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Perspective

Rewilding a vanishing taxon – Restoring aquatic ecosystems using amphibians

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ABSTRACT

The increasing rate of biodiversity loss and the number of threatened or endangered species worldwide has accelerated conservation and recovery strategies, emphasising fish, birds, and mammals. This focus has mostly neglected amphibians, which are currently facing the most existential crisis among all vertebrates, with declining populations across most habitats. The factors driving global amphibian declines are diverse, often synergistic, and predominantly anthropogenic. Amphibians urgently require rapid conservation action, and we cannot afford to wait while the most important critical elements required to initiate effective recovery efforts are known. We recommend the rapid (re)introduction of this "forgotten" taxon via the guidelines of trophic rewilding. Amphibian rewilding initiatives may provide early indications of ecological health and better contribute to conservation goals, by simultaneously protecting highly endangered species, and promoting ecological stability in these species ecosystems.

1. Introduction

The current human-driven extinction rate of biodiversity is estimated to be greater than any known in the last 100,000 years, although the exact number of species being lost is unknown (Barnosky et al., 2011; Hussain and Pandit, 2012; Cowie et al., 2022). For amphibians, the threat of extinction is imminent in every order (Fig. 1; Luedtke et al., 2023). Their extinction rate is estimated to be the highest among terrestrial vertebrates, with 41 % of amphibian species threatened with extinction, compared to 26 %, 21 %, 14 % and 12 % of mammal, reptiles, bony fish and bird species, respectively (IUCN, 2023). This disproportional difference in extinction rate among groups is attributed to the fact that amphibians have the highest proportion of species with no protected area coverage: 18 % among all amphibians as opposed to only 3 % in birds or 6 % for mammals (Butchart et al., 2015; Nowakowski et al., 2023). The causes of amphibian declines and extinctions are complex and multifactorial, and include habitat loss and fragmentation, pollution, climate change, invasive species, overexploitation, and, most critically, infectious diseases (e.g., *Batrachochytrium dendrobatidis*; Bishop et al., 2012). These drivers of extinction differ among species and localities (Stuart et al., 2004; Stark et al., 2023). Although evidence from other taxa provides solutions, or at least a starting point for addressing most of these extinction drivers, significant conservation challenges (e.g., chytrid infections) must be tackled to counter amphibian declines worldwide.

Concerns regarding declining amphibian populations are partly due

Glossary: Reinforcement, Releasing conspecifics from breeding captive programs or sourced from other larger wild populations, into an existing, small or declining population; Reintroduction, The introduction of one or more individuals into a previously occupied area to enhance the species' conservation efforts; Assisted migration, (formerly known as assisted colonisation) The deliberate introduction of a species beyond its native habitat to prevent its decline or extinction. This usually occurs when it is deemed more feasible to protect the species in locations outside its current range rather than within it, and when species cannot adapt to captive conditions; Ecological replacement, The deliberate movement and introduction of a species outside its native range to fulfill a specific ecological function; Soft-release protocol, Any measures that provide released individuals with an easier or more gradual transition to the wild habitat, such as teaching predatory skills and providing supplementary food; Hard-release protocol, Release of a species into the wild without taking any preliminary or post-release measures; Trophic Rewilding, An ecological restoration strategy that uses species (re)introductions to restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems.

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to their value as indicators of environmental stress in freshwater and terrestrial ecosystems (Blaustein and Wake, 1995; Kiesecker et al., 2001). Most amphibians experience both aquatic and terrestrial stressors, as they depend on freshwater habitats for reproduction and larval development, and terrestrial habitats for foraging (Blaustein and Wake, 1995). Because they depend on both freshwater and terrestrial habitats, they are especially vulnerable to the ongoing global anthropogenic impact on the natural world (Bishop et al., 2012). Moreover, amphibians are essential to many ecosystems, acting as prey, predators, or herbivores (Wells, 2007). Due to their impact on trophic dynamics and freshwater environments, amphibians' loss can exacerbate the decline of the ecosystem's health and functionality.

Amphibians are a diverse group, comprising more than 8600 species worldwide (AmphibiaWeb, 2023). Amphibians are also the least-known group of vertebrates in several geographic areas (Howard and Bickford, 2014), with more than 150 newly described species per year over the last two decades (AmphibiaWeb, 2023). Even though amphibians are recognised as the most critically endangered vertebrate group, most conservation efforts worldwide focus on mammals (n = ~6400), birds (n = ~11,000), and to some extent, reptile species (n = ~12,000; Bajomi et al., 2010; Gilbert et al., 2017; Burgin et al., 2018; Bubac et al., 2019; Callaghan et al., 2021; IUCN, 2023; Uetz, 2023). Additionally, despite their great diversity and central role in ecosystem functioning (Rohr et al., 2008; Collins et al., 2009; Hocking and Babbitt, 2014; Amaral et al., 2019), amphibians are the most underrepresented group in reintroduction projects worldwide (only 1 % out of all projects globally; Seddon et al., 2005; Bajomi et al., 2010; Gilbert et al., 2017; Bubac et al., 2019).

Conservation strategies such as trophic rewilding use the reintroduction of species into areas where they have been extirpated, or introducing ecological proxies (taxonomic substitutions for extinct native species, that once underpinned, deliver key ecological functions; Hansen, 2010) into novel habitats to restore ecosystem functionality (Svenning et al., 2016). Trophic rewilding may thus provide an effective conservation solution for impoverished environments worldwide (Foreman, 2004; Svenning et al., 2016). The main argument for promoting rewilding projects has been that this strategy can help conserve endangered species (e.g., tropical frogs) and restore ecosystem functionality for other organisms (Perino et al., 2019). In this perspective, we aim for the first time, to raise awareness of the potential of the use of amphibians in rewilding projects for conservation efforts. We establish the claim that amphibians can serve a double purpose as both bioindicators for the restored ecosystem's health, and as key elements in the ecosystem's trophic cascade. We finally bring forth a conservation scheme for potential future rewilding-based conservation projects.

2. Amphibians as key participants in ecological trophic cascades and ecosystem functioning

The complex life cycles of amphibians make them pivotal parts of both terrestrial and aquatic food chains (Valencia-Aguilar et al., 2013). In some ecosystems, amphibian species may play the role of keystone herbivores or predators, whose removal can cause alterations to the food web and ecosystem functioning (Fauth and Resetarits Jr, 1991; Holomuzki et al., 1994; Wissinger et al., 1999; Whiles et al., 2006; Smith, 2006; Davenport and Chalcraft, 2012; West, 2018). Adults and tadpoles can act as predators of invertebrates (Fig. 2 [2.1]), fish (Fig. 2 [2.2]), and other amphibians (Fig. 2 [2.3]), and many species are generalists that consume all life stages of their prey (eggs, larvae, juveniles, and adults; Wells, 2007). They can thus also prey on different life stages of invasive species, potentially controlling their numbers and restraining their harmful effects on their habitat and other species (Smith, 2006; Fig. 2 [2.4]). Eggs, tadpoles, adults, and decomposing carcasses can serve as a high-quality nutritional source for certain species of invertebrates (Fig. 2 [2.5]), fish (Fig. 2 [2.6]), other amphibians (Fig. 2 [2.7]), reptiles (Fig. 2 [2.8]), birds (Fig. 2 [2.9]), and mammals (Fig. 2 [2.10]), thus seasonally enhancing the energy and nutrient sources that support the aquatic food web (Schiesari et al., 2009). This fact is attributable to amphibians'

Fig. 1. The most threatened amphibian species according to the IUCN Red List assessment representing each order (or family) across various habitats worldwide. (a) Anura (Hylidae); The lemur leaf frog (*Agalychnis lemur*; photo: WIkimedia Commons), (b) Anura (Bufonidae); The Bleeding Toad (*Leptophryne cruentata*; photo: Farits Alhadi), (c) Urodela; the Lanza's Alpine Salamander (*Salamandra lanzai*; photo: Alexandre Roux), (d) Gymnophiona; The Sagalla Caecilian (*Boulengerula niedeni*; photo: Matt Muir). All images (not edited) are published online and attributable to licenses: CC-BY-SA 3.0/ CC BY-NC-ND 2.0/CC BY-NC-SA 4.0. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

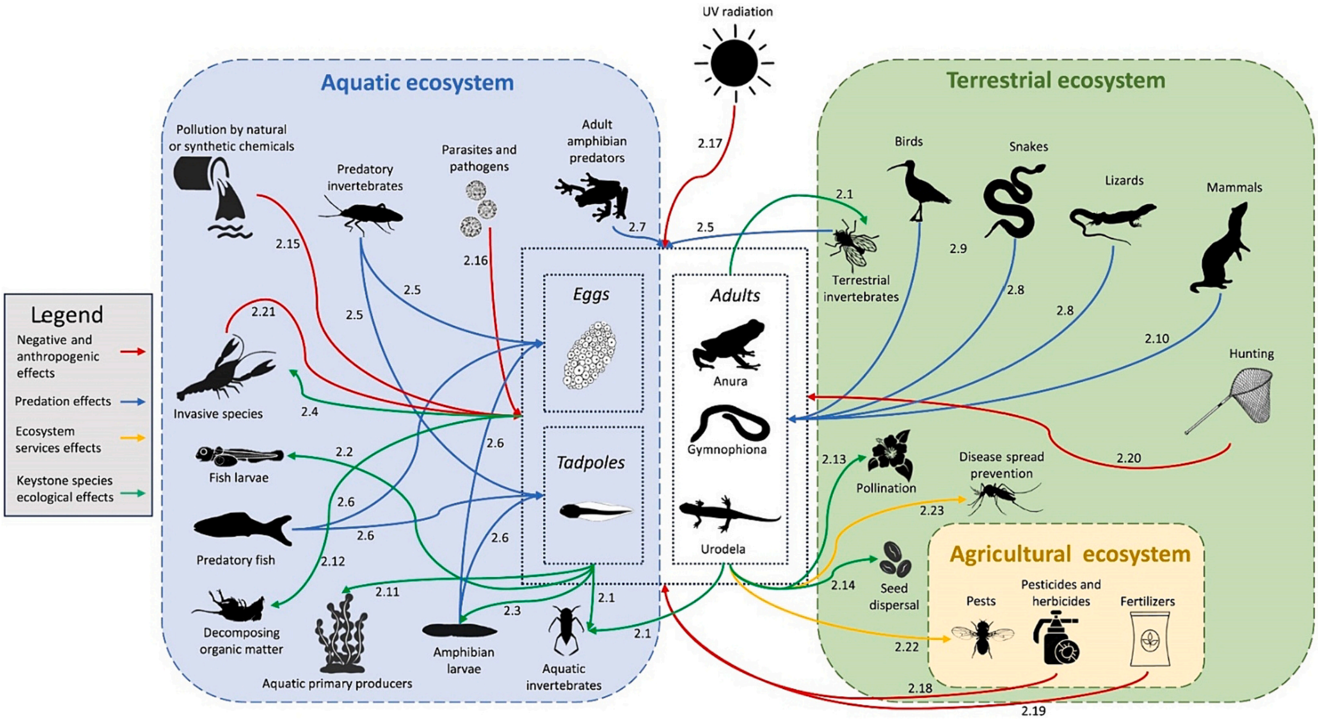

Fig. 2. A scheme portraying the direct and indirect ecosystem roles played by the different amphibian groups (Anura, Urodela and Gymnophiona) in different stages (eggs, tadpoles, adults) and their interactions with aquatic and terrestrial ecosystems. Keystone ecosystemic interactions are in green, negative natural and anthropogenic effects are in red, predatory interactions are in blue, and ecosystem services provided by the amphibians are portrayed in yellow. The numbers indicate the pathways detailed throughout chapters 2, 3, and 4. All silhouettes were taken from the PhyloPic website [https://www.phylopic.org; accessed on 24.02.2024] and other publicly available clipart deposits. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ability to reach high densities and biomass due to their fast-paced life histories, including fast reproductive rates and relatively short lifespans (Allen et al., 2017; Stark and Meiri, 2018; Stark et al., 2020). Tadpoles of most amphibian species are herbivorous, and thus, they affect primary producer species in freshwater ecosystems (Fig. 2 [2.11]; McDiarmid and Altig, 1999). For instance, tadpoles are known to act as keystone species, significantly affecting algal and periphyton community structures and biomass in lentic systems, thus reducing sediment accumulation and resulting in a slowing of the stream of nitrogen cycling (Kupferberg, 1997; Pankaj and Nath, 2023). Additionally, many frogs can digest various organic materials such as keratin and chitin (Wells, 2007), thereby they play an important keystone role as detritivores, enhancing organic matter dynamics and nutrient flow in various ecosystems (Flecker et al., 1999; Fig. 2 [2.12]). By having multiple life stages, often in different habitats, amphibians have been found to enhance the flow of nutrients in the ecosystem via energy transfer in the food chain between habitats (Wells, 2007; Collins et al., 2009; Valencia-Aguilar et al., 2013). Finally, frogs can potentially play a role in tropical ecosystems via pollination (Fig. 2 [2.13]) and seed dispersal (Fig. 2 [2.14]) of certain species of plants (through frugivory, e.g., *Xenohyla truncata* feeding on fruit and defecating seeds in moist microhabitats in Brazilian forests; da Silva et al., 1989; de-Oliveira-Nogueira et al., 2023). These different life cycle roles emphasise the importance of amphibians for ecosystem functionality.

3. Amphibians as bioindicators of ecosystem health

The complex life cycle of amphibians (aquatic larvae and terrestrial adults) makes them doubly susceptible to environmental disturbances (Becker et al., 2007). Amphibians have moist, permeable skin and unshelled eggs that are directly exposed to soil, water, and sunlight (Wells, 2007). They can, therefore, readily absorb toxic substances (Wells, 2007), and are sensitive to certain natural and synthetic chemicals (e.g., iodine and pesticides; Baier et al., 2016; Thambirajah et al., 2019). As the metamorphosis process depends on the concentration of iodine in the water (Thambirajah et al., 2019), the desiccation of water bodies, which is accelerated by rising temperatures, can have an impact on the timing of metamorphosis onset, its success, and the morphological characteristics of adults (Miyata and Ose, 2012). Pollution by chemicals (Fig. 2 [2.15]), the presence of pathogens and parasites (Fig. 2 [2.16]), and UV light (Fig. 2 [2.17]) can cause frogs to become malformed (Ankley et al., 2002; Johnson et al., 2002; Taylor et al., 2005). The interaction between pollution and rising temperatures due to global warming can intensify the negative effects on amphibians further (Hooper et al., 2013; Baier et al., 2016). Frogs can be indicators of various environmental disturbances, e.g., habitat loss and defragmentation, prolonged droughts, pollution by pesticides and herbicides (Fig. 2 [2.18]), fertilisers (Fig. 2 [2.19]), UV radiation (Fig. 2 [2.17]), overhunting (Fig. 2 [2.20]), viral/fungal/parasite infections (Fig. 2 [2.16]), and the presence of non-native invasive predators or competitors (Fig. 2 [2.21]; Andrade, 2015; West, 2018). These issues, however, are what make amphibians an important biological indicator of habitat degradation, pollution, and environmental health (Stuart et al., 2004) in both aquatic and terrestrial habitats (Fig. 2).

4. Amphibians as providers of ecosystem services

In addition to contributing non-ecological services to humans through food and medicine, adult amphibians can serve as excellent pest control (Fig. 2 [2.22]) in agricultural fields such as rice fields (Raghavendra et al., 2008). For instance, it has been found that 50 frog individuals can keep an acre of rice paddy free of pest insects (Raghavendra et al., 2008). Amphibians can also control the number of airborne insects such as mosquitos, as it has been found that up to

500,000 individuals per hectare are able to remove a large number of mosquitos in wetlands, ponds, streams, and rivers (West, 2018). By consuming a large number of insects, amphibians (both adults and tadpoles) regulate mosquito and fly populations, and thus decrease vectors of human pathogens such as malaria (Fig. 2 [2.23]; DuRant and Hopkins, 2008; Benelli et al., 2016). In some areas of the world where amphibian populations have declined, agricultural pests and human diseases have increased (Springborn et al., 2022). The decline of amphibians may thus also carry financial costs, because more money has to be spent on pesticides (West, 2018; Propper et al., 2020). In this age of human-induced climate change, tropical mosquito-borne diseases are migrating further away from the equator and will affect more people yearly as global temperatures continue to rise (West, 2018; Tidman et al., 2021). Tropical amphibians have co-evolved with the vectors of diseases such as malaria, dengue, and Zika fever, and have evolved to be efficient consumers of them (Mahr and Ridgway, 1993; West, 2018; Springborn et al., 2022). Thus, with the decline of tropical amphibians, there will be a reduction in predators that can consume tropical disease vectors with the same efficiency (Springborn et al., 2022). Because the trends of rising temperatures and pathogen migrations are likely to continue in the near future, amphibians have the potential to be a helpful tool in reducing the number of pathogen-bearing insects (West, 2018). This consideration further highlights the importance of conserving amphibian species, especially the highly threatened populations from tropical regions.

5. Current amphibian conservation efforts

Most conservation initiatives for amphibians today focus on ex-situ breeding programs in different facilities (e.g., zoos, aquariums and botanical gardens), with the ultimate goal of releasing suitable candidates into natural or restored habitats (Griffiths and Pavajeau, 2008; Harding et al., 2016; Bradfield et al., 2023). From a life-history point of view, amphibians are highly suitable for ex-situ conservation measures, due to several characteristics: their body size is comparatively small and requires very little space, they possess high fecundity, short generation time, and lack parental care (Smith and Sutherland, 2014; Tapley et al., 2015; Pincheira-Donoso et al., 2021). They also have relatively small home ranges compared to mammals and birds (Trochet et al., 2014), and in some cases, they cope with captivity, both physiologically and behaviourally, better than some other taxa (Biega et al., 2017). Yet, ex-situ conservation initiatives for amphibians are fewer than those for mammals (20 %) and birds (25 %), despite a recent rise in the last 20 years (from 4 % to almost 11 %; Dawson et al., 2016; Biega et al., 2017). These ex-situ programs are subjected to the logistical challenges and financial costs of captive breeding (e.g., high average annual costs of $130,000 USD for Australian species; Harley et al., 2018), which results in a limited number of initiatives worldwide. According to previous calculations, some ~1,000 species are in need of these programs, while there are only resources to hold approximately 50 amphibian species globally in captive programs (Zippel et al., 2011; Bishop et al., 2012; Murphy and Gratwicke, 2017; Luedtke et al., 2023). Although ex-situ programs can offer an important solution for rescuing critically endangered species and vanishing populations, they may sometimes be "too little too late" for many endangered species, because they may take too long, or because some species cannot adapt to captive conditions (Zippel et al., 2011). Thus, the need for more pragmatic actions (such as trophic rewilding or assisted migration) must be at the forefront of conservation initiatives worldwide (Svenning et al., 2016; Kracke et al., 2021; Ricciardi and Simberloff, 2021).

6. Steps in (re)introducing amphibians in trophic rewilding programs to enhance conservation efforts

Amphibian species may be considered optimal candidates for trophic rewilding programs, due to various advantages (see above), apparent at all (re)introduction stages, over other vertebrates used in rewilding projects, such as mammals, birds, reptiles or invertebrates (Gilbert et al., 2017; Bubac et al., 2019; Macdonald, 2019; Garrido et al., 2021, 2022; Brevé et al., 2022; Vasile, 2023; Stark and Galetti, 2024). Most critically, their (re)introduction can help conservationists to assess the human impact (e.g., clearance for crops, logging, clear-cutting, urbanisation and industrial development; Bishop et al., 2012) that has led in the first place to the degraded state of the ecosystem (Stuart et al., 2004). These advantages (as bioindicators of ecosystem health) may convince conservationists to increase the use of amphibians in trophic rewilding projects, and, through it, enhance conservation efforts of endangered species, and restore the habitats into which they are (re)introduced (Polak and Saltz, 2011). Several steps, detailed henceforth and presented in Fig. 3, need to be taken in the (re)introduction of amphibians into natural habitats:

First, it is critical to assess the state of the focal site, and to understand whether the environment is in a degraded, recovering, or stable condition (Fig. 3A). If the target site is in a stable state, conservationists should continuously monitor it and be aware of any new anthropogenic interference. Suppose the focal habitat is in a recovering state (i.e., species populations and trophic interactions are not stable); conservationists should reinforce existing declining amphibian populations while also engaging in repeated monitoring of the overall state of the aquatic ecosystem (Fig. 3A).

If the site is in a degraded state, however, e.g., the aquatic ecosystem is polluted and depauperate of amphibians, the first step would require an initial purification of the aquatic system. Before and while restoring the local vegetation, harmful abiotic toxins (e.g., fertilisers, pesticides, heavy metals, road deicers, nitrogenous and phosphorous compounds; Egea-Serrano et al., 2012) need to be removed from the focal habitat (Fig. 3A). Due to the sensitivity of amphibians to chytrid infections and its deleterious impact on amphibian populations worldwide (Stuart et al., 2004; Bishop et al., 2012), it is imperative to examine the prevalence of these fungi species (e.g., *Batrachochytrium dendrobatidis* and *Batrachochytrium salamandrivorans*; Fisher and Garner, 2020) in the designated rewilding area, and attempt to remove it before the (re)introduction of amphibians can take place. Following an efficient habitat recovery process, choosing the most suitable candidate for (re)introduction is essential. An ideal candidate would be a generalist species that would play a key role in the trophic interactions in the restored ecosystem, and would serve as a bioindicator for the health of the habitat (Fig. 3A). The generalist candidate could be a local species, whose population needs to be enhanced (i.e., reinforcement), reintroduced from neighbouring habitats (i.e., reintroduction or assisted migration), or a species that is introduced into the focal habitat from outside its native range, but is expected to perform the same ecological role (i.e., ecological replacement). If the chosen candidate species is not available in existing captive breeding programs, one can be established (Fig. 3B). If such a program is logistically not feasible (for the reasons described in Section 5), translocations of breeding individuals from neighbouring habitats can be performed, without captive breeding (i.e., assisted migration). Alternatively, it is also possible to collect egg masses from different populations to improve the genetic diversity of the released species, thereby increasing its chances of survival in the new habitat. Suppose the local species is unavailable for collection or translocation from other habitats. In such a case one must consider the collection and release of other species from outside their indigenous range, which can act as ecological proxies and perform similar ecological functions in the restored habitat (Linhoff et al., 2021). Subsequently, an initial release (hard/soft) of selected individuals of the candidate generalist species can occur, with repeated monitoring for population establishment and growth (Fig. 3B).

If the released population does not manage to establish itself, it is necessary to understand the reason and attempt a reinforcement by releasing more individuals (Fig. 3B), or consider the release of another candidate species. However, if the released population manages to

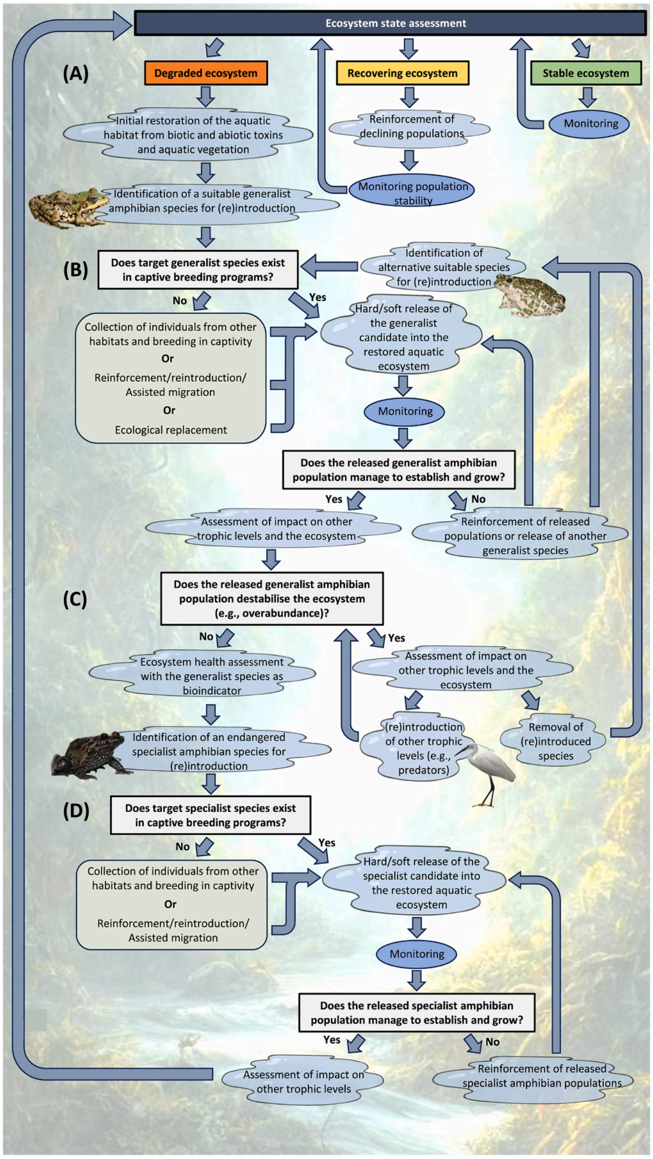

Fig. 3. Schematic description (based on the guidelines of the IUCN; Griffiths and Pavajeau, 2008; Harding et al., 2016; Linhoff et al., 2021) of proposed steps for the trophic rewilding of habitats, to conserve threatened amphibian species, and restore the natural environment. *Pelophylax bedriagae* (left; photo: Petra & Wilfried- Flickr) and *Bufotes viridis* (right; photo: Skampetsky) are given as examples of generalist amphibian species that can be (re)introduced, *Egretta garzetta* (photo: El Golli Mohamed) is given as an example of a predator of *Bufotes viridis*, and *Latonia nigriventer* (photo: Frank Glaw) is given as an example of an endangered specialist amphibian species that can be subsequently (re)introduced. The bold text in grey boxes suggests decision points where conservationists must answer a question to proceed to the next stage.

establish and grow, an assessment of the impact of the (re)introduced species on the aquatic ecosystem and other trophic levels should subsequently be made (Fig. 3B). Suppose the long-term effect on the recovering site can be categorised as stable (e.g., functioning trophic cascades and interactions). In that case, the focal ecosystem's health should be continuously monitored with the generalist species as a bioindicator, to ensure that the habitat is recovering, and that the ecosystem is functioning (Fig. 3C). However, in case the effect of the (re)introduced species is destabilising the recovering ecosystem (e.g., the (re)introduced species becomes overabundant and detrimental to other trophic interactions), it might be necessary to control its population, or attempt its removal from the habitat (Fig. 3C). When removing and controlling the species is impossible or undesired, the focal habitat can be reassessed, with the intention to (re)introduce another species belonging to a different trophic level. (Re)introducing a predator, for instance, may help to regulate and control the numbers of the targeted amphibian species, and potentially indirectly improve its impact on the focal restored habitat, and the ecological interactions therein (Fig. 3C).

After the generalist amphibian species has managed to perform an initial recovery of the habitat, and its survivability in the habitat is a testament to the habitat's health, it is possible to proceed and attempt the (re)introduction of a critically endangered amphibian species (e.g., one of the species depicted in Fig. 1). Such a species would often be a specialist, requiring specific niches or conditions, or depending on other species or ecological interactions (Fernandez et al., 2017; Galetti et al., 2017), which would be available at this point in the rewilding program (Fig. 3D). The specialist endangered species of choice can then be (re)introduced to the focal habitat from captive breeding programs or via assisted migration (Fig. 3D). If the released species fails to establish in the habitat (i.e. population reduction or extinction), conservationists may need to reinforce the population by releasing more breeding individuals, or by improving the genetic pool of the populations (e.g., releasing individuals from other captive programs/natural populations). If the released specialist species, however, does manage to establish itself, an assessment of its impact on other species and trophic levels needs to be done before reassessing the state of the whole habitat (Fig. 3D).

7. Conclusion

In our opinion, the best solution for the amphibian crisis lies in emphasising their potential for (re)introduction in rewilding projects worldwide. Their ability to serve as biological indicators of ecological health in certain ecosystems (e.g., freshwater habitats) can improve the results of initial rewilding initiatives. This step is beneficial in "laying the ground" for more complex and expensive (re)introduction attempts (e.g., mammalian herbivores or carnivores), which usually entail considering social and economic factors beforehand (Pettorelli et al., 2018; Perino et al., 2019). Rewilding using targeted amphibian species in certain regions worldwide (especially in the tropics) can help conservationists achieve a win-win situation. This doubly important goal includes the reinforcement and (re)introduction of declining populations of the most endangered vertebrate taxa on Earth (Amaral et al., 2019), while also helping to restore depauperate, ecologically dysfunctional habitats. We hope that considering and implementing the steps we propose in this perspective will help future conservation initiatives be more effective and successful.

CRediT authorship contribution statement

Gavin Stark: Conceptualization, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Rachel Schwarz:** Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

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

Data availability

No data was used for the research described in the article.

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