WILDLIFE DISEASE

Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity

Ben C. Scheele^{1,2,3*}, Frank Pasmans⁴, Lee F. Skerratt³, Lee Berger³, An Martel⁴, Wouter Beukema⁴, Aldemar A. Acevedo^{5,6}, Patricia A. Burrowes⁷, Tamilie Carvalho⁸, Alessandro Catenazzi⁹, Ignacio De la Riva¹⁰, Matthew C. Fisher¹¹, Sandra V. Flechas^{12,13}, Claire N. Foster¹, Patricia Frías-Álvarez³, Trenton W. J. Garner^{14,15}, Brian Gratwicke¹⁶, Juan M. Guayasamin^{17,18,19}, Mareike Hirschfeld²⁰, Jonathan E. Kolby^{3,21,22}, Tiffany A. Kosch^{3,23}, Enrique La Marca²⁴, David B. Lindenmayer^{1,2}, Karen R. Lips²⁵, Ana V. Longo²⁶, Raúl Maneyro²⁷, Cait A. McDonald²⁸, Joseph Mendelson III^{29,30}, Pablo Palacios-Rodriguez¹², Gabriela Parra-Olea³¹, Corinne L. Richards-Zawacki³², Mark-Oliver Rödel²⁰, Sean M. Rovito³³, Claudio Soto-Azat³⁴, Luís Felipe Toledo⁸, Jamie Voyles³⁵, Ché Weldon¹⁵, Steven M. Whitfield^{36,37}, Mark Wilkinson³⁸, Kelly R. Zamudio²⁸, Stefano Canessa⁴

Anthropogenic trade and development have broken down dispersal barriers, facilitating the spread of diseases that threaten Earth's biodiversity. We present a global, quantitative assessment of the amphibian chytridiomycosis panzootic, one of the most impactful examples of disease spread, and demonstrate its role in the decline of at least 501 amphibian species over the past half-century, including 90 presumed extinctions. The effects of chytridiomycosis have been greatest in large-bodied, range-restricted anurans in wet climates in the Americas and Australia. Declines peaked in the 1980s, and only 12% of declined species show signs of recovery, whereas 39% are experiencing ongoing decline. There is risk of further chytridiomycosis outbreaks in new areas. The chytridiomycosis panzootic represents the greatest recorded loss of biodiversity attributable to a disease.

ighly virulent wildlife diseases are contributing to Earth's sixth mass extinction (1). One of these is chytridiomycosis, which has caused mass amphibian die-offs worldwide (2, 3). Chytridiomycosis is caused by two fungal species, Batrachochytrium dendrobatidis [discovered in 1998, (4)] and B. salamandrivorans [discovered in 2013, (5)]. Both Batrachochytrium species likely originated in Asia, and their recent spread has been facilitated by humans (5, 6). Twenty years after the discovery of chytridio-

mycosis, substantial research has yielded insights about its epidemiology (2, 3, 7, 8), yet major knowledge gaps remain. First, the global extent of species declines associated with chytridiomycosis is unknown [see (2, 9) for initial assessments]. Second, although some regional declines are well studied, global spatial and temporal patterns of chytridiomycosis impacts remain poorly quantified. Third, ecological and life history traits have been examined only for a portion of declined species (10, 11). Finally, after initial declines, it is

unknown what proportion of declined species exhibit recovery, stabilize at lower abundance, or continue to decline. Here we present a global epidemiological analysis of the spatial and temporal extent of amphibian biodiversity loss caused by chytridiomycosis.

We conducted a comprehensive examination of evidence from multiple sources, including the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (12), peerreviewed literature, and consultation with amphibian experts worldwide (data S1). We classified declined species into five decline-severity categories corresponding to reductions in abundance. Species declines were attributed to chytridiomycosis on the basis of diagnosis of infection causing mortalities in the wild or, if this was unavailable, evidence consistent with key epidemiological characteristics of this disease. Most evidence is retrospective because many species declined before the discovery of chytridiomycosis (data S1).

We conservatively report that chytridiomycosis has contributed to the decline of at least 501 amphibian species (6.5% of described amphibian species; Figs. 1 and 2). This represents the greatest documented loss of biodiversity attributable to a pathogen and places B. dendrobatidis among the most destructive invasive species, comparable to rodents (threatening 420 species) and cats (Felis catus) (threatening 430 species) (13). Losses associated with chytridiomycosis are orders of magnitude greater than for other high-profile wildlife pathogens, such as white-nose syndrome (Pseudogymnoascus destructans) in bats (six species) (14) or West Nile virus (Flavivirus sp.) in birds (23 species) (15). Of the 501 declined amphibian species, 90 (18%) are confirmed or presumed extinct in the wild, with a further 124 (25%) experiencing a >90% reduction in abundance (Figs. 1 and 2). The declines of all species except one (Salamandra salamandra affected by B. salamandrivorans) were attributed to B. dendrobatidis.

Declines were proportional to taxonomic abundance, with anurans having 93% of severe

¹Fenner School of Environment and Society, Australian National University, Canberra, ACT 2601, Australia. ²National Environmental Science Programme, Threatened Species Recovery Hub, Canberra, ACT 2601, Australia. ³One Health Research Group, Melbourne Veterinary School, The University of Melbourne, Werribee, VIC 3030, Australia. ⁴Wildlife Health Ghent, Department of Pathology, Bacteriology, and Avian Diseases, Faculty of Veterinary Medicine, Ghent University, B-9820 Merelbeke, Belgium. ⁵Programa de Doctorado en Ciencias Biológicas, Laboratorio de Biología Evolutiva, Pontificia Universidad Católica de Chile, Avenida Libertador Bernardo O'Higgins 340, Santiago, Chile. 6Grupo de Investigación en Ecología y Biogeografía, Universidad de Pamplona, Barrio El Buque, Km 1, Vía a Bucaramanga, Pamplona, Colombia. Department of Biology, University of Puerto Rico, P.O. Box 23360, San Juan, Puerto Rico. Laboratório de História Natural de Anfibios Brasileiros (LaHNAB), Departamento de Biologia Animal, Instituto de Biologia, Üniversidade Estadual de Campinas, Campinas, Brazil. Departamento de Biologia Animal, Instituto de Biologia, Üniversidade Estadual de Campinas, Campinas, Brazil. Florida International University, Miami, FL 33199, USA. 10 Museo Nacional de Ciencias Naturales-CSIC, C/ José Gutiérrez Abascal 2, Madrid 28006, Spain. 11 MRC Centre for Global Infectious Disease Analysis, School of Public Health, Imperial College London, London W2 IPG, UK. ¹²Department of Biological Sciences, Universidad de los Andes, Bogotá, Colombia. ¹³Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Sede Venado de Oro, Paseo Bolívar 16-20, Bogotá, Colombia. ¹⁴Institute of Zoology, Zoological Society London, Regents Park, London NW1 4RY, UK. ¹⁵Unit for Environmental Sciences and Management, North-West University, Potchefstroom 2520, South Africa. ¹⁶Smithsonian National Zoological Park and Conservation Biology Institute, Washington, DC 20008, USA. ¹⁷Universidad San Francisco de Quito USFQ, Colegio de Ciencias Biológicas y Ambientales COCIBA, Instituto de Investigaciones Biológicas y Ambientales BIOSFERA, Laboratorio de Biología Evolutiva, Campus Cumbayá, Quito, Ecuador. 18 Centro de Investigación de la Biodiversidad y Cambio Climático (BioCamb), Ingeniería en Biodiversidad y Cambio Climático, Facultad de Medio Ambiente, Universidad Tecnológica Indoamérica, Calle Machala y Sabanilla, Quito, Ecuador. 19 Department of Biology, Colorado State University, Fort Collins, CO 80523, USA. 20 Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstr. 43, Berlin 10115, Germany. 21 Honduras Amphibian Rescue and Conservation Center, Lancetilla Botanical Garden and Research Center, Tela, Honduras. ²²The Conservation Agency, Jamestown, RI 02835, USA. ²³AL Rae Centre for Genetics and Breeding, Massey University, Palmerston North 4442, New Zealand. ²⁴School of Geography, Faculty of Forestry Engineering and Environmental Sciences, University of Los Andes, Merida, Venezuela. ²⁵Department of Biology, University of Maryland, College Park, MD 20742, USA. ²⁶Department of Biology, University of Florida, Gainesville, FL 32611, USA. ²⁷Laboratorio de Sistemática e Historia Natural de Vertebrados. Facultad de Ciencías, Universidad de la República. Igua 4225, CP 11400, Montevideo, Uruguay. 28 Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA. ²⁹Zoo Atlanta, Atlanta, GA 30315, USA. ³⁰School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA 30332, USA. ³¹Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, México. 32 Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, USA. 33 Unidad de Genómica Avanzada (Langebio), Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, km 9.6 Libramiento Norte Carretera Irapuato-León, Irapuato, Guanajuato CP36824, México. ³⁴Centro de Investigación para la Sustentabilidad, Facultad de Ciencias de la Vida, Universidad Andres Bello, Santiago 8370251, Chile. ³⁵Department of Biology, University of Nevada, Reno, NV 89557, USA. 36Zoo Miami, Conservation and Research Department, Miami, FL 33177, USA. 37Florida International University School of Earth, Environment, and Society, 11200 SW 8th St., Miami, FL 33199, USA. 38 Department of Life Sciences, The Natural History Museum, London SW7 5BD, UK. *Corresponding author. Email: ben.scheele@anu.edu.au

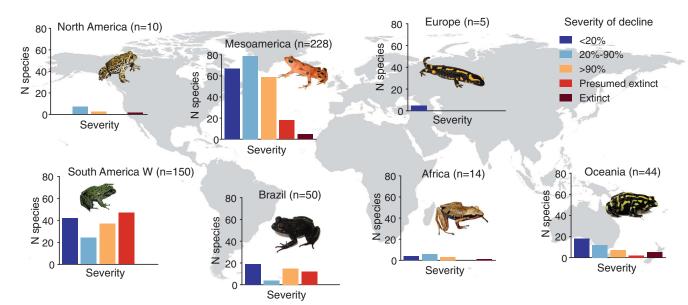


Fig. 1. Global distribution of chytridiomycosis-associated amphibian species declines. Bar plots indicate the number (N) of declined species, grouped by continental area and classified by decline severity. Brazilian species are plotted separately from all other South American species (South America W); Mesoamerica includes Central America, Mexico, and the Caribbean Islands; and Oceania includes Australia and New Zealand.

No declines have been reported in Asia. n, total number of declines by region. [Photo credits (clockwise from top left): Anaxyrus boreas, C. Brown, U.S. Geological Survey; Atelopus varius, B.G.; Salamandra salamandra, D. Descouens, Wikimedia Commons; Telmatobius sanborni, I.D.I.R; Cycloramphus boraceiensis, L.F.T.; Cardioglossa melanogaster, M.H.; and Pseudophryne corroboree, C. Doughty]

declines (they comprise 89% of all amphibian species). Within anurans, there has been marked taxonomic clustering of declines, with 45% of severe declines and extinctions occurring in the Neotropical genera Atelopus, Craugastor, and Telmatobius (Fig. 2) (16). Chytridiomycosis is lethal to caecilians (17), but there have been no caecilian declines due to the disease, although data are limited. The capacity for B. dendrobatidis to cause major declines is attributable to its maintenance of high pathogenicity (2, 18), broad host range (8), high transmission rate within and among host species (2, 7), and persistence in reservoir host species and the environment (19). For many species, chytridiomycosis is the principal driver of decline, exemplified by precipitous mass mortalities in undisturbed environments (2). In other species, chytridiomycosis acts in concert with habitat loss, altered climatic conditions, and invasive species to exacerbate species declines (20).

Most amphibian declines have occurred in the tropics of Australia, Mesoamerica, and South America (Fig. 1), supporting the hypothesis that B. dendrobatidis spread from Asia into the New World (6). Asia, Africa, Europe, and North America have had notably low numbers of declines attributable to chytridiomycosis, despite widespread occurrence of B. dendrobatidis (8). Relative lack of documented declines could reflect less knowledge of amphibian populations in Asia and Africa (3, 21), early introduction and potential coevolution of amphibians and B. dendrobatidis in parts of Africa and the Americas [e.g., (22)], the comparatively recent emergence of B. dendrobatidis in Western and Northeast Africa (6), or unsuit-

able conditions for chytridiomycosis. It remains unknown whether chytridiomycosis contributed to widespread amphibian declines reported in North America and Europe in the 1950s to 1960s (3, 21, 22) or current enigmatic salamander declines in eastern North America. Although the number of new declines has now eased (Fig. 3), additional declines could occur if B. dendrobatidis or B. salamandrivorans are introduced into new areas, highly virulent lineages are introduced into areas that currently have less-virulent lineages (6), and/or environmental changes alter previously stable pathogen-host dynamics (3).

Chytridiomycosis-associated declines peaked globally in the 1980s, between one and two decades before the discovery of the disease (Fig. 3 and table S1), and coincident with anecdotal recognition of amphibian declines in the 1990s (23). A second, smaller peak occurred in the early 2000s, associated with an increase in declines in western South America (Fig. 3 and fig. S1). Regionally, temporal patterns of decline are variable (fig. S1). For example, in some areas of South America and Australia, declines commenced in the late 1970s(2, 24), whereas in other areas, declines started in the 2000s (25). B. dendrobatidis is associated with ongoing declines in 197 assessed species. Ongoing declines after a transition to enzootic disease dynamics (19) might be driven by a lack of effective host defenses, maintenance of high pathogenicity (18), and presence of B. dendrobatidis in amphibian and nonamphibian reservoirs (7, 19).

We examined host life history traits and environmental conditions to understand why some species declined more severely than others, using multinomial logistic regression and accounting for the degree of evidence that chytridiomycosis was implicated in each species's decline (fig. S2 and table S2). Decline severity was greatest for larger-bodied species, those occurring in consistently wet regions, and those strongly associated with perennial aquatic habitats. These patterns are likely due to favorable environmental conditions for B. dendrobatidis in wet regions (7), because the fungus dies when desiccated, as well as the general pattern of increased time to maturity in large-bodied amphibians resulting in less reproductive potential to offset mortality due to chytridiomycosis (26). Declines were less severe for species with large geographic and elevational ranges (Fig. 4), potentially owing to the greater chance of their range encompassing environmental conditions unfavorable for B. dendrobatidis (3) and/or information bias, because population extinctions can be assessed with more certainty in restricted-range species. Our results are consistent with previous studies that show that the risk of chytridiomycosis is associated with host aquatic habitat use, large body size, and narrow elevational range (10, 11).

Encouragingly, of the 292 surviving species for which population trends are known, 60 (20%) have shown initial signs of recovery. However, recoveries generally represent small increases in abundance of individual populations, not complete recovery at the species level. Logistic regression showed the probability of recovery was lower for species that experienced more recent or more severe declines, for large-bodied or nocturnal species, and for species occurring at higher elevations (fig. S2 and table S3). When

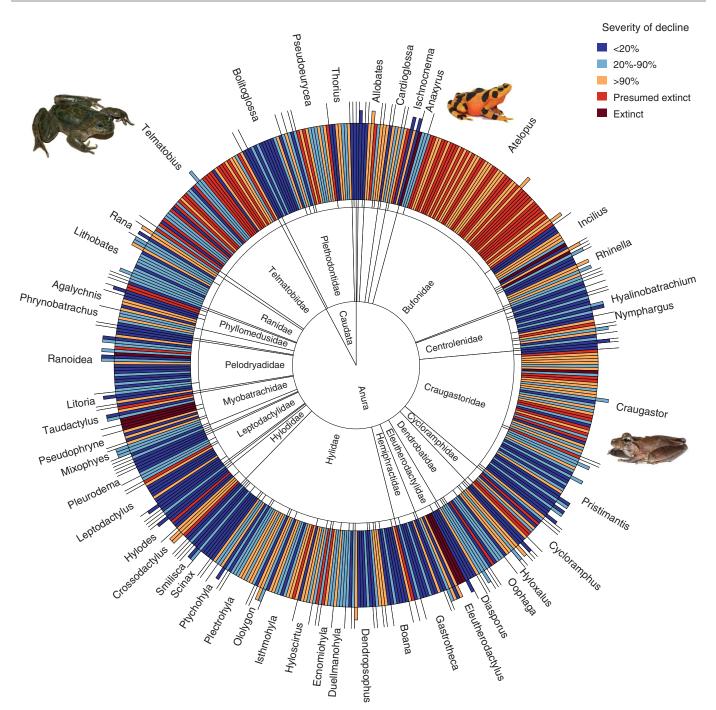


Fig. 2. Taxonomic distribution of chytridiomycosis-associated amphibian declines. Each bar represents one species, and color denotes the severity of its decline. Concentric circles indicate, from inner to outer, order (Caudata or Anura), family, and genus. Full names are given only for families and genera that include >5 and >2 species,

respectively; details for all taxa are in table S4. Within each taxonomic level, sublevels are ordered alphabetically. Protruding bars indicate species for which there is evidence of recovery. [Photo credits (left to right): Telmatobius bolivianus, I.D.I.R.; Atelopus zeteki, B.G.; and Craugastor crassidigitus, B.G.]

holding those predictors of recovery at their mean value, the chance of a species recovering from a severe (>90%) decline was less than 1 in 10. Low probability of recovery for high-elevation species might be related to suitable climatic conditions for fungal persistence as well as limited connectivity to source populations and/or longer host generation time (26). Some recoveries may be underpinned by selection for increased host resistance (18), whereas management of concurrent threats may have facilitated other recoveries (a promising avenue for conservation interventions) (27). Unfortunately, the remaining 232 species have shown no signs of recovery.

The unprecedented lethality of a single disease affecting an entire vertebrate class highlights the threat from the spread of pathogens in a globalized world. Global trade has recreated a functional Pangaea for infectious diseases in wildlife, with far-reaching impacts on biodiversity (this study), livestock (28), and human health (29). Effective biosecurity and an immediate reduction in wildlife trade are urgently needed to reduce the risk of pathogen spread. As mitigation of chytridiomycosis in nature remains unproven (30), new research and intensive monitoring that utilizes emerging

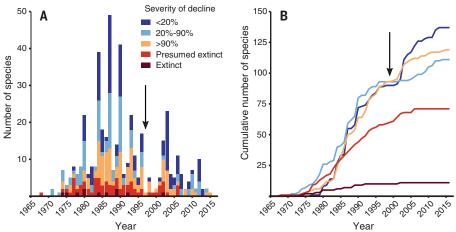


Fig. 3. Timing of chytridiomycosis-associated amphibian declines. (A) Declines by year. Bars indicate the number of declines in a given year, stacked by decline severity. For species for which the exact year of decline is uncertain, the figure shows the middle year of the interval of uncertainty, as stated by experts or inferred from available data. (B) Cumulative declines. Curves indicate the cumulative number of declines in each decline-severity category over time. In (A) and (B), the arrows mark the discovery of chytridiomycosis in 1998.

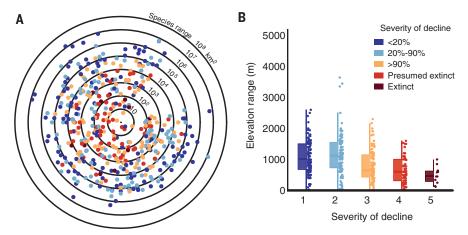


Fig. 4. Severity of chytridiomycosis-associated amphibian declines in relation to the geographic and elevational ranges of species. (A) Declines in relation to geographic range. Each dot indicates a species, located randomly along the perimeter of a circle with radius equal to the log₁₀ of the species's geographic range in kilometers squared. (B) Declines in relation to elevational range. Horizontal bars, boxes, and vertical bars indicate, respectively, mean, first and second quartiles, and 95% quantiles of elevation ranges within each category of decline severity.

technologies are needed to identify mechanisms of species recovery and develop new mitigation actions for declining species.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/363/6434/1459/suppl/DC1 Materials and Methods

Figs. S1 and S2 Tables S1 to S4 References (31-47)

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The demise of amphibians?

Rapid spread of disease is a hazard in our interconnected world. The chytrid fungus *Batrachochytrium dendrobatidis* was identified in amphibian populations about 20 years ago and has caused death and species extinction at a global scale. Scheele *et al.* found that the fungus has caused declines in amphibian populations everywhere except at its origin in Asia (see the Perspective by Greenberg and Palen). A majority of species and populations are still experiencing decline, but there is evidence of limited recovery in some species. The analysis also suggests some conditions that predict resilience.

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