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Ongoing harlequin toad declines suggest the amphibian extinction crisis is still an emergency

Biodiversity loss is extreme in amphibians. Despite ongoing conservation action, it is difficult to determine where we stand in overcoming their extinction crisis. Among the most threatened amphibians are the 131 Neotropical harlequin toads. Many of them declined since the 1980s with several considered possibly extinct. Recently, more than 30 species have been rediscovered, raising hope for a reversing trend in the amphibian extinction crisis. We use past and present data available for harlequin toads (*Atelopus*), to examine whether the amphibian extinction crisis is still in an emergency state. Since 2004 no species has improved its population status, suggesting that recovery efforts have not been successful. Threats include habitat change, pathogen spread and climate change. More mitigation strategies need implementation, especially habitat protection and disease management, combined with captive conservation breeding. With harlequin toads serving as a model, it is clear that the amphibian extinction crisis is still underway.

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The Anthropocene is characterized by high levels of biodiversity loss[1]. At the UN Biodiversity Conference (COP15) held in December 2022 in Montreal almost 200 countries committed to reducing the extinction rate tenfold by 2050[2]. Extreme declines have been noted in amphibians, which are among the most threatened vertebrates[3–7]. While populations are experiencing severe declines worldwide, strategies and tools have been identified to prevent further amphibian loss[8]. Extinction risk is unequally distributed across amphibians[7]. Some genera stand out as highly threatened, particularly those that contain many species with restricted ranges and high rates of population declines[4]. One of these 'worst-cases' are the Neotropical harlequin toads, genus *Atelopus*, which scientists have closely monitored since the early 1990s and of which several species were expected to be extinct[4,6,9]. In recent years, more than 30 *Atelopus* species have been rediscovered[10]. This raises hope and given the extreme declines in harlequin toads, they might be appropriate to explore where we stand in managing the amphibian crisis.

We analyse trends in population status of 131 harlequin toads from 2004 to 2022 and explore current and future threats and their mitigation in this highly imperiled genus. We find that neither population status of the species nor the threats have changed. Using harlequin toads as a 'worst-case' amphibian decline model, we conclude that the amphibian extinction crisis is still an emergency. Despite invaluable efforts in amphibian conservation[3,8], we so far have not been able to reverse the massive declines. Implementation of mitigation strategies needs more attention.

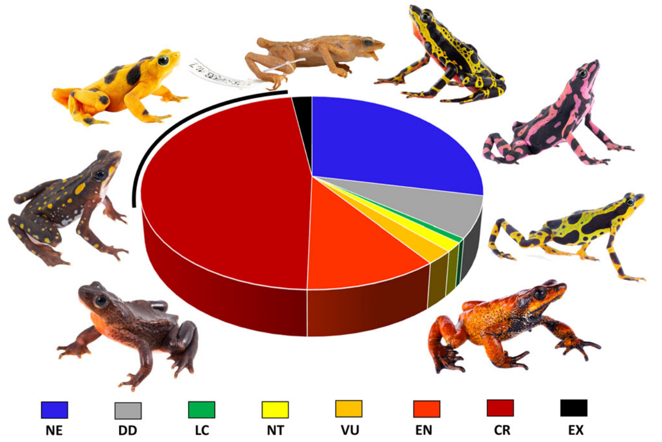

Fig. 1 Harlequin toads are a prime example of a worst-case scenario of amphibian declines, with most species threatened with extinction. Of 131 species, 94 have been assessed by the IUCN Red List:[7] NE – Not Evaluated (37), DD – Data Deficient (9), LC – Least Concern (1), NT – Near Threatened (2), VU – Vulnerable (3), EN – Endangered (14), CR – Critically Endangered (62), EX – Extinct (3). The black line indicates that 39 CR species are possibly extinct. Representatives of different categories are shown, clockwise from above: *Atelopus vogli*, only known in preservative (EX), *A.* sp. "wampukrum" (NE), *A. hoogmoedi* (NE), *A. spurrelli* (NT), *A. carrikeri* (EN), *A. ignescens* (CR), *A. longirostris* (CR), and *A. zeteki* (CR), which is possibly extinct in the wild (photos: Christopher Heine (*A. vogli*), Jaime Culebras).

Background

The global amphibian extinction crisis. In the late 1980s, researchers started to witness amphibian declines at alarming rates with sudden and rapid population crashes all over the globe[11,12]. The 2004 IUCN Global Amphibian Assessment revealed that about 32% of 5743 species were threatened with extinction and 34 species were already extinct[5]. The most up-to-date IUCN Red List of Threatened Species (version 2022-2) now indicates that almost 35% of 7486 evaluated species are threatened with extinction and 38 are extinct[7]. In addition to 'traditional' threats (e.g., habitat destruction or degradation), novel and synergistically acting threats have been identified including climate change and emerging infectious diseases[5,7,13,14]. Of particular importance are pathogenic skin fungi from the genus *Batrachochytrium* causing the infectious disease chytridiomycosis. Human-mediated spread of these fungi has resulted in mass mortality events in many amphibians worldwide[6,15].

The IUCN Amphibian Conservation Action Plan, regularly updated since 2007, frames strategies and tools to escape the amphibian emergency. Among others, this includes research at all levels from ecology to systematics, evolutionary biology, increased monitoring and continuous status assessments, habitat protection, disease mitigation efforts, in-country capacity building, community-based work, and ex situ conservation breeding[8].

While extinction threatens many amphibians, new species are continuously being discovered, with more than 150 species descriptions per year over the last two decades[16]. This makes assessing the amphibian crisis difficult as the true number of living amphibians is hard to estimate, and for this reason, it is challenging to assess our progress in overcoming the amphibian extinction crisis.

Dramatic declines of harlequin toads. More than 100 species of harlequin toads occur in tropical lowland and montane forests up to the paramos, from sea level to almost snowline in Central and South America (Supplementary Table 1). Scientists have closely monitored them since the early 1990s documenting the alarming situation of most of them to call for conservation action[9,17–20]. At least 27 species declined rapidly from 1984 to 2004 (Supplementary Table 2). By 2005, more than half of all species had not been seen for one decade or longer, and only 10 species had stable populations[9]. The latest IUCN Red List assessed 94 harlequin toads and listed two thirds (62) of these as Critically Endangered (Fig. 1), of which 39 are Possibly Extinct. Only one species is categorized as Least Concern[7].

While these numbers clearly demonstrate why *Atelopus* represent a 'worst-case' amphibian decline scenario, the fear of witnessing the unprecedented extinction of an entire species-rich amphibian genus[21] has not yet materialized. Since 2005, only three species were added to the list of harlequin toads in decline (Supplementary Table 2). This is remarkable, given that *Atelopus* are among the best-studied and most sought-after amphibians in the Neotropics[10,20,22]. Instead, 30 species that had not been seen by scientists for many years have been rediscovered (Supplementary Table 3), suggesting a hypothetical reverse population trend in at least some species[10]. This also includes two species the IUCN Red List categorized as Extinct (*Atelopus ignescens* and *A. longirostris*; Fig. 1)[23].

We define two phases: (i) the crisis with dramatic population declines, ca. 1984–2004; and (ii) post-2004, a hypothetical improvement of the population status in at least some species. Two features provide unique opportunities to explore this apparent change. This is different to many other 'worst-case' amphibian groups (e.g. *Centrolene*, *Gastrotheca*, *Pseudophryne*, *Strabomantis*, *Telmatobius*), why we consider *Atelopus* a potential model for them. First, population monitoring data from two periods led to the assessment of population status of all known species in 2004[9] and 2022. These are based on expert knowledge, which is common practice in conservation assessments[24]. As done in 2004, we assigned one of three population status categories to each species in 2022, resulting in two sets of standardized data 15 years apart (Fig. 2; Supplementary Table 1).

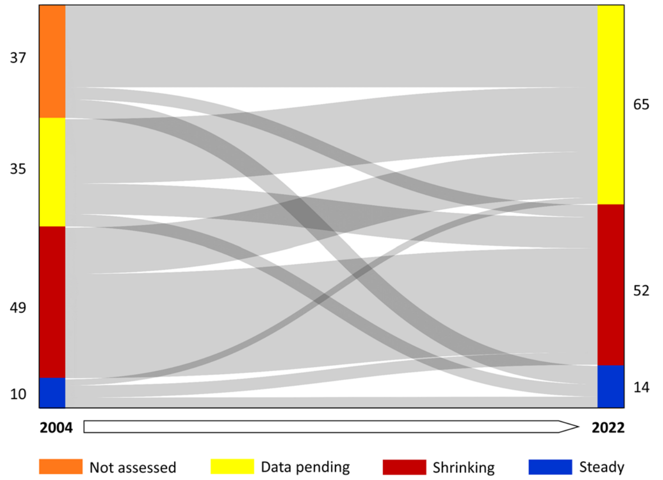

Fig. 2 Harlequin toad population status 2004–2022. Change in population status of 131 *Atelopus* species over time, based on two standardized datasets with a span of more than 15 years between them. Not a single species has improved its population status. For details see Supplementary Table 1.

The second feature making harlequin toads an exemplary group is that we take a high degree of accuracy in taxonomy for granted, which is essential for effective species conservation[25]. Several of the authors have contributed to the taxonomy of *Atelopus* for many years and have established the contemporary taxonomic architecture of the genus. With this unparalleled advantage, we have a comprehensive data set on this genus far beyond the available published information, so that species status data are not markedly behind the taxonomic progress, as in other amphibians. In total, we evaluated 131 *Atelopus* species, of which 37 (28.2%) are not yet assessed on the IUCN Red List (Fig. 1; Supplementary Table 1). Next to acknowledging the taxonomic progress (i.e., new and revalidated species), our 2022 database includes 31 species identified but not yet formally described (e.g. *A.* sp. "wampukrum", Fig. 1).

Results and discussion

We did not detect change in the population status of the species assessed in 2004 and 2022 (Fig. 2), (Freeman-Halton extension of Fisher's exact test for RxC table: $p = 0.152$; $N = 131$), including for a 2022 reduced dataset containing only the species listed in the 2004 assessment ($p = 0.826$; $N = 94$). Since 2004, no species have had an improvement in population status from shrinking to steady (Fig. 2), even the shrinking species that were rediscovered after 2004 remain shrinking. This is supported by the observation that specimens occur in densities apparently lower than in the past, so that it is hard to consider them 'true' recoveries with the demographic potential to contribute to population expansions. Most of the findings were new discoveries at formerly unknown localities[10]. Most historical localities, which have been regularly visited, have remained empty of harlequin toads for many years.

Harlequin toads with shrinking population status mostly occur in Andean areas and Central America, while none of the species from the lower Amazon basin, the Guianas, the Colombian Sierra Nevada de Santa Marta and part of the species from the Chocó have shrinking populations (13 species in total) (Fig. 3a). Alarmingly, 61 species (46.6%) have 'year last seen' (YLS) in 2004 or earlier. These species have population status data pending or shrinking (depending on the knowledge on the population status prior their YLS) and 37 have probably vanished (Supplementary Table 1).

Persisting threats. The main drivers of *Atelopus* declines are habitat destruction and degradation[5,7] and the skin fungus *Batrachochytrium dendrobatidis* (*Bd*)[6,26]. The 2022 expert data demonstrate that habitat destruction and degradation are a threat to 93 (71.0%) species (Fig. 3b), of which 37 have YLS 2004 or earlier (Supplementary Table 1). We noted the presence of *Bd* in 50 (38.2%) species, and of the 42 species with *Bd* whose population status is categorized as shrinking or data pending (Fig. 3b), 16 have YLS 2004 or earlier (Supplementary Table 1).

Habitat destruction and degradation as well as *Bd* continue to threaten harlequin toads today. The situation is dire, considering how habitat change can dramatically affect *Atelopus* populations[27]. A vivid example is the recently rediscovered *A. longirostris* (Fig. 1) from the Intag Valley of Ecuador which is now the focus of a large copper mining project[28]. Regarding *Bd*, some populations compensate high mortality rates with a high reproductive output, which might cause life history shifts, e.g. in *A. cruciger*. That is, some *Atelopus* species can persist once the fungus becomes enzootic, using different strategies[29–32]. There are five species that continue to have steady populations despite the presence of *Bd* (see Supplementary Table 1) However, these are fragile systems, because effects of *Bd* are more complex due to co-stressors[6].

Climate change as a future threat. Some studies suggest that unusual climatic conditions may play a role in *Atelopus* declines and might also exacerbate the effects of *Bd*[26,33,34]. Climatic change is associated with an increase in the frequency of extreme weather events. Climate change for the period from present (1970–2000) to the year 2100 can be assessed using the Climatic Stability Index, CSI[35]. CSI values are higher in lowlands (i.e. climate is unstable), where most harlequin toads with steady populations occur (Fig. 3a), suggesting that climate change might become an important threat to currently steady lowland *Atelopus* in the future (Fig. 3c). However, this does not preclude species living at high altitudes from the effects of climate change. Especially high-Andean taxa are potentially limited in their capacities to undergo range shifts as a response to warming. They may also become more exposed to an increased solar radiation.

The number of *Atelopus* species in protected areas has increased from 84 to 96 from 2004 to 2022 (64.1 to 73.3%; Supplementary Table 1). Given that the populations of 43 of these species are shrinking, it is evident that habitat protection alone is not sufficient. So far, multi-disciplinary approaches to improve the conservation status of *Atelopus* have been proposed, next to habitat protection, additionally including scientific research, monitoring, environmental education, and conservation breeding[19]. Recently, these were reinforced in the *Atelopus* Conservation Action Plan 2021–2041 along with elaborated targets for the coming decades. The plan was launched by the recently founded *Atelopus* Survival Initiative[36], a multistakeholder collaborative and participative effort to stop the loss of this imperiled genus[20].

Other initiatives, such as the El Valle Amphibian Conservation Center[37], Project Golden Frog[38] and the Panama Amphibian Rescue and Conservation Project[39], have operated for more than 10 years now and have contributed to direct conservation efforts on Central American *Atelopus* species. They have promoted research to further understand the effects of *Bd* on population genetic structures[40] and to explore the response of *Bd* to an altered skin microbiome[15,41] or to skin secretions[32,42]. In addition, ex situ assisted reproductive technologies are being developed to preserve genetic diversity of some harlequin toads, for instance for Ecuadorian species[43]. Various local initiatives have been initiated recently to conserve particular species through community-based

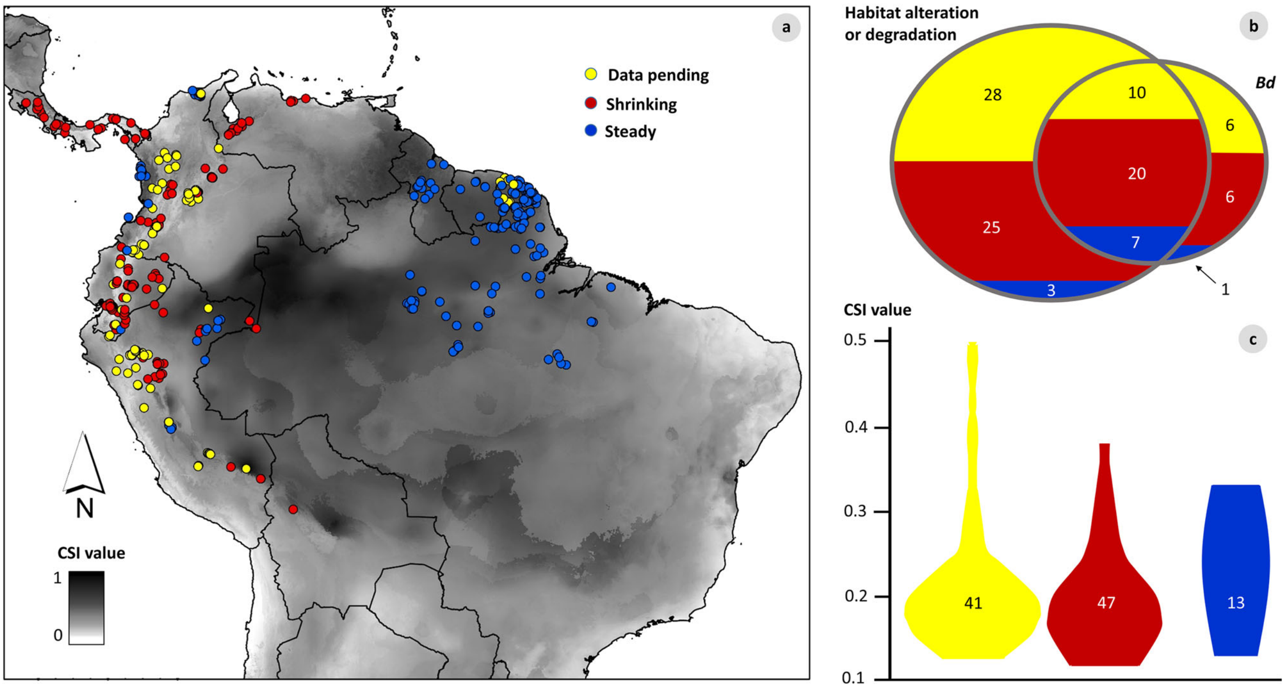

Fig. 3 Threats to harlequin toads. a Climatic Stability Index (CSI, Shared Socioeconomic Pathway 8.5 scenario[35]) map of South America showing the distribution of harlequin toads and their current population status. **b** Number of species affected by habitat destruction and degradation or by the presence of the skin fungus *Batrachochytrium dendrobatidis* (*Bd*) or both arranged by population status. **c** Distribution of CSI values among species according to their population status. In **b**, **c** the number of species is given per population status. For details see Supplementary Table 1.

conservation action and habitat protection[44,45], but their impact remains difficult to assess.

The special role of ex situ conservation breeding. For highly threatened species, captive assurance populations are strongly recommended as a potentially powerful tool allowing for reintroductions once the threat(s) can be mitigated. This is an extreme measure, especially for amphibian species that are vulnerable to *Bd*. In practice, ex situ conservation breeding allows us to buy time while appropriate mitigation and conservation strategies are developed and applied[8]. Thus, conservation breeding is a crucial action to enhance the chances of harlequin toad survival[19,35,46]. So far, captive assurance colonies have been established for 26 *Atelopus* species and scientists have now started to study reintroductions of captive-born individuals in *A. limosus*;[47] studies on additional species are in progress (authors' unpubl. data). So far, 16 species (13 with shrinking populations) have already successfully reproduced at least once at one institution, with offspring reaching maturity. However, only six *Atelopus* species have reproduced at two or more institutions with at least one institution successfully reproducing for more than one generation (Supplementary Table 4), showing that conservation breeding needs more efforts. Conservation breeding of *A. zeteki* (Fig. 1) has been a story of remarkable success[38,46], with more than a thousand individuals being held in more than 50 institutions in three countries, independent from wild caught founders, for roughly 20 years. This species is considered shrinking and has likely already vanished in the wild. As a sharp contrast, in three *Atelopus* species, conservation breeding attempts have failed, with all individuals lost (Supplementary Table 4).

Captive breeding initiatives are regionally biased, with several in-country colonies covering mainly Ecuadorian and Panamanian species, while Brazil, Colombia and Venezuela have recently launched programs for one species each. Ex situ conservation efforts are lacking in other countries where harlequin toads occur, yet some species are or were bred in Europe and North America (Supplementary Table 4).

Conclusion

Our comparison of the 2004 and 2022 databases reveals that no harlequin toad went from status shrinking to steady. We reject the hypothesis that we have entered a hypothetical post-decline phase of improvement. Although reports on sudden and rapid population declines have lessened (Supplementary Table 2), many species continue to have shrinking populations, which implies that over time declines continue to happen more silently. This is reinforced by the observations that of the 29 species rediscovered since 2004, six have not been seen again for the past 10 years, despite targeted searches[10]. These harlequin toads either occur in low numbers or are possibly extinct emphasizing that rediscoveries are not equating recoveries. At the same time habitat destruction and *Bd* persist to threaten harlequin toads, despite that 96 (75%) of the species occur in protected areas and (at least) some *Atelopus* can somehow cope with *Bd*. In addition, future threats through changing climate are expected.

Using harlequin toads as a worst-case model for amphibian species with high extinction risk[4,7], the situation of these amphibians has not improved over the past two decades. Despite invaluable efforts, we so far have not been able to reverse the massive declines. The amphibian extinction crisis is still an emergency.

The goal to massively reduce extinction rates within the next 20–30 years[2] will require immense efforts and investments, which need to be massively scaled up. More in situ mitigation strategies need to be implemented, including effective habitat protection and management. This also addresses the development of innovative methods to mitigate the effects of infectious diseases (such as *Bd*). The expansion of ex situ capacities might address to strengthen the technical and scientific capacities for in country-captive breeding. Increased storage capacities for germplasm and genetic material as well as the implementation of genome resource banks are additional steps for safeguarding amphibian species with high extinction risk. In line with these strategies, programs aiming at reintroductions and translocations of species are a key step to mitigate the amphibian extinction crisis. Other strategies are to improve the baseline knowledge, to increase the visibility of the problem and to create mechanisms for multi-stakeholder collaboration and participation including local communities.

For harlequin toads, these aspects are described in detail in the *Atelopus* Conservation Action Plan 2021–2041[36]. Given proper funding and support and the collaborative coalition of on-the-ground conservation organizations, zoos, governments and local communities, there is improvement in sight for the remaining harlequin toads[20]. For most other threatened amphibians such focal plans and coordinated conservation efforts are still lacking.

Methods

We used the original database of La Marca et al.[9], which compiled information from experts on *Atelopus* population trends through February 2004. This database was updated with the revised taxonomy, as well as additional input and data from experts, and our study period was defined as March 2004 to December 2022 (Supplementary Table 1). We interviewed 105 experts (a diverse group of scientists and conservationists with considerable knowledge on *Atelopus* species), sometimes on multiple occasions, from October 2019 to December 2022. All 75 original database contributors to La Marca et al.[9] were contacted, but we received updated information from only 13. The additional 92 contributing researchers were *Atelopus* taxonomists and conservationists. Original contributions included initial estimates on population status and general threats as well as field data on the species ecology and threats at the site level. Data was reviewed and summarized species-wise prior to a second round, where experts were able to provide corrected estimates, as has been proven successful for obtaining robust expert data[48,49]. Still, we are well-aware that expert opinions carry an unavoidable uncertainty and need to be considered carefully[49,50]. Most of the experts who contributed data also contributed to the writing of this paper and became co-authors.

In this study, we refer the term 'species' to described taxa that we consider valid and to forms that are undescribed and are expected to represent valid species. Also, we tentatively consider suggested subspecies as species here. According to this, we refer to 131 species of which 100 are formally described, while the 2004 database considered 94 taxa. Alphataxonomic problems remain for some harlequin toads, e.g. *A. hoogmoedi* which could be more than one species[51].

Following La Marca et al[.9], for each species we updated the information on distribution, the known altitudinal range, and local endemism by number of known populations (1, 2, >2). We recorded: species population status; the year last seen (YLS); information on *Bd* presence; occurrence in any governmental or private protected area. In order to address threats that have been identified to play a key role in *Atelopus* declines[9,34], we additionally assessed the potential future impact of climate change for each species. For detailed data see Supplementary Table 1. Details on how data were assessed are described below.

The population status was coded following definitions of La Marca et al.[9]. However, we change the terminology to avoid confusion with terms used by the IUCN Red List of Threatened Species. We used 'steady' (= stable) when one or more populations are known to have persisted and no population has declined by more than 50%; 'shrinking' (= declining) when at least one population has declined by more than 50%; 'data pending' (= data deficient) when insufficient population trend data are available to judge whether a decline has occurred. This also includes species where unsystematic survey efforts were invested, but the species could not be detected. We additionally coded species as 'probably vanished' or 'probably vanished in the wild', when experts agreed that the particular species has possibly gone extinct (or extinct in the wild). However, as extinction is difficult to confirm, and as rediscoveries of formerly thought to be extinct species are common in the genus, this is not a separate status category. Freeman-Halton extension of Fisher's exact tests (one-sided, with sequential Bonferroni-Holm correction) were performed to explore the population status change between the 2004 and 2022 databases using the following online web statistical calculator: https://astatsa.com/FisherTest/ (accessed 7 January 2023).

In addition to information on *Bd* presence through direct testing of *Atelopus* specimens (including diagnosis both by PCR or histology), we provide information on presumed *Bd* presence for *Atelopus* species that have not been tested for *Bd*. We consider likely presence of *Bd* in an *Atelopus* species when *Bd* infection is known in other amphibian species at *Atelopus* localities. For this purpose, we used *Bd* records available from the Aquatic Parasite Observatory (http://www.aquaticparasites.org/, accessed 8 June 2022) and the Amphibian Disease Portal (https://amphibiandisease.org/, accessed 28 September 2022). Employing ArcGIS Pro (ESRI), we then buffered (5 km) 776 georeferenced *Atelopus* records of 102 species. If a *Bd* record was within a buffer, we considered the *Atelopus* species to potentially have *Bd*.

To assess the potential future impact of climate change at *Atelopus* sites, we used the Climate Stability Index (CSI). It provides information on climate vulnerability for the time span Pliocene (3.3 Ma) to the year 2100 [35]. The CSI operates using the standard deviation over time at grid cells with resolution 2.5 arcmin. It is based on 9 general circulation models and 19 bioclimatic variables[52] available from WorldClim 2[53]. Of the different underlying climate change scenarios (Shared Socioeconomic Pathways, SSP), we chose, a priori, SSP5–8.5 from present (1970–2000) to the year 2100 for our study because it is among the most extreme ('worst-case') scenarios for Central and South America[35]. CSI data were downloaded from Figshare (https://doi.org/10.6084/m9.figshare.14672637, accessed 2 March 2022). CSI values range 0-1 (most to least stable).

With the goal of obtaining information on *Atelopus* conservation breeding, we contacted all existing institutions, to our knowledge, that hold or held captive assurance colonies of harlequin toads to compile a dataset on the species kept and breeding success (Supplementary Table 4). We received information from all seven institutions located in *Atelopus* range countries as well as from numerous North American and European institutions, partially coordinated through the multinational Project Golden Frog[38].

Reporting summary. Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The authors declare that all other relevant data supporting the findings of this study are included in the paper and in the Supplementary Information. All data used in this paper is found at https://doi.org/10.5061/dryad.jm63xsjhh.

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References

1. Barnosky, A. D. et al. Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011).

2. Convention on Biological Diversity. COP 15: Nations adopt four goals, 23 targets for 2030 in Landmark UN Biodiversity Agreement. *Official CBD Press Release* https://www.cbd.int/article/cop15-cbd-press-release-final-19dec2022 (2022).
3. Mendelson, J. R. et al. Confronting amphibian declines and extinctions. *Science* **313**, 48 (2006). 1128396.
4. *Threatened Amphibians of the World*. (Lynx Editions, 2008).
5. Stuart, S. N. et al. Status and trends of amphibian declines and extinctions worldwide. *Science* **306**, 1783–1786 (2004).
6. Scheele, B. C. et al. Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. *Science* **363**, 1459–1463 (2019).
7. IUCN. The IUCN Red List of Threatened Species. Version 2022-2. https://www.iucnredlist.org (2022).
8. IUCN SSC Amphibian Specialist Group. The Amphibian Conservation Action Plan (ACAP): a status review and roadmap for global amphibian conservation. Preprint. https://doi.org/10.32942/osf.io/brfas (2022).
9. La Marca, E. et al. Catastrophic population declines and extinctions in Neotropical harlequin frogs (Bufonidae: *Atelopus*). *Biotropica* **37**, 190–201 (2005).
10. Jaynes, K. E. et al. Harlequin frog rediscoveries provide insights into species persistence in the face of drastic amphibian declines. *Biol. Conserv.* **276**, 109784 (2022).
11. Barinaga, M. Where have all the froggies gone. *Science* **247**, 1033 (1990).
12. Blaustein, A. R. & Wake, D. B. Declining amphibian populations: A global phenomenon? *Trends Ecol. Evol.* **5**, 203–204 (1990).
13. Kiesecker, J., Blaustein, A. R. & Belden, L. K. Complex causes of amphibian population declines. *Nature* **410**, 681–684 (2001).
14. Collins, J. P. & Storfer, A. Global amphibian declines: Sorting the hypotheses. *Divers. Distrib.* **9**, 89–98 (2003).
15. Woodhams, D. C. et al. Prodigiosin, Violacein, and Volatile organic compounds produced by widespread cutaneous bacteria of amphibians can inhibit two *Batrachochytrium* fungal pathogens. *Microb. Ecol.* **75**, 1049–1062 (2018).
16. AmphibiaWeb. Newly described species by year. *University of California, Berkeley* https://amphibiaweb.org/amphibian/newspecies.html (2023).
17. La Marca, E. & Reinthaler, H. P. Population changes in *Atelopus* species of the Cordillera de Mérida, Venezuela. *Herpetol. Rev.* **22**, 125–128 (1991).
18. Pounds, J. A. & Crump, M. L. Amphibian declines and climate disturbance: The case of the golden toad and the harlequin frog. *Conserv. Biol.* **8**, 72–85 (1994).
19. Lötters, S. The fate of the harlequin toads – help through a synchronous multi-disciplinary approach and the IUCN 'Amphibian Conservation Action Plan'? *Mitt. Mus. Naturkunde Berl., Zoolog. Reihe.* **83**, 69–73 (2007).
20. Valencia, L. M. & Marin da Fonte, L. F. Collaborative work brings hope for threatened harlequin toads. *Oryx* **56**, 12 (2022).
21. Lötters, S., La Marca, E., Stuart, S., Gagliardo, R. & Veith, M. A new dimension of current biodiversity loss? *Herpetotropicos* **1**, 29–31 (2004).
22. *Ranas Arlequines*. (Conservación Internacional, 2005).
23. Tapia, E. E., Coloma, L. A., Pazmiño-Otamendi, G. & Peñafiel, N. Rediscovery of the nearly extinct longnose harlequin frog *Atelopus longirostris* (Bufonidae) in Junín, Imbabura, Ecuador. *Neotrop. Biodivers.* **3**, 157–167 (2017).
24. Drescher, M. et al. Toward rigorous use of expert knowledge in ecological research. *Ecosphere* **4**, 1–26 (2013).
25. de Magalhães, R. F., Rocha, P. C., Santos, F. R., Strüssmann, C. & Giaretta, A. A. Integrative taxonomy helps to assess the extinction risk of anuran species. *J. Nat. Conserv.* **45**, 1–10 (2018).
26. Lips, K. R. et al. Riding the Wave: Reconciling the roles of disease and climate change in amphibian declines. *PLoS Biol.* **6**, e72 (2008).
27. Tarvin, R. D., Peña, P. & Ron, S. R. Changes in population size and survival in *Atelopus spumarius* (Anura: Bufonidae) are not correlated with chytrid prevalence. *J. Herpetol.* **48**, 291–297 (2014).
28. Murphy, D. International and Local Conservation Groups Condemn Ecuadorian Court's Decision to Allow Copper Mining in Intag Valley Cloud Forests. *Froglog* **124**, 23–24 (2022).
29. Ballestas, O., Lampo, M. & Rodríguez, D. Living with the pathogenic chytrid fungus: exploring mechanisms of coexistence in the harlequin toad *Atelopus cruciger*. *PLoS ONE* **16**, e0254439 (2021).
30. Lampo, M., Señaris, C. & García, C. Z. Population dynamics of the Critically Endangered toad *Atelopus cruciger* and the fungal disease chytridiomycosis. *PLoS ONE* **12**, e0179007 (2017).
31. Lampo, M., Señaris, C., González, K. & Ballestas, O. Smaller size of harlequin toads from populations long exposed to the lethal fungal disease chytridiomycosis. *Biotropica* **55**, 699–705 (2023).
32. Voyles, J. et al. Shifts in disease dynamics in a tropical amphibian assemblage are not due to pathogen attenuation. *Science.* **30**, 1517–1519 (2018).
33. Rohr, J. R., Raffel, T. R., Romansic, J. M., McCallum, H. & Hudson, P. J. Evaluating the links between climate, disease spread, and amphibian declines. *Proc. Natl. Acad. Sci. USA.* **105**, 17436–17441 (2008).
34. Ron, S. R., Duellman, W. E., Coloma, L. A. & Bustamante, M. R. Population decline of the jambato toad *Atelopus ignescens* (Anura: Bufonidae) in the Andes of Ecuador. *J. Herpetol.* **37**, 116–126 (2003).
35. Herrando-Moraira, S. et al. Climate Stability Index maps, a global high resolution cartography of climate stability from Pliocene to 2100. *Sci. Data.* **9**, 48 (2022).
36. Atelopus Survival Initiative. Save harlequin Toads. https://www.atelopus.org/ (2021).
37. El Valle Amphibian Conservation Center. https://www.evaccfoundation.org (2023).
38. Project Golden Frog. https://www.ranadorada.org/ (2023).
39. Gratwicke, B. et al. Evaluating the probability of avoiding disease-related extinctions of Panamanian amphibians through captive breeding programs. *Anim. Conserv.* **19**, 324–336 (2016).
40. Byrne, A. Q. et al. Whole exome sequencing identifies the potential for genetic rescue in iconic and critically endangered Panamanian harlequin frogs. *Glob. Chang. Bio.* **27**, 50–70 (2020).
41. Becker, M. H. et al. Genetically modifying skin microbiome to produce violacein and augmenting microbiome did not defend Panamanian golden frogs from disease. *ISME Communic.* **4281**, 57 (2021).
42. Gass, J. & Voyles, J. When defences fail: *Atelopus zeteki* skin secretions increase growth of the pathogen *Batrachochytrium dendrobatidis*. *Integr. Comp. Biol.* **62**, 1595–1605 (2022).
43. Naranjo, R. E. et al. Development of assisted reproductive technologies for the conservation of *Atelopus* sp. (*spumarius* complex). *Cryobiology* **105**, 20–31 (2022).
44. Alianza Jambato. https://alianzajambato.org/ (2023).
45. Fundación Atelopus. https://www.fundacionatelopus.org (2023).
46. Lewis, C. H. R. et al. Conserving Panamanian harlequin frogs by integrating captive breeding and research programs. *Biol. Cons.* **236**, 180–187 (2019).
47. Estrada, A., Medina, D., Gratwicke, B., Ibáñez & Belden, L. K. Body condition, skin bacterial communities and disease status: insights from the first release trial of the limosa harlequin frog. *Atelopus limosus. Proc. Biol. Sci.* **289**, 20220586 (2022).
48. McBride, M. F. et al. Structured elicitation of expert judgments for threatened species assessment: a case study on a continental scale using email. *Methods Ecol. Evol.* **3**, 906–620 (2012).
49. Sutherland, W. J. & Burgman, M. A. Use experts wisely. *Nature* **526**, 317–318 (2015).
50. Krueger, T., Page, T., Hubacek, K., Smith, L. & Hiscock, K. The role of expert opinion in environmental modelling. *Environ. Model. Softw.* **36**, 4–18 (2012).
51. Lötters, S. et al. The gastromyzophorous tadpole of the pink harlequin frog from Suriname with comments on the taxonomy of Guianan Clade *Atelopus* (Amphibia, Bufonidae). *Zootaxa* **5087**, 591–598 (2022).
52. Booth, T. H., Nix, H. A., Busby, J. R. & Hutchinson, M. F. Bioclim: the first species distribution package, its early applications and relevance to mot current MaxEnt studies. *Divers. Distrib.* **20**, 1–9 (2014).
53. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).

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