. Thomson, J. D. Kratovil, B. P. Noonan, R. A. Pyron, P. L. V. Peloso, M. L. Kortyna, J. S. Keogh, S. C. Donnellan, R. L. Mueller . . . D. W. Weisrock. 2021. Phylogenomics reveals ancient gene tree discordance in the amphibian tree of life. Systematic Biology 70:49–66.

Hopkins, W. A., J. Congdon, and J. K. Ray. 2000. Incidence and impact of axial malformations in larval bullfrogs (*Rana catesbeiana*) developing in sites polluted by a coal-burning power plant. Environmental Toxicology and Chemistry 19:862–868.

Huang, J., A. J. Gates, R. Sinatra, and A. L. Barabási. 2020. Historical comparison of gender inequality in scientific careers across countries and disciplines. Proceedings of the National Academy of Sciences of the United States of America 117:4609–4616.

Hutter, C. R., K. A. Cobb, D. M. Portik, S. L. Travers, P. L. Wood Jr., and R. M. Brown. 2021. FrogCap: a modular sequence capture probe-set for phylogenomics and population genetics for all frogs, assessed across multiple phylogenetic scales. Molecular Ecology Resources 22:1100–1119.

IUCN. 2021. The IUCN Red List of Threatened Species. Version 2021–2. https://www.iucnredlist.org (accessed 1 December 2021).

Iwanowicz, D. D., W. B. Schill, D. H. Olson, M. J. Adams, C. Densmore, R. S. Cornman, C. Adams, J. Figiel, C. W. Anderson, A. R. Blaustein, and T. Chestnut. 2017. Potential concerns with analytical methods used for the detection of *Batrachochytrium salamandrivorans* from archived DNA of amphibian swab samples, Oregon, USA. Herpetological Review 48:352–355.

Jiang, K., F. Yan, K. Wang, D.-H. Zou, C. Li, and J. Che. 2016. A new genus and species of treefrog from Medog, southeastern Tibet, China (Anura, Rhacophoridae). Zoological Research 37:15–20.

Joanisse, D. R., and K. B. Storey. 1996. Oxidative damage and antioxidants in *Rana sylvatica*, the freeze-tolerant wood frog. The American Journal of Physiology 271: R545–R553.

Joven, A., A. Elewa, and A. Simon. 2019. Model systems for regeneration: salamanders. Development 146:dev167700.

Kamei, R. G., D. San Mauro, D. J. Gower, I. Van Bocxlaer, E. Sherratt, A. Thomas, S. Babu, F. Bossuyt, M. Wilkinson, and S. D. Biju. 2012. Discovery of a new family of amphibians from northeast India with ancient links to Africa. Proceedings of the Royal Society B: Biological Sciences 279:2396–2401.

Kerby, J. L., K. L. Richards-Hrdlicka, A. Storfer, and D. K. Skelly. 2010. An examination of amphibian sensitivity to environmental contaminants: are amphibians poor canaries? Ecology Letters 13:60–67.

Kerney, R. 2011. Embryonic staging table for a direct-developing salamander, *Plethodon cinereus* (Plethodontidae). Anatomical Record 294:1796–1808.

Kerney, R. R., D. C. Blackburn, H. Müller, and J. Hanken. 2012. Do larval traits re-evolve? Evidence from the embryogenesis of a direct-developing salamander, *Plethodon cinereus*. Evolution 66:252–262.

Kleeberger, S. R., and J. K. Werner. 1982. Home range and homing behavior of *Plethodon cinereus* in northern Michigan. Copeia 1982:409–415.

Klein, S. L., R. L. Strausberg, L. Wagner, J. Pontius, S. W. Clifton, and P. Richardson. 2002. Genetic and genomic tools for *Xenopus* research: the NIH *Xenopus* Initiative. Developmental Dynamics 225:384–391.

Knapp, R. A., G. M. Fellers, P. M. Kleeman, D. A. W. Miller, V. T. Vredenburg, E. B. Rosenblum, and C. J. Briggs. 2016. Large-scale recovery of an endangered amphibian despite ongoing exposure to multiple stressors. Proceedings of the National Academy of Sciences of the United States of America 113:11889–11894.

Koepfli, K. P., B. Paten, Genome 10K Community of Scientists, and S. J. O'Brien. 2015. The Genome 10K Project: a way forward. Annual Review of Animal Biosciences 3:57–111.

Koo, M. S., V. T. Vredenburg, J. B. Deck, D. H. Olson, K. L. Ronnenberg, and D. B. Wake. 2021. Tracking, synthesizing, and sharing global *Batrachochytrium* data at AmphibianDisease.org. Frontiers in Veterinary Science 8:728232.

Kosch, T. A., A. Bataille, C. Didinger, J. A. Eimes, S. Rodríguez-Brenes, M. J. Ryan, and B. Waldman. 2016. Major histocompatibility complex selection dynamics in pathogen-infected túngara frog (*Physalaemus pustulosus*) populations. Biology Letters 12:20160345.

Kosch, T. A., C. N. S. Silva, L. A. Brannelly, A. A. Roberts, Q. Lau, G. Marantelli, L. Berger, and L. F. Skerratt. 2019. Genetic potential for disease resistance in critically endangered amphibians decimated by chytridiomycosis. Animal Conservation 22:238–250.

Kriegman, S., D. Blackiston, M. Levin, and J. Bongard. 2021. Kinematic self-replication in reconfigurable organisms. Proceedings of the National Academy of Sciences of the United States of America 118:e2112672118.

Kubiak, L. 2020. Why the world must commit to protecting 30 percent of the planet by 2030 (30X30). National Resource Defense Council.

Lalremsanga, H. T., J. Purkayastha, L. Biakzuala, M. Vabeiryureilai, L. Murasanga, and G. Z. Hmar. 2021. A new striped species of *Ichthyophis fitzinger*, 1826 (Amphibia: Gymnophiona: Ichthyophiidae) from Mizoram, northeast India. Amphibian and Reptile Conservation 15:198–209.

Lambert, M. R., M. C. Womack, A. Q. Byrne, O. Hernández-Gómez, C. F. Noss, A. P. Rothstein, D. C. Blackburn, J. P. Collins, M. L. Crump, M. S. Koo, P. Nanjappa, L. Rollins-Smith, V. T. Vredenburg, and E. B. Rosenblum. 2020. Comment on "Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity." Science 367:eaay1838.

Lang, D. T. 2021. XML: tools for parsing and generating XML within R and S-Plus. https://CRAN.R-project.org/package=XML

Laufer, G., and N. Gobel. 2017. Habitat degradation and biological invasions as a cause of amphibian richness loss: a case report in Aceguá, Cerro Largo, Uruguay. Phyllomedusa: Journal of Herpetology 16:289–293.

Lefcort, H., R. A. Meguire, L. H. Wilson, and W. F. Ettinger. 1998. Heavy metals alter the survival, growth, metamorphosis, and antipredatory behavior of Columbia spotted frog (*Rana luteiventris*) tadpoles. Archives of Environmental Contamination and Toxicology 35:447–456.

Leinonen, R., H. Sugawara, and M. Shumway, on behalf of the International Nucleotide Sequence Database Collaboration. 2011. The sequence read archive. Nucleic Acids Research 39:D19–D21.

Lemmon, A. R., and E. M. Lemmon. 2012. High-throughput identification of informative nuclear loci for shallow-scale phylogenetics and phylogeography. Systematic Biology 61:745–761.

Levis, N. A., E. M. X. Reed, D. W. Pfennig, and M. O. Burford Reiskind. 2020. Identification of candidate loci for adaptive phenotypic plasticity in natural populations of spadefoot toads. Ecology and Evolution 10:8976–8988.

Levis, N. A., S. de la Serna Buzón, and D. W. Pfennig. 2015. An inducible offense: carnivore morph tadpoles induced by tadpole carnivory. Ecology and Evolution 5:1405–1411.

Liedtke, H. C., D. J. Gower, M. Wilkinson, and I. Gomez-Mestre. 2018. Macroevolutionary shift in the size of amphibian genomes and the role of life history and climate. Nature Ecology and Evolution 2:1792–1799.

Liévano-Latorre, L. F., R. A. da Silva, R. R. S. Vieira, F. M. Resende, B. R. Ribeiro, F. J. A. Borges, L. Sales, and R. Loyola. 2020. Pervasive gender bias in editorial boards of biodiversity conservation journals. Biological Conservation 251:108767.

Maas, B., R. J. Pakeman, L. Godet, L. Smith, V. Devictor, and R. Primack. 2021. Women and Global South strikingly underrepresented among top-publishing ecologists. Conservation Letters 14:e12797.

Magnus, R., and R. Rannap. 2019. Pond construction for threatened amphibians is an important conservation tool, even in landscapes with extant natural water bodies. Wetlands Ecology and Management 27:323–341.

Marshall, A. F., C. Bardua, D. J. Gower, M. Wilkinson, E. Sherratt, and A. Goswami. 2019. High-density three-dimensional morphometric analyses support conserved static (intraspecific) modularity in caecilian (Amphibia: Gymnophiona) crania. Biological Journal of the Linnean Society 126:721–742.

Martel, A., A. Spitzen-van der Sluijs, M. Blooi, W. Bert, R. Ducatelle, M. C. Fisher, A. Woeltjes, W. Bosman, K. Chiers, F. Bossuyt, and F. Pasmans. 2013. *Batrachochy-*

trium salamandrivorans sp. nov. causes lethal chytridiomycosis in amphibians. Proceedings of the National Academy of Sciences of the United States of America 110:15325–15329.

Mayani-Parás, F., F. Botello, S. Castañeda, and V. Sánchez-Cordero. 2019. Impact of habitat loss and mining on the distribution of endemic species of amphibians and reptiles in Mexico. Diversity 11:210.

McCaffery, R., C. L. Richards-Zawacki, and K. R. Lips. 2015. The demography of *Atelopus* decline: Harlequin frog survival and abundance in central Panama prior to and during a disease outbreak. Global Ecology and Conservation 4:232–242.

McCoy, K. A., and A. L. Peralta. 2018. Pesticides could alter amphibian skin microbiomes and the effects of *Batrachochytrium dendrobatidis*. Frontiers in Microbiology 9:748.

Mendoza-Henao, A. M., Á. M. Cortes-Gomez, M. A. Gonzalez, O. D. Hernandez-Córdoba, A. R. Acosta-Galvis, F. Castro-Herrera, J. M. Daza, J. M. Hoyos, M. P. Ramirez-Pinilla, N. Urbina-Cardona, and B. Salgado-Negret. 2019. A morphological database for Colombian anuran species from conservation-priority ecosystems. Ecology 100:e02685.

Meredith, H., C. Van Buren, and R. E. Antwis. 2016. Making amphibian conservation more effective. Conservation Evidence 13:1–6.

Moore, C. E., J. S. Helmann, Y. Chen, S. M. St. Amour, M. A. Hallmark, L. E. Hughes, N. Wax, and M. C. Mims. 2021. Anuran Traits of the United States (ATraiU): a database for anuran traits-based conservation, management, and research. Ecology 102:e03261.

Murphy, R. W. 2016. Advances in herpetological research emanating from China. Zoological Research 37:4–6.

NCBI Resource Coordinators. 2016. Database resources of the National Center for Biotechnology Information. Nucleic Acids Research 44:D7–D19.

Nowakowski, A. J., L. O. Frishkoff, M. E. Thompson, T. M. Smith, and B. D. Todd. 2018a. Phylogenetic homogenization of amphibian assemblages in human-altered habitats across the globe. Proceedings of the National Academy of Sciences of the United States of America 115:E3454–E3462.

Nowakowski, A. J., J. I. Watling, M. E. Thompson, G. A. Brusch IV, A. Catenazzi, S. M. Whitfield, D. J. Kurz, Á. Suárez-Mayorga, A. Aponte-Gutiérrez, M. A. Donnelly, and B. D. Todd. 2018b. Thermal biology mediates responses of amphibians and reptiles to habitat modification. Ecology Letters 21:345–355.

Nowakowski, A. J., S. M. Whitfield, E. A. Eskew, M. E. Thompson, J. P. Rose, B. L. Caraballo, J. L. Kerby, M. A. Donnelly, and B. D. Todd. 2016. Infection risk decreases with increasing mismatch in host and pathogen environmental tolerances. Ecology Letters 19:1051–1061.

Nowoshilow, S., S. Schloissnig, J.-F. Fei, A. Dahl, A. W. C. Pang, M. Pippel, S. Winkler, A. R. Hastie, G. Young, J. G. Roscito, F. Falcon, D. Knapp, S. Powell, A. Cruz . . . E. W. Myers. 2018. The axolotl genome and the evolution of key tissue formation regulators. Nature 554:50–55.

Nürnberger, B., K. Lohse, A. Fijarczyk, J. M. Szymura, and M. L. Blaxter. 2016. Para-allopatry in hybridizing fire-bellied toads (*Bombina bombina* and *B. variegata*): inference from transcriptome-wide coalescence analyses. Evolution 70:1803–1818.

Nye, H. L. D., J. A. Cameron, E. A. G. Chernoff, and D. L. Stocum. 2003. Regeneration of the urodele limb: a review. Developmental Dynamics 226:280–294.

O'Connell, L. A. 2020. Frank Beach Award Winner: lessons from poison frogs on ecological drivers of behavioral diversification. Hormones and Behavior 126:104869.

Oliveira, B. F., V. A. São-Pedro, G. Santos-Barrera, C. Penone, and G. C. Costa. 2017. AmphiBIO, a global database for amphibian ecological traits. Scientific Data 4: 170123.

Olson, D. H., D. M. Aanensen, K. L. Ronnenberg, C. I. Powell, S. F. Walker, J. Bielby, T. W. J. Garner, G. Weaver, Bd Mapping Group, and M. C. Fisher. 2013. Mapping the global emergence of *Batrachochytrium dendrobatidis*, the amphibian chytrid fungus. PLoS ONE 8:e56802.

Olson, D. H., K. L. Ronnenberg, C. K. Glidden, K. R. Christiansen, and A. R. Blaustein. 2021. Global patterns of the fungal pathogen *Batrachochytrium dendrobatidis* support conservation urgency. Frontiers in Veterinary Science 8:685877.

Páez, N. B., and S. R. Ron. 2019. Systematics of *Huicundomantis*, a new subgenus of *Pristimantis* (Anura, Strabomantidae) with extraordinary cryptic diversity and eleven new species. ZooKeys 868:1–112.

Palomar, G., J. Bosch, and J. M. Cano. 2016. Heritability of *Batrachochytrium dendrobatidis* burden and its genetic correlation with development time in a population of Common toad (*Bufo spinosus*). Evolution 70:2346–2356.

Paluh, D. J., K. Riddell, C. M. Early, M. M. Hantak, G. F. Jongsma, R. M. Keeffe, F. Magalhães Silva, S. V. Nielsen, M. C. Vallejo-Pareja, E. L. Stanley, and D. C. Blackburn. 2021. Rampant tooth loss across 200 million years of frog evolution. eLife 10:e66926.

Paradis, E., and K. Schliep. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35:526–528.

Parrott, J. C., A. Shepack, D. Burkart, B. LaBumbard, P. Scimè, E. Baruch, and A. Catenazzi. 2017. Survey of pathogenic chytrid fungi (*Batrachochytrium dendrobatidis* and *B. salamandrivorans*) in salamanders from three mountain ranges in Europe and the Americas. EcoHealth 14:296–302.

Pennell, M. W., J. M. Eastman, G. J. Slater, J. W. Brown, J. C. Uyeda, R. G. FitzJohn, M. E. Alfaro, and L. J. Harmon. 2014. geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. Bioinformatics 30:2216–2218.

Phillips, S. J., R. P. Anderson, M. Dudík, R. E. Schapire, and M. E. Blair. 2017. Opening the black box: an open-source release of Maxent. Ecography 40:887–893.

Pollet, I., and L. I. Bendell-Young. 2000. Amphibians as indicators of wetland quality in wetlands formed from oil sands effluent. Environmental Toxicology and Chemistry 19:2589–2597.

Portik, D. M., L. L. Smith, and K. Bi. 2016. An evaluation of transcriptome-based exon capture for frog phylogenomics across multiple scales of divergence (class: Amphibia, order: Anura). Molecular Ecology Resources 16:1069–1083.

Powers, R. P., and W. Jetz. 2019. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nature Climate Change 9:323–329.

Poyarkov, N. A., Jr., C. Suwannapoom, P. Pawangkhanant, A. Aksornneam, T. Van Duong, D. V. Korost, and J. Che.

2018. A new genus and three new species of miniaturized microhylid frogs from Indochina (Amphibia: Anura: Microhylidae: Asterophryinae). Zoological Research 39: 130–157.

QGIS Development Team. 2021. QGIS Geographic Information System. QGIS Association. https://www.qgis.org

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Randhawa, S. S., and R. Pawar. 2021. Fish genomes: sequencing trends, taxonomy and influence of taxonomy on genome attributes. Journal of Applied Ichthyology 37: 553–562.

Reeder, A. L., G. L. Foley, D. K. Nichols, L. G. Hansen, B. Wikoff, S. Faeh, J. Eisold, M. B. Wheeler, R. Warner, J. E. Murphy, and V. R. Beasley. 1998. Forms and prevalence of intersexuality and effects of environmental contaminants on sexuality in cricket frogs (*Acris crepitans*). Environmental Health Perspectives 106:261–266.

Reeves, R. A., C. L. Pierce, K. L. Smalling, R. W. Klaver, M. W. Vandever, W. A. Battaglin, and E. Muths. 2016. Restored agricultural wetlands in central Iowa: habitat quality and amphibian response. Wetlands 36:101–110.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Richgels, K. L. D., R. E. Russell, M. J. Adams, C. L. White, and E. H. C. Grant. 2016. Spatial variation in risk and consequence of *Batrachochytrium salamandrivorans* introduction in the USA. Royal Society Open Science 3:150616.

Rock, K. N., I. N. Barnes, M. S. Deyski, K. A. Glynn, B. N. Milstead, M. E. Rottenborn, N. S. Andre, A. Dekhtyar, O. Dekhtyar, and E. N. Taylor. 2021. Quantifying the gender gap in authorship in herpetology. Herpetologica 77:1–13.

Roland, A. B., and L. A. O'Connell. 2015. Poison frogs as a model system for studying the neurobiology of parental care. Current Opinion in Behavioral Sciences 6:76–81.

Rollins-Smith, L. A. 2017. Amphibian immunity—stress, disease, and climate change. Developmental and Comparative Immunology 66:111–119.

Rozenblit, F., and T. Gollisch. 2020. What the salamander eye has been telling the vision scientist's brain. Seminars in Cell and Developmental Biology 106:61–71.

Ryan, M. J., J. H. Fox, W. Wilczynski, and A. S. Rand. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. Nature 343:66–67.

Salerno, P. E., M. Páez-Vacas, J. M. Guayasamin, and J. L. Stynoski. 2019. Male principal investigators (almost) don't publish with women in ecology and zoology. PLoS ONE 14:e0218598.

Saporito, R. A., M. A. Donnelly, T. F. Spande, and H. M. Garraffo. 2012. A review of chemical ecology in poison frogs. Chemoecology 22:159–168.

Savage, A. E., and K. R. Zamudio. 2016. Adaptive tolerance to a pathogenic fungus drives major histocompatibility complex evolution in natural amphibian populations. Proceedings of the Royal Society B: Biological Sciences 283:20153115.

Scheele, B. C., D. A. Hunter, S. C. Banks, J. C. Pierson, L. F. Skerratt, R. Webb, and D. A. Driscoll. 2016. High adult mortality in disease-challenged frog populations increases vulnerability to drought. Journal of Animal Ecology 85: 1453–1460.

Scheele, B. C., F. Pasmans, L. F. Skerratt, L. Berger, A. Martel, W. Beukema, A. A. Acevedo, P. A. Burrowes, T. Carvalho, A. Catenazzi, I. De la Riva, M. C. Fisher, S. V. Flechas, C. N. Foster . . . S. Canessa. 2019. Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. Science 363:1459–1463.

Scherz, M. D., C. R. Hutter, A. Rakotoarison, J. C. Riemann, M.-O. Rödel, S. H. Ndriantsoa, J. Glos, S. Hyde Roberts, A. Crottini, M. Vences, and F. Glaw. 2019. Morphological and ecological convergence at the lower size limit for vertebrates highlighted by five new miniaturised microhylid frog species from three different Madagascan genera. PLoS ONE 14:e0213314.

Schmeller, D. S., R. Utzel, F. Pasmans, and A. Martel. 2020. *Batrachochytrium salamandrivorans* kills alpine newts (*Ichthyosaura alpestris*) in southernmost Germany. Salamandra 56:230–232.

Schmidt, B. R., C. Bozzuto, S. Lötters, and S. Steinfartz. 2017. Dynamics of host populations affected by the emerging fungal pathogen *Batrachochytrium salamandrivorans*. Royal Society Open Science 4:160801.

Schneider-Maunoury, L., V. Lefebvre, R. M. Ewers, G. F. Medina-Rangel, C. A. Peres, E. Somarriba, N. Urbina-Cardona, and M. Pfeifer. 2016. Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forest landscapes. Biological Conservation 200:207–215.

Seimon, T. A., A. Seimon, K. Yager, K. Reider, A. Delgado, P. Sowell, A. Tupayachi, B. Konecky, D. McAloose, and S. Halloy. 2017. Long-term monitoring of tropical alpine habitat change, Andean anurans, and chytrid fungus in the Cordillera Vilcanota, Peru: results from a decade of study. Ecology and Evolution 7:1527–1540.

Session, A. M., Y. Uno, T. Kwon, J. A. Chapman, A. Toyoda, S. Takahashi, A. Fukui, A. Hikosaka, A. Suzuki, M. Kondo, S. J. van Heeringen, I. Quigley, S. Heinz, H. Ogino . . . D. S. Rokhsar. 2016. Genome evolution in the allotetraploid frog *Xenopus laevis*. Nature 538:336–343.

Shen, X. X., D. Liang, Y. J. Feng, M. Y. Chen, and P. Zhang. 2013. A versatile and highly efficient toolkit including 102 nuclear markers for vertebrate phylogenomics, tested by resolving the higher level relationships of the Caudata. Molecular Biology and Evolution 30:2235–2248.

Silbiger, N. J., and A. D. Stubler. 2019. Unprofessional peer reviews disproportionately harm underrepresented groups in STEM. PeerJ 7:e8247.

Simpkins, C. A., J. G. Castley, J. D. Shuker, C. Morrison, and J.-M. Hero. 2021. Battling habitat loss: suitability of anthropogenic waterbodies for amphibians associated with naturally acidic, oligotrophic environments. Pacific Conservation Biology 28:174–183.

Smart, U., G. C. Sarker, U. Arifin, M. B. Harvey, I. Sidik, A. Hamidy, N. Kurniawan, and E. N. Smith. 2017. A new genus and two new species of arboreal toads from the highlands of Sumatra with a phylogeny of Sundaland toad genera. Herpetologica 73:63–75.

Spitzen-van der Sluijs, A., A. Martel, J. Asselberghs, E. K. Bales, W. Beukema, M. C. Bletz, L. Dalbeck, E. Goverse, A. Kerres, T. Kinet, K. Kirst, A. Laudelout, L. F. Marin da Fonte, A. Nöllert . . . S. Lötters. 2016. Expanding distribution of lethal amphibian fungus *Batrachochytrium salamandrivorans* in Europe. Emerging Infectious Diseases 22:1286–1288.

Stegen, G., F. Pasmans, B. R. Schmidt, L. O. Rouffaer, S. Van Praet, M. Schaub, S. Canessa, A. Laudelout, T. Kinet, C. Adriaensen, F. Haesebrouck, W. Bert, F. Bossuyt, and A. Martel. 2017. Drivers of salamander extirpation mediated by *Batrachochytrium salamandrivorans*. Nature 544: 353–356.

Streicher, J. W., E. C. Miller, P. C. Guerrero, C. Correa, J. C. Ortiz, A. J. Crawford, M. R. Pie, and J. J. Wiens. 2018. Evaluating methods for phylogenomic analyses, and a new phylogeny for a major frog clade (Hyloidea) based on 2214 loci. Molecular Phylogenetics and Evolution 119:128–143.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

Subba, B., S. Sen, G. Ravikanth, and M. P. Nobis. 2018. Direct modelling of limited migration improves projected distributions of Himalayan amphibians under climate change. Biological Conservation 227:352–360.

Sun, Y.-B., T.-T. Fu, J.-Q. Jin, R. W. Murphy, D. M. Hillis, Y.-P. Zhang, and J. Che. 2018. Species groups distributed across elevational gradients reveal convergent and continuous genetic adaptation to high elevations. Proceedings of the National Academy of Sciences of the United States of America 115:E10634–E10641.

Sun, Y.-B., Z.-J. Xiong, X.-Y. Xiang, S.-P. Liu, W.-W. Zhou, X.-L. Tu, L. Zhong, L. Wang, D.-D. Wu, B.-L. Zhang, C.-L. Zhu, M.-M. Yang, H.-M. Chen, F. Li . . . Y.-P. Zhang. 2015. Whole-genome sequence of the Tibetan frog *Nanorana parkeri* and the comparative evolution of tetrapod genomes. Proceedings of the National Academy of Sciences of the United States of America 112:E1257–E1262.

Sun, Y.-B., Y. Zhang, and K. Wang. 2020. Perspectives on studying molecular adaptations of amphibians in the genomic era. Zoological Research 41:351–364.

Suwannapoom, C., M. Sumontha, J. Tunprasert, T. Ruangsuwan, P. Pawangkhanant, D. V. Korost, and N. A. Poyarkov. 2018. A striking new genus and species of cave-dwelling frog (Amphibia: Anura: Microhylidae: Asterophryinae) from Thailand. PeerJ 6:e4422.

Suzuki, S., K. Awai, A. Ishihara, and K. Yamauchi. 2016. Cold temperature blocks thyroid hormone-induced changes in lipid and energy metabolism in the liver of *Lithobates catesbeianus* tadpoles. Cell and Bioscience 6:19.

Tarvin, R. D., C. M. Borghese, W. Sachs, J. C. Santos, Y. Lu, L. A. O'Connell, D. C. Cannatella, R. A. Harris, and H. H. Zakon. 2017. Interacting amino acid replacements allow poison frogs to evolve epibatidine resistance. Science 357: 1261–1266.

Thein, J., U. Reck, C. Dittrich, A. Martel, V. Schulz, and G. Hansbauer. 2020. Preliminary report on the occurrence of *Batrachochytrium salamandrivorans* in the Steigerwald, Bavaria, Germany. Salamandra 56:227–229.

Thompson, M. E., and M. A. Donnelly. 2018. Effects of secondary forest succession on amphibians and reptiles: a review and meta-analysis. Copeia 106:10–19.

Thompson, M. E., A. J. Nowakowski, and M. A. Donnelly. 2016. The importance of defining focal assemblages when evaluating amphibian and reptile responses to land use. Conservation Biology 30:249–258.

Tomkins, A., M. Zhang, and W. D. Heavlin. 2017. Reviewer bias in single- versus double-blind peer review. Proceedings of the National Academy of Sciences of the United States of America 114:12708–12713.

Trochet, A., S. Moulherat, O. Calvez, V. M. Stevens, J. Clobert, and D. S. Schmeller. 2014. A database of life-history traits of European amphibians. Biodiversity Data Journal 2:e4123.

Uetz, P., M. S. Koo, R. Aguilar, E. Brings, A. Catenazzi, A. T. Chang, and D. B. Wake. 2021. A quarter century of reptile and amphibian databases. Herpetological Review 52:246–255.

Urbina-Blanco, C. A., S. Z. Jilani, I. R. Speight, M. J. Bojdys, T. Friščić, J. F. Stoddart, T. L. Nelson, J. Mack, R. A. S. Robinson, E. A. Waddell, J. L. Lutkenhaus, M. Godfrey, M. I. Abboud, S. O. Aderinto . . . Y.-W. Yang. 2020. A diverse view of science to catalyse change. Journal of the American Chemical Society 142:14393–14396.

Vasconcelos, T. S., F. R. da Silva, T. G. dos Santos, V. H. M. Prado, and D. B. Provete. 2019. South American anurans: species diversity and description trends through time and space, p. 9–84. *In*: Biogeographic Patterns of South American Anurans. T. S. Vasconcelos, F. R. da Silva, T. G. dos Santos, V. H. M. Prado, and D. B. Provete (eds.). Springer International Publishing, Cham.

Vences, M., and S. Lötters. 2020. The salamander plague in Europe—a German perspective. Salamandra 56:169–171.

Vijayakumar, S. P., R. A. Pyron, K. P. Dinesh, V. R. Torsekar, A. N. Srikanthan, P. Swamy, E. L. Stanley, D. C. Blackburn, and K. Shanker. 2019. A new ancient lineage of frog (Anura: Nyctibatrachidae: Astrobatrachinae subfam. nov.) endemic to the Western Ghats of Peninsular India. PeerJ 7:e6457.

Voyles, J., D. C. Woodhams, V. Saenz, A. Q. Byrne, R. Perez, G. Rios-Sotelo, M. J. Ryan, M. C. Bletz, F. A. Sobell, S. McLetchie, L. Reinert, E. B. Rosenblum, L. A. Rollins-Smith, R. Ibáñez . . . C. L. Richards-Zawacki. 2018. Shifts in disease dynamics in a tropical amphibian assemblage are not due to pathogen attenuation. Science 359:1517–1519.

Waddle, J. H., D. A. Grear, B. A. Mosher, E. H. C. Grant, M. J. Adams, A. R. Backlin, W. J. Barichivich, A. B. Brand, G. M. Bucciarelli, D. L. Calhoun, T. Chestnut, J. M. Davenport, A. E. Dietrich, R. N. Fisher . . . M. E. Winzeler. 2020. *Batrachochytrium salamandrivorans* (Bsal) not detected in an intensive survey of wild North American amphibians. Scientific Reports 10:13012.

Wake, D. B., and M. S. Koo. 2018. Amphibians. Current Biology 28:R1237–R1241.

Wake, D. B., and V. T. Vredenburg. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences of the United States of America 105:11466–11473.

Wang, G.-D., B.-L. Zhang, W.-W. Zhou, Y.-X. Li, J.-Q. Jin, Y. Shao, H.-C. Yang, Y.-H. Liu, F. Yan, H.-M. Chen, L. Jin, F. Gao, Y. Zhang, H. Li . . . J. Che. 2018. Selection and environmental adaptation along a path to speciation in the Tibetan frog *Nanorana parkeri*. Proceedings of the National Academy of Sciences of the United States of America 115: E5056–E5065.

Warren, R., J. VanDerWal, J. Price, J. A. Welbergen, I. Atkinson, J. Ramirez-Villegas, T. J. Osborn, A. Jarvis, L. P. Shoo, S. E. Williams, and J. Lowe. 2013. Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. Nature Climate Change 3:678–682.

Wells, D. E., L. Gutierrez, Z. Xu, V. Krylov, J. Macha, K. P. Blankenburg, M. Hitchens, L. J. Bellot, M. Spivey, D. L. Stemple, A. Kowis, Y. Ye, S. Pasternak, J. Owen . . . A. K. Satera. 2011. A genetic map of *Xenopus tropicalis*. Developmental Biology 354:1–8.

Wickham, H. 2007. Reshaping data with the reshape package. Journal of Statistical Software 21:1–20.

Wickham, H. 2010. Stringr: modern, consistent string processing. The R Journal 2:38.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag, New York.

Wickham, H. 2017. tidyr: easily tidy data with spread and gather functions. https://CRAN.R-project.org/package=tidyr

Wickham, H., M. Averick, J. Bryan, W. Chang, L. D'Agostino McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, M. Kuhn, T. L. Pedersen, E. Miller, S. M. Bache . . . H. Yutani. 2019. Welcome to the tidyverse. Journal of Open Source Software 4:1686.

Wickham, H., R. François, L. Henry, and K. Müller. 2021. dplyr: a grammar of data manipulation. https://dplyr.tidyverse.org, https://github.com/tidyverse/dplyr

Wilke, C. O. 2020. cowplot: streamlined plot theme and plot annotations for "ggplot2". R package version 0.9.2. https://CRAN.R-project.org/package=cowplot

Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. Ecology 95:2027–2027.

Wilson, D. S. 1998. Patterns in publishing in three north American herpetological journals: gender biases. Herpetologica 54(Suppl.):S35–S42.

Winter, D. 2017. rentrez: an R package for the NCBI eUtils API. The R Journal 9:520.

Wyman, R. L., and D. S. Hawksley-Lescault. 1987. Soil acidity affects distribution, behavior, and physiology of the salamander *Plethodon cinereus*. Ecology 68:1819–1827.

Yakushiji, N., H. Yokoyama, and K. Tamura. 2009. Repatterning in amphibian limb regeneration: a model for study of genetic and epigenetic control of organ regeneration. Seminars in Cell and Developmental Biology 20:565–574.

Yap, T. A., N. T. Nguyen, M. Serr, A. Shepack, and V. T. Vredenburg. 2017. *Batrachochytrium salamandrivorans* and the risk of a second amphibian pandemic. EcoHealth 14: 851–864.

Yuan, Z.-Y., B.-L. Zhang, C. J. Raxworthy, D. W. Weisrock, P. M. Hime, J.-Q. Jin, E. M. Lemmon, A. R. Lemmon, S. D. Holland, M. L. Kortyna, W.-W. Zhou, M.-S. Peng, J. Che, and E. Prendini. 2018. Natatanuran frogs used the Indian Plate to step-stone disperse and radiate across the Indian Ocean. National Science Review 6:10–14.

Zellmer, A. J., P. Slezak, and T. S. Katz. 2020. Clearing up the crystal ball: understanding uncertainty in future climate suitability projections for amphibians. Herpetologica 76:108–120.

Zipkin, E. F., G. V. DiRenzo, J. M. Ray, S. Rossman, and K. R. Lips. 2020. Tropical snake diversity collapses after widespread amphibian loss. Science 367:814–816.