


Evolutionary principles guiding amphibian conservation

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Abstract

The Anthropocene has witnessed catastrophic amphibian declines across the globe. A multitude of new, primarily human-induced drivers of decline may lead to extinction, but can also push species onto novel evolutionary trajectories. If these are recognized by amphibian biologists, they can be engaged in conservation actions. Here, we summarize how principles stemming from evolutionary concepts have been applied for conservation purposes, and address emerging ideas at the vanguard of amphibian conservation science. In particular, we examine the consequences of increased drift and inbreeding in small populations and their implications for practical conservation. We then review studies of connectivity between populations at the landscape level, which have emphasized the limiting influence of anthropogenic structures and degraded habitat on genetic cohesion. The rapid pace of environmental changes leads to the central question of whether amphibian populations can cope either by adapting to new conditions or by shifting their ranges. We gloomily conclude that extinction seems far more likely than adaptation or range shifts for most species. That said, conservation strategies employing evolutionary principles, such as selective breeding, introduction of adaptive variants through translocations, ecosystem interventions aimed at decreasing phenotype–environment mismatch, or genetic engineering, may effectively counter amphibian decline in some areas or for some species. The spread of invasive species and infectious diseases has often had disastrous consequences, but has also provided some premier examples of rapid evolution with conservation implications. Much can be done in terms of setting aside valuable amphibian habitat that should encompass both natural and agricultural areas, as well as designing protected areas to maximize the phylogenetic and functional diversity of the amphibian community. We conclude that an explicit consideration and application of evolutionary principles, although certainly not a silver bullet, should increase effectiveness of amphibian conservation in both the short and long term.

KEYWORDS

amphibians, conservation biology, conservation genetics, habitat degradation, host parasite interactions, natural selection and contemporary evolution

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1 | INTRODUCTION

The Anthropocene has witnessed the demise of many amphibian populations across the globe (Cushman, 2006). Approximately 40% of extant amphibian species are threatened with extinction (IUCN Red List Data version 2019-1) and 34-170 are likely already extinct, at least in the wild. In addition, species with insufficient data for assessment (~21% of assessed species) are predicted to be more threatened with extinction than previously recognized (González-del-Pliego et al., 2019).

Extant amphibians live in environments exposed to a multitude of primarily human-induced drivers of decline. These drivers have been exhaustively reviewed elsewhere (e.g., Collins & Crump, 2009) and are briefly summarized in Box 1. Apart from causing demographic crashes and extinction, these stressors have a more nuanced effect on amphibian populations by inducing phenotypic and evolutionary change. For instance, adaptation to changing conditions might mitigate some of the detrimental effects of environmental degradation (Flynn, Love, Coleman, & Lance, 2019). Pathogens may remodel amphibian communities by altering biotic interactions among species with different levels of susceptibility (Bosch & Rincón, 2008). Climate change has allowed some species to colonize previously

unavailable habitat or expand demographically in some areas (Bosch, Fernández-Beaskoetxea, Garner, & Carrascal, 2018). Human encroachment has created new types of habitat (artificial water bodies, canals, rice paddies) that can be colonized by a few species that can adapt to and exploit altered environmental conditions (e.g., Davies, Hill, McGeoch, & Clusella-Trullas, 2019). Some of these examples, and others mentioned further in the text, reflect evolution in action in current amphibian populations. The challenge for amphibian conservationists is to manage the evolution of natural populations in a way that will secure their fate into the future.

The need to incorporate evolutionary considerations to understand and mitigate amphibian declines was clearly voiced more than a decade ago (Blaustein & Bancroft, 2007). Several reviews, particularly those focusing on the use of molecular markers, discussed evolutionary aspects of amphibian conservation (e.g., Allentoft & O'Brien, 2010; Beebee, 2005; McCartney-Melstad & Shaffer, 2015; Shaffer et al., 2015). However, an overview structured according to the major evolutionary mechanisms in a conservation context is unavailable and we hope to fill this gap. In this review, we examine how major evolutionary mechanisms relate to current amphibian population status (current threats) and what they mean for practical amphibian conservation. We summarize how evolutionary

BOX 1 The complexity of amphibian declines

No single remedy for the global amphibian decline exists because it is driven by a multitude of interacting factors (Figure 1, reviewed in Blaustein & Kiesecker, 2002; Blaustein et al., 2018; Collins & Crump, 2009; Cushman, 2006). Degradation or **destruction of habitat** due to changes in land use is probably the foremost threat to amphibians. The spread and outbreak of **emerging infectious diseases**, mostly by chytrid fungi and ranaviruses, but also trematodes *Ribeiroia ondatrae*s, fungi *Saprolegnia ferax*, and protists *Amphibocystidium ranae*, have triggered widespread declines and commanded the attention of conservation biologists in recent decades. The introduction of **harmful chemicals** (fertilizers, pesticides, and other environmental contaminants) into the world's air, soil, and particularly water supply alters development and physiology of amphibians and increases mortality. Furthermore, pollution can compromise host immune response or its protective microbiome, increasing pathogen virulence (Jiménez & Sommer, 2017). The introduction of **alien species** that predate, compete, hybridize with, or spread infectious diseases in autochthonous amphibian populations (Kraus, 2008) has taken a heavy toll on amphibian communities. A factor that is usually ignored in studies on amphibian declines is the role of population density and community composition. High densities increase not only competition but also the probability of infection. The natural composition of amphibian communities affects predation, competition, hybridization, and spread of emerging diseases, although higher diversity of an assembly can have a dilution effect on pathogens. In addition, the local or regional causes of decline are exasperated by global stressors. Rapid changes in temperature and precipitation patterns due to **global change** are affecting amphibians by shifting ranges and modifying life-history traits as well as biological and ecological interactions. For instance, climate change can increase temperature up to the optimum of pathogen development triggering a disease outbreak (Bosch, Carrascal, Duran, Walker, & Fisher, 2007). Desiccation caused by climate change can elevate levels of UV-B radiation in shallow waters increasing the effect of *Saprolegnia* fungus and environmental changes, and contamination can act as a cofactor influencing chytrid outbreaks in tropical America. Amphibians are overharvested for consumption and trade. The **global trade** in amphibians is causing or at least facilitating disease transmission and the establishment of non-native species. In conclusion, the global and local drivers of amphibian declines seldom act single-handedly. Instead, many amphibian populations are under the influence of two or more factors at once and the synergistic interactions between them oftentimes prove deadly to susceptible species (e.g., Cohen, Civitello, Venesky, McMahon, & Rohr, 2019). Despite their important role in amphibian decline, these interactions are poorly understood and, since the severity of each of the drivers varies in space and time, their interactions also vary. Hence, the main challenge for amphibian conservation is to find solutions to a local–global phenomenon occurring at multiple scales, identifying the specific drivers and their complex interactions, and dealing with them at the appropriate spatial scale (Grant et al., 2016).

principles have been applied in amphibian conservation, identify gaps, and provide recommendations as to where the application of evolutionary principles is likely to provide immediate and long-term progress in practical conservation. Our goal is to discuss how (and if) evolutionary mechanisms can be exploited toward the benefit of declining amphibian populations. Two important themes permeate this review. First, it is becoming widely appreciated that ecological and evolutionary processes are coupled at temporal scales that are relevant for conservation (Hendry, 2016; Stockwell, Hendry, & Kinnison, 2003). One pertinent amphibian example implicates an evolutionary response in the Sierra Nevada yellow-legged frog (*Rana sierra*) involving reduced susceptibility to the frog-killing chytrid fungus (Knapp et al., 2016). The remarkable recovery of this species in Yosemite National Park after decades of decline implies that evolutionary changes in imperiled amphibian species may occur at temporal and spatial scales compatible with human-aided recovery programs. Second, the field of applied evolution has emerged, with the aim of harnessing evolutionary processes to address global challenges, including biodiversity conservation (Carroll et al., 2014), providing a useful framework to conceptualize conservation work in light of evolutionary principles.

This review is structured according to evolutionary mechanisms and processes pertinent to amphibian conservation, starting at the scale of generations in local populations and ending with macroevolutionary processes (Figure 2). We emphasize factors that dictate population genetics (e.g., migration, drift, and selection), reflecting the large body of literature on the subject, but also highlight the effects of species interactions (invasives versus locals, pathogens versus hosts, hybridization) and macroevolutionary patterns meaningful for conservation. A notable exception is the lack of a section on mutation—because pressure from *de novo* mutations *per se* is unlikely to be of relevance at the temporal scale of a typical conservation horizon. We discuss, however, mechanisms affecting the dynamics of mutations segregating in populations, as these are important for conservation.

2 | DRIFT AND INBREEDING

Understanding the evolutionary effects of reduction in population size has been a major goal in conservation biology (Frankham, Ballou, & Briscoe, 2010). The main consequences of increased drift in small populations, collectively termed “genetic erosion,” are loss of genetic variation and increased inbreeding. The former leads to the loss of adaptive potential, while the latter exposes the phenotypic effects of deleterious recessive mutations, leading to inbreeding depression. The effective population size (N_e , Box 2), which measures the strength of drift, is a key parameter of conservation relevance (Hoffmann, Sgrò, & Kristensen, 2017) that generally negatively correlates with extinction risk (Frankham, 2005).

Fragmented populations of widespread European anurans show loss of genetic diversity and reduced fitness (Johansson, Primmer, & Merilä, 2007; Luquet et al., 2011; Rowe & Beebee, 2003). However,

heterozygosity–fitness correlations (HFCs) at the individual level have been observed only in a subset of amphibian studies (Allentoft & O'Brien, 2010). This is expected because HFCs, reflecting the effect of inbreeding depression, are only detectable in cases when substantial variance in inbreeding occurs between individuals. Two sources of reduced fitness due to deleterious mutations can be distinguished: (a) fixation of slightly deleterious mutations causing fixation load detectable by interpopulation comparisons and (b) the effects of strongly deleterious recessive mutations that segregate in populations and are exposed by inbreeding, detectable as HFCs at the individual level. In the European tree frog (*Hyla arborea*), larval fitness in small fragmented populations suffered from fixation load but HFCs were undetectable (Luquet et al., 2011). Moreover, neither fixation load nor HFCs were detected for adults in the wild, indicating either differences between traits in sensitivity to the accumulation of deleterious mutations, or the confounding effect of environmental variation (Luquet et al., 2013). The prediction that inbreeding depression should be more severe in the wild was corroborated by finding HFCs in the wood frog (*Lithobates sylvaticus*) in the field but not in the laboratory (Halverson, Skelly, & Caccone, 2006). If inbreeding depression is manifested at the larval stage, many pond-breeding amphibians characterized by high fecundity and high larval mortality may purge deleterious mutations without an excessive demographic cost of selection. Evidence for strong selection against inbreeding acting at the larval stage was found in a small population of the Italian agile frog (*Rana latastei*) (Ficetola, Garner, Wang, & De Bernardi, 2011). This mechanism may buffer the negative effects of small population size, allowing quick population recovery following habitat restoration. In another study on *R. latastei*, Ficetola, Garner, and De Bernardi (2007) showed that while variation within populations was affected by both habitat fragmentation and distance from the glacial refugium, fitness declined as a function of the former but not the latter. It is thus important to distinguish between old and recent reductions in variation, as their consequences for population viability and conservation may differ.

Threatened amphibians often have low census and effective population sizes, but N_e 's of local populations are naturally small in many widespread species (Box 2). Small populations of threatened amphibians may nonetheless harbor levels of genetic variation comparable to those of larger populations of the same or related species. For example, the ancient and highly endangered Hula painted frog (*Latonia nigriventer*), with contemporary N_e of several tens of individuals, still retains substantial microsatellite variation (Perl et al., 2018). Detailed historical records of fire salamander (*Salamandra salamandra*) occurrence in Oviedo, Spain, showed that despite isolation for hundreds of generations, populations in the city center still harbor substantial genetic variation (Lourenço, Álvarez, Wang, & Velo-Antón, 2017). Even in small populations, the loss of genetic variation can be a lengthy process, so a time lag is expected before the reduction of variation becomes apparent. Nevertheless, examples of endangered species that probably have always been small and isolated, such as the Montseny brook newt (*Calotriton arnoldi*) (Valbuena-Ureña, Soler-Membrives, Steinfartz, Orozco-terWengel,

Evolutionary-based conservation

Information ↑ ↓ Application

Evolutionary processes

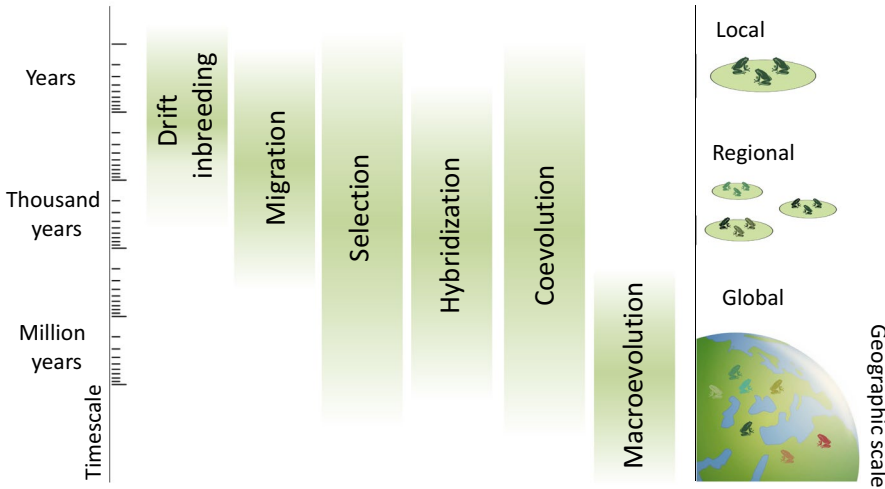


FIGURE 1 The framework of evolutionary conservation integrates processes operating at various scales

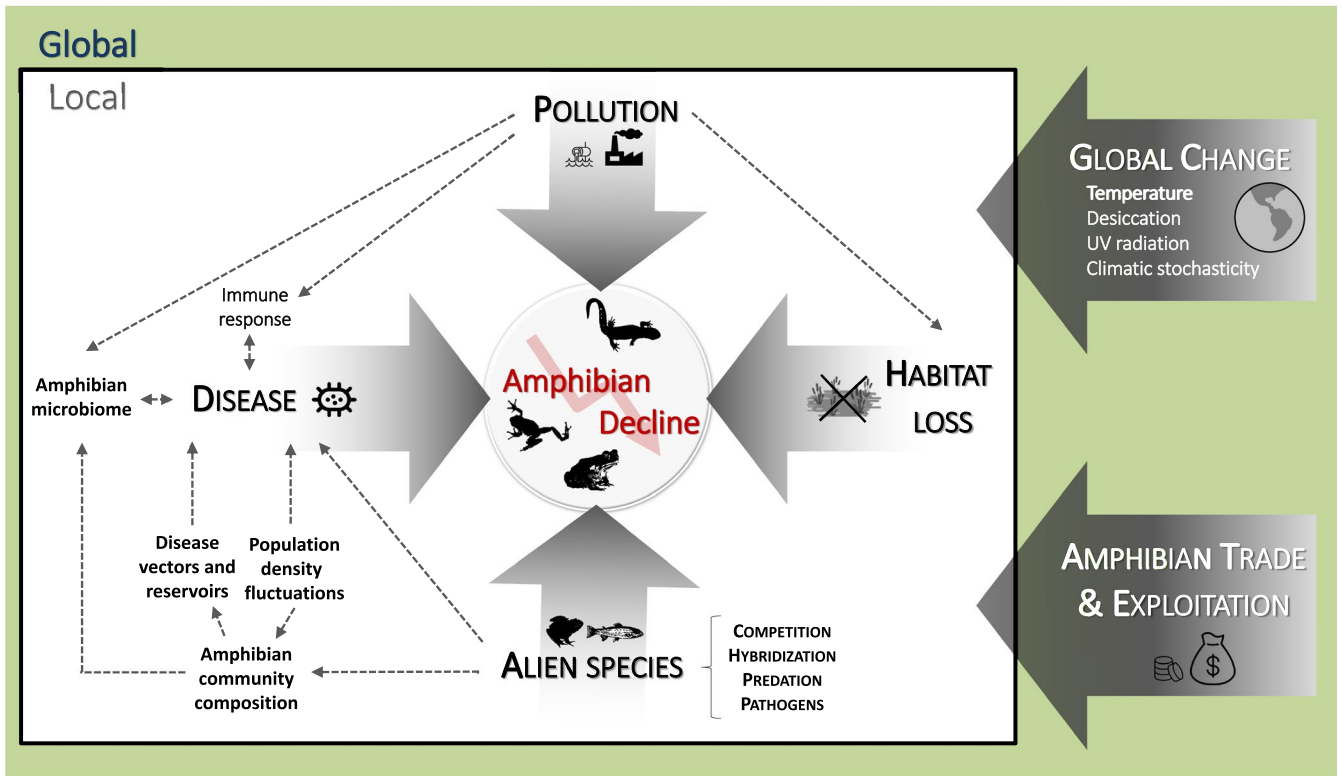


FIGURE 2 Drivers of amphibian decline and their complex interactions

& Carranza, 2017), indicate that even those can exhibit substantial variation.

A potentially highly effective conservation intervention alleviating the adverse genetic effects of reduced *N_e* is genetic rescue, involving the introduction of individuals from a different gene pool to improve fitness in the recipient population (Frankham, 2015). Surprisingly, we could not find any well-documented reports of

genetic rescue in amphibians, despite strong advocacy of the approach (Beauclerc, Johnson, & White, 2010). Beebee (2018) described a possible case of apparent genetic rescue in a peripheral natterjack toad (*Epidalea calamita*) population in the UK due to the inadvertent release of tadpoles from another population.

A recent example of using the principles described in this section for conservation is the case of the critically endangered dusky

gopher frog (*Lithobates sevosus*). The implementation of intense conservation efforts, including a headstarting program (raising hatchlings or juveniles in captivity and then releasing them into the wild) in 2002, resulted in an increase in N_e , as assessed using microsatellite markers, over a 17-year period (Hinkson & Richter, 2016), suggesting the effectiveness of management practices.

2.1 | Implications for conservation

Strong links exist between demography, evolutionary potential, and conservation. In recent years, our understanding of N_e in amphibians has improved, with the crucial insight that N_e of local populations is often modest (Box 2), although more data from directly developing tropical taxa are needed. Nevertheless, genetic variation may be considerable even in small populations. It appears that the effect of fragmentation on genetic variation is stronger in widespread species with high population connectivity than in naturally highly subdivided species. It is possible that in the latter, populations are largely independent in the medium term, so the effects of increased isolation are only gradually manifested and not yet clearly visible. Therefore, it is important to distinguish between recent fragmentation in high gene flow species and historical fragmentation of species of naturally low connectivity. Conservation actions improving connectivity may be of more immediate effect in the former, but are also important for the latter in the long term. In any case, the success of conservation

interventions may be assessed by following temporal trends in N_e using available tools (Boxes 2 and 3). Cautious optimism regarding the prospects of small amphibian populations is warranted because of genetic compensation (Box 2) and potential for selection against inbreeding without excessive demographic cost. To increase N_e in captive colonies even above census size, breeding schemes such as equalizing the number of progeny between families or subdivision can be used (Wang et al., 2016).

3 | MIGRATION

3.1 | Connectivity

Habitat fragmentation is a major cause of global biodiversity loss (Haddad et al., 2015). At the genetic level, fragmentation is associated with reduced gene flow, increased inbreeding, loss of diversity within populations, increased differentiation among populations, and elevated risk of extinction (Frankham, 2005). Understanding how changes in landscape composition and configuration affect intraspecific genetic variation and population viability is, however, an extremely challenging task, mainly due to the highly dynamic nature of landscapes (Epps & Keyghobadi, 2015; Richardson, Brady, Wang, & Spear, 2016). Nonetheless, studies at landscape genetic scales are widely recognized for their conservation potential (McCartney-Melstad & Shaffer, 2015; Richardson et al., 2016) and

BOX 2 Estimation and estimates of N_e in amphibians

Effective population size (N_e) is usually lower than census size and depends on sex ratio among breeders, variance in reproductive success between individuals, and, crucially, population size fluctuations across generations. Probably most relevant for conservation is contemporary, current, or recent (several generations) N_e of individual populations. These N_e estimates in amphibians usually go in tens, and only rarely in hundreds or thousands of individuals (Phillipsen, Funk, Hoffman, Monsen, & Blouin, 2011; Schmelzer & Merilä, 2007). The ratio of N_e/N varies from <0.01 to close to 1, but often is relatively high. Interestingly, elevated N_e/N ratios have been reported for small amphibian populations (Álvarez, Lourenço, Oro, & Velo-Antón, 2015; Beebee, 2009). The mechanisms behind genetic compensation of this sort are poorly understood but may involve reduced competition between males (Beebee, 2009) and have also been linked to intraspecific variation in phenotypic traits such as body size (Coles, Reading, & Jehle, 2019). Contemporary N_e is usually estimated using molecular markers. Historically, approaches based on temporal changes of allele frequency have been popular, but recently single-sample methods that explore linkage disequilibrium among unlinked markers or relatedness among individuals in a sample tend to dominate (Wang, Santiago, & Caballero, 2016).

Modest contemporary N_e values contrast markedly with estimates of tens or hundreds of thousands of individuals inferred from nucleotide variation using evolutionary models (e.g., Pabijan, Zieliński, Dudek, Stuglik, & Babik, 2017). Species-wide effective population size is conveniently defined in terms of the expected time to coalescence in a sample of DNA sequences (Charlesworth & Charlesworth, 2010). Such defined metapopulation N_e depends not only on population sizes but also on migration between them and can greatly exceed the sum of the census population sizes if migration between populations is low. To make things more complicated, estimates depend critically on the way DNA sequences are sampled. For example, under the assumption of a large number of populations, to estimate species-wide N_e , a single sequence per locus should be sampled from multiple populations. A sum of (long-term) effective sizes of a number of populations connected by migration can be inferred from DNA sequences sampled from a single population. The distinction between different aspects and timescales of N_e is well understood in the population genetic literature, but not sufficiently appreciated in the conservation context. Thus, paradoxically, a highly subdivided species harboring as a whole substantial genetic variation and characterized by large species-wide N_e can actually consist of very small populations on the verge of extinction.

BOX 3 An expanding molecular toolbox aids amphibian conservation

Conservation efforts can be severely hampered by incomplete distributional and taxonomic information. The proportion of unknown or undescribed amphibian taxa, particularly in tropical communities, can be staggering (Vieites et al., 2009), and some groups are particularly deficient in relevant conservation data (e.g., caecilians, Gower & Wilkinson, 2005). Molecular assessments of diversity, using rule-of-thumb sequence divergence thresholds in mtDNA, can be applied to screen for candidate species to be confirmed by integrative taxonomy approaches. Environmental DNA (eDNA) has emerged as a complementary or even alternative tool for monitoring amphibian species composition and has been particularly successful for secretive and rare species (e.g., hellbenders, Wineland et al., 2019). With improvements in sampling design (Goldberg, Strickler, & Fremier, 2018) and proof-of-concept studies for tropical batrachofauna (Bálint et al., 2018), eDNA metabarcoding has the potential to advance biodiversity assessment as well as long-term monitoring over large spatial scales. Community metabarcoding is also used to study diversity of amphibian microbiomes and has applications in disease mitigation and captive breeding for reintroduction purposes (Jiménez & Sommer, 2017).

Although full genomes are still a rare commodity in amphibian research, genome-scale molecular data are now accessible through the application of reduced representation techniques such as transcriptome sequencing, restriction-site-associated DNA sequencing, anchored enrichments, and other methods (reviewed in Funk, Zamudio, & Crawford, 2018). Genome-wide data have improved species delimitation in amphibians, but its applications are much farther ranging and have immediate conservation implications. For instance, Pabijan et al. (2017) have shown that the well-studied smooth newt complex of Europe contains eight different evolutionary lineages. Coalescent-based demographic modeling revealed that four southern lineages have been genetically isolated for a substantial amount of time and deserve species status. These species harbor a significant amount of the phylogenetic and morphological diversity of the complex and have rather restricted distributions; a revision of their conservation status is therefore timely.

The new standard in pathogen detection and quantification (particularly *Bd* and *Bsal* spp., Ranavirus) in amphibians is quantitative PCR (qPCR) which has eliminated the need for laborious and unreliable histological examinations of amphibian skin (Boyle, Boyle, Olsen, Morgan, & Hyatt, 2004). This technique is being applied to an expanding assortment of pathogen species (Karwacki, Atkinson, Ossiboff, & Savage, 2018). Creative solutions using new techniques have been suggested for combating cane toad expansion; for instance, Tingley et al. (2017) floated the idea of using CRISPR/Cas9-mediated targeted mutagenesis to knock out the toxin production pathway in toads and then use gene drive to spread the mutant in populations.

aid conservation in three main ways (Bolliger, Lander, & Balkenhol, 2014): (a) by providing baseline information on dispersal and movement patterns; (b) advising conservation strategies; and (c) evaluating the effectiveness of conservation measures.

Strong links between landscapes and population connectivity in amphibians result from their relatively low mobility and limited ecological versatility, with most species showing pronounced phylogeographic and population genetic structure (Vences & Wake, 2007; Zeisset & Beebee, 2008), while some may function as classic metapopulations (Smith & Green, 2005), especially aquatic-breeding species (e.g., Heard, Scroggie, & Malone, 2012). Regular extinction of local populations and dependence on recolonization make fragmentation a serious threat to the persistence of such species (Cushman, 2006; Rivera-Ortiz, Aguilar, Arizmendi, Quesada, & Oyama, 2015). Recently, a summary of 42 amphibian landscape genetic studies confirmed that anthropogenic landscape features (e.g., urban areas, roads, and agricultural fields) had an overall negative effect on genetic connectivity (Cayuela et al., 2018), in agreement with studies at phylogeographic scales (see Section 8). Furthermore, Cayuela et al. (2018) identified other general patterns, such as the negative relationship between topographic complexity and gene flow or the importance of forested areas and networks of aquatic habitat for connectivity. Nonetheless, the applicability of these findings in conservation is limited because connectivity patterns vary widely across

taxa and landscapes. Recent comparative landscape genetic studies on amphibians revealed contrasting connectivity patterns at all levels of evolutionary distinctiveness: urodeles versus anurans (Gutiérrez-Rodríguez, Gonçalves, Civantos, & Martínez-Solano, 2017), closely related frog species (Robertson et al., 2018), and even at intraspecific levels (Lourenço, Gonçalves, Carvalho, Wang, & Velo-Antón, 2019). This finding has stimulated interest in multispecies inference and predictive frameworks, such as trait-based approaches (Mims, Kirk, Lytle, & Olden, 2018). To give an example, in a species-rich tropical anuran assemblage in Madagascar, small-bodied species are poorer dispersers and thus show lower connectivity and stronger genetic structure over landscapes (Pabijan, Wollenberg, & Vences, 2012). Conservation measures maintaining or promoting population connectivity in the smaller species should safeguard most other species in this community. This approach has considerable conservation potential, especially given the growing availability of amphibian trait data (Mims et al., 2018), but it should be kept in mind that the relationships between traits and population connectivity will likely vary among regions and species assemblages.

The potential of genetic tools to advance connectivity research and aid conservation has long been recognized, but direct applications in amphibian conservation are still rare. Genetic evidence has linked pond network density with increased population connectivity in, for example, *H. arborea* (Angelone & Holderegger, 2009), *Ambystoma*

macrodictylum (Savage, Fremier, & Bradley Shaffer, 2010), and *L. sylvaticus* (Coster, Babbitt, & Kovach, 2015). Landscape genetic studies following pond restoration include an assessment of European tree frog populations in Switzerland (Angelone & Holderegger, 2009) and palmate newt (*Lissotriton helveticus*) populations in France (Isselin-Nondedeu et al., 2017). Both studies confirmed the restoration of ponds in a stepping-stone manner as an effective measure to re-establish connectivity among populations. Further genetic surveys are necessary to better understand the effects of such strategies on long-term patterns of population genetic diversity and viability.

An important factor that is expected to further empower connectivity research and, by extension, practical conservation strategies is increased resolution of molecular markers. A recent study reassessing connectivity in the New York-endangered eastern tiger salamanders (*Ambystoma tigrinum*) exemplifies the power of genome-wide data in detecting effects of anthropogenic fragmentation (McCartney-Melstad, Vu, & Shaffer, 2018). Using thousands of nuclear SNPs, the authors detected restricted connectivity between ponds separated by major roads, in stark contrast with a previous study based on microsatellites that apparently lacked power.

3.2 | Range expansion

Although global change has had detrimental effects on most amphibians, a handful of generalist species have thrived in its wake by extending their ranges into formerly unoccupied areas. It is useful to differentiate between range expansion as the development of new population foci in the proximity of the native range of a species, and the expansion of introduced alien or invasive species far beyond their natural ranges (e.g., Zeisset & Hoogesteger, 2018). Although there are many parallels between the two, there are also differences (Moran & Alexander, 2014). Most notably, the establishment of an alien involves the removal of a species from its evolutionary context and places it within an entirely novel environment (see Section 6). In comparison, native populations only rarely undergo abrupt and severe environmental change and may also benefit from higher N_e , conducive toward adapting to new circumstances. Recent range expansions have been studied in the context of climate change in high-altitude populations. Bosch et al. (2018) report expansions for three species into newly available habitat in the Peñalara region of Spain, and altitudinal expansion of three amphibian species in the Andes has been linked to recent deglaciation (Seimon et al., 2007). Habitat conversion has been implicated in the expansion of several generalist amphibian species, for example, *Hyperolius* in South Africa (Davies, Clusella-Trullas, Hui, & McGeoch, 2013) and *Polypedates leucomystax* in South-East Asia (Brown et al., 2010). The evolutionary implications of climate- or landscape-related, recent range shifts in amphibians have not been explored thoroughly. However, an ongoing expansion of plains spadefoot toads (*Spea bombifrons*) into similar habitat (grassland) does not seem to decrease population connectivity or genetic diversity (measured as microsatellite variation) in the new populations; in contrast, expansion into novel

habitat (desert) resulted in strong population differentiation, likely the result of bottlenecks and lack of connectivity (Pierce, Gutierrez, Rice, & Pfennig, 2017).

3.3 | Implications for conservation

Genetic evidence clearly shows that human-induced habitat fragmentation is the main factor behind the loss of genetic connectivity, leading to genetic erosion (see Section 2) and thus compromising the long-term viability of amphibian populations. The process is predicted to accelerate through synergistic interactions with global climate change (Mantyka-Pringle et al., 2015). European amphibians illustrate this problem, with numerous species expected to expand their ranges in response to climate change (Araújo, Thuiller, & Pearson, 2006). However, if dispersal and range expansion are constrained by habitat loss and fragmentation, amphibian populations will necessarily depend on their capacity for rapid adaptation for survival in the long term (see Section 4). On a more positive note, land cover can potentially buffer the negative effects of climate change because of its greater influence on patterns of connectivity among populations compared to climate, at least at local scales. Taking these factors into consideration, protecting the existing primary habitat patches and securing or increasing their quality should be the default conservation strategy (Ralls et al., 2018). However, the negative effects of increased connectivity (e.g., maladaptive gene flow, spread of disease and invasive species) should also be considered. For instance, among population gene flow has the potential to erase locally evolved, disease-resistant genotypes in isolated populations of *Lithobates yavapaiensis* (Savage, Becker, & Zamudio, 2015). In this case, effective management should encompass activities aimed at preserving genetic diversity within populations (e.g., increasing effective population size) rather than promoting connectivity. Keeping in mind both the benefits and potential pitfalls of gene flow in a quickly changing world, we advocate considering the available genetic evidence directly linking landscape features and connectivity patterns in specific areas (mostly at local scales) when designing conservation strategies (Bolliger et al., 2014; Grant, Muths, Schmidt, & Petrovan, 2019).

The translocation of individuals is an important tool in the conservation of small, inbred populations through demographic or genetic restoration. Usually, nearby locations are chosen as donor sites because it is thought that individuals from distant populations will fare worse due to local adaptation and increased risk of outbreeding depression (Frankham et al., 2011). In a translocation experiment spanning nearly four decades, Zeisset and Beebee (2013) showed that repeated translocations of common toads (*Bufo bufo*) from nearby donor populations consistently failed to establish at a receptor site, whereas a single translocation from a distant site with different environmental characteristics became established and eventually thrived. The authors suggest that success was determined by the large size of the distant donor population, and by its higher mean fitness or more adaptive variation than the local but smaller donor sites. After 10 years, the receptor population retained allele frequency distributions at microsatellite loci similar to the donor site, but intriguingly

MHC allele frequencies shifted to resemble local ones. This study implies that the risks of losing local adaptation can be offset if the introduced individuals originate from large populations because of a strong correlation between population size and fitness or adaptive variation in amphibians. Moreover, local selection acting on some loci of the genome can be very rapid (~3 toad generations), and these loci may often be involved in disease resistance. At a practical level, this study adds weight to the suggestion that the release of many individuals (>1,000) increases the chances of success of a translocation project (Germano & Bishop, 2009). Obtaining large numbers of animals for translocation by removal of eggs or larvae is entirely feasible for many species of aquatic-breeding amphibians. Targeted or assisted gene flow involves moving individuals with advantageous traits to imperiled populations in an effort to increase viability (Kelly & Phillips, 2016). While promising, this approach has caveats including unpredictability and the potential for undesirable side effects such as the loss of genome-wide genetic variation and adaptive potential. Management and decisions should carefully balance these liabilities against the risk of local extinction without intervention (O'Donnell, Drost, & Mock, 2017).

4 | SELECTION

Literature abounds in examples of rapid phenotypic response to biotic and abiotic environmental factors, often of anthropogenic origin (Hoffmann & Sgro, 2011). Phenotypic shifts may not necessarily involve genetic changes, but can also be due to phenotypic plasticity, and distinguishing between the two is challenging (Merilä & Hendry, 2014). Only adaptation can prevent extinction in species unable to track suitable environment via range shifts (the concept of “evolutionary rescue,” reviewed in Bell (2017)). However, phenotypic plasticity and other nongenetic mechanisms may “buy time” and provide an opportunity for evolutionary rescue. Such nongenetic mechanisms may thus set the stage for adaptation (but also prevent it, see Ghalambor, McKay, Carroll, & Reznick (2007)) and also contribute to adaptation more directly, through genetic assimilation (Ehrenreich & Pfennig, 2015). Finally, plasticity itself can evolve. Because plastic responses of amphibians to environmental changes have recently been reviewed (Levis & Pfennig, 2019; Urban, Richardson, & Freidenfelds, 2014), we do not cover them here. Instead, we focus on genuine adaptive response and discuss two seemingly disparate, but closely linked issues: (a) whether the adaptive potential of amphibians is sufficient or can be increased to the point that it becomes relevant for conservation and (b) whether conservation interventions can prevent unwanted evolution.

4.1 | The extent and rate of rapid adaptation in amphibians

A substantial fraction of the rapid phenotypic response to climate change in amphibians involves adaptive genetic changes (estimated proportion of genetic responses was 0.65, Urban et al. (2014)). This,

and examples in Table 1, indicate considerable potential for rapid adaptation in amphibians. Other spectacular examples of fast phenotypic response also implicate genetic effects (e.g., Halfwerk et al., 2019; Vimercati, Davies, & Measey, 2018).

A leading amphibian example for rapid adaptation to temperature change is provided by studies on the wood frog demonstrating shifts in thermal tolerance and preference as well as temperature-specific developmental rate (Freidenburg & Skelly, 2004; Skelly & Freidenburg, 2000). Modeling by Skelly et al. (2007) suggested rapid evolution of critical thermal maxima, with estimated change of 3.2°C in 50 years, potentially mitigating the effects of predicted climate warming. However, this model assumes no loss of relevant variation during adaptation and ignores accompanying environmental change, and may therefore be too optimistic. Furthermore, the predicted rates of climate change probably dramatically exceed past rates of climatic niche evolution in vertebrates, including amphibians (Quintero & Wiens, 2013). Further examples document swift adaptation to, for example, novel predators, urbanization, insecticides, or contaminants (Table 1).

Of particular interest, given the threat it currently poses for amphibians worldwide, is the adaptive response to invasive fungal pathogens *Batrachochytrium dendrobatidis* (*Bd*) and *B. salamandrivorans* (*Bsal*). The adaptive potential to overcome the pathogen has been demonstrated for some amphibian populations (Kosch et al., 2019; Palomar, Bosch, & Cano, 2016). Changes in MHC allele frequencies (Savage & Zamudio, 2016) and other components of the immune system (Voyles et al., 2018) have been documented in response to *Bd* (see Section 7). Amphibian species often harbor considerable MHC variation providing raw material for adaptation (e.g., Fijarczyk, Dudek, Niedzicka, & Babik, 2018), which can, however, be rapidly lost, for example, following range expansion (Wielstra, Babik, & Arntzen, 2015). It is also known that particular sequence motifs, detected in multiple species, may affect susceptibility to *Bd* (Bataille et al., 2015). These two observations suggest that direct interventions promoting the spread of resistant alleles, such as selective breeding and targeted gene flow, may be conservation measures of immediate effect.

4.2 | Preventing unwanted adaptation

The importance of ex situ amphibian conservation through captive breeding programs (CBP) is likely to increase (<http://www.amphibiana.org/>), even though captive assurance programs outnumber programs aimed at reintroductions (Harding, Griffiths, & Pavajeau, 2016). A major issue specific to CBP is adaptation to captivity, which can occur even in a single generation (Christie, Marine, French, & Blouin, 2012), and is detrimental to fitness in the wild (Frankham, 2008). Although origin of donor animals (wild, captive, or a combination) did not seem to affect translocation success (Germano & Bishop, 2009), only a small number of studies have looked into the issue. Indeed, a study on the Mallorcan midwife toad (*Alytes muletensis*) found that more than eight generations in captivity negatively affected not only

TABLE 1 Examples of recent or contemporary adaptation in amphibians

Taxon	Adaptation to	Response	Plasticity involved?	Evidence for genetic change	References
<i>Ambystoma maculatum</i>	Proximity of breeding site to roads	Environment-dependent survival	ND (maternal effects cannot be excluded)	Genotype-by-environment interaction in a reciprocal transplant experiment	Brady (2012)
<i>Plethodon cinereus</i>	Habitat (forest cover) and temperature change	Proportion of two discrete color morphs differs between habitats	No	Color morph is genetically based	Cosentino, Moore, Karraker, Ouellet, & Gibbs (2017), but see Evans, Forester, Jockusch, & Urban (2018)
<i>Taricha granulosa</i>	Road deicing salts	Adaptive potential for salinity tolerance	ND	Variance in tolerance among families	Hopkins, French, & Brodie (2013)
<i>Lithobates sylvaticus</i>	Temperature change	In <40 years, thermal tolerance, preference, and temperature-specific development rate have changed	No	Genotype-by-environment interaction in a reciprocal transplant experiment	Freidenburg & Skelly (2004); Skelly & Freidenburg (2000)
<i>Lithobates sylvaticus</i>	Insecticide	Higher constitutive insecticide tolerance close to agriculture, but higher induced tolerance far from agriculture	Yes	Differences in tolerance between populations in a gradient of distance from agriculture; pattern consistent with genetic assimilation	Hua et al. (2015)
<i>Lithobates sylvaticus</i>	Predation from <i>Ambystoma opacum</i> (predator range expands due to climate change)	Morphology, developmental rate, and behavior changed in response to predator presence	Yes	Genotype-by-environment interaction in a reciprocal transplant experiment	Urban et al. (2017)
<i>Lithobates sylvaticus</i>	Anthropogenic noise	Decreased physiological response to noise in populations exposed to anthropogenic noise	ND	Population-level differences in response	Tennessen et al. (2018)
<i>Lithobates sylvaticus</i>	Urbanization	Directional changes in allele frequencies	ND	Genome-wide association study supported an association between environment type and F_{ST} outlier loci identified in urban-rural comparison	Homola et al. (2019)
<i>Lithobates yavapaiensis</i>	<i>Bd</i> infection	Change in MHC allele frequencies	No	Signatures of ongoing positive selection on MHC alleles and supertypes in field and laboratory studies	Savage & Zamudio (2016)
<i>Rana arvalis</i>	Acid stress tolerance	Higher acid tolerance in populations exposed to acid conditions since the 1900s	Yes (maternal effect on survival under acid stress)	In reciprocal crosses between frogs from acid-exposed and nonexposed populations, genetic effects found in development and growth	Räsänen, Laurila, & Merilä (2003)
<i>Rana temporaria</i>	Different pool-drying patterns	Different growth rates and development rates caused probably by different foraging efforts	Yes	Support for a model assuming selection on standing genetic variation	Lind & Johansson (2011)
<i>Rhinella marina</i>	Dispersal opportunity	Dispersal abilities increased at the invasion front	ND	Heritable variation within and differences between populations	Phillips et al. (2010)
<i>Rhinella marina</i>	Low temperature (following invasion of new area)	Populations from cooler area have lower critical thermal minima	Yes	Persistent differences between populations after acclimation	Mittan & Zamudio (2019)

Abbreviations: *Bd*, *Batrachochytrium dendrobatidis*; ND, not determined.

genetic variation, but also a trait clearly related to fitness—induced antipredator defense (Kraaijeveld-Smit, Griffiths, Moore, & Beebee, 2006). A recent modeling study revealed that even a small amount of adaptation to captivity can have a long-term detrimental effect on natural populations supplemented with captive stock, with stronger consequences predicted for species with shorter life spans and higher rates of population replacement (Willoughby & Christie, 2019). Adaptation to captivity could be mitigated by applying the obvious but oftentimes impractical strategies of minimizing time spent in captivity or by ensuring that husbandry conditions are similar to those in the wild. The prospects of applying cryopreservation as an alternative for preventing unwanted evolution are unclear (Silla & Byrne, 2019). Another available strategy entails eliminating selection between families through equalization of family sizes (reviewed in Frankham, 2008). A further promising approach, supported by experimental evidence, is fragmentation, that is, the maintenance of several subpopulations in captivity and mixing before reintroduction. This slows down adaptation and effectively maintains variation and fitness at the level of the entire species/colony (Frankham, 2008). The effectiveness of this approach has not been examined in amphibians.

4.3 | Implications for conservation

It remains largely unknown whether the rate and magnitude of adaptation in amphibians will be sufficient to prevent declines and extinction given the expected scale of environmental change in the coming decades. The prospects for successful adaptation are best in widespread species which could thus be subject to proactive conservation measures (Sterrett et al., 2019) but at the same time are, understandably, of lower conservation priority. Priority species often exhibit characteristics (i.e., small population size, depleted variation, large distance from fitness optimum) that reduce the likelihood of evolutionary rescue (Bell, 2017; Hoffmann et al., 2017). The scale of reduction of adaptive potential in endangered amphibians is currently unknown. However, there are reasons for moderate optimism regarding the prospect of adaptation to pathogen assault (Christie & Searle, 2018; Kosch et al., 2019; Voyles et al., 2018). Even threatened species often harbor the necessary genetic variation. Selective breeding, translocations that promote gene flow, and even interspecific introgression may be effective in some situations (see Section 5), while the risks of such interventions may be overestimated (Frankham et al., 2011). Conservation actions that increase fitness by reducing the mismatch between phenotype and environment, for example, the establishment of thermal refugia (see Section 7), are also worthy of further exploration, as they may reduce the demographic cost of selection that could otherwise lead to extinction. Finally, although the adaptive potential of amphibians in the context of global change may be limited, it is nevertheless important to consider the effect of contemporary evolution in projections of the future loss of amphibian biodiversity. Otherwise, the predicted loss is likely to be overestimated (Razgour et al., 2019).

5 | HYBRIDIZATION

Hybridization, defined as mating between genetically distinct populations or species, can have a variety of evolutionary outcomes. It can cause the breakdown of reproductive barriers and fusion of lineages or, conversely, strengthen reproductive isolation and complete the speciation process. Hybridization can fuel adaptive radiations by providing ample genetic variation. From the conservation perspective however, the most important are shorter-term (several tens of generations) consequences of hybridization and we focus on them here.

5.1 | Hybridization as a challenge for conservation

Hybridization can disproportionately affect species of conservation concern, sometimes driving them to extinction (Todesco et al., 2016). Low hybrid fitness may cause demographic swamping, that is, when population growth rates of parental species fall due to wasted reproductive effort, leading to extinction. For instance, human-mediated hybridization between the Gulf Coast toad (*Incilius nebulifer*) and Fowler's toad (*Anaxyrus fowleri*) has contributed to a decline of the latter due to strong postzygotic isolation (Vogel & Johnson, 2008). Hybrids of *Lithobates blairi* and *L. sphenocephalus* may cope less efficiently with emergent pathogens (Parris, 2004).

If hybrids are fit and population growth rates exceed replacement rates, then the parental species may be replaced by hybrids, a process referred to as genetic swamping (Todesco et al., 2016). Genetic swamping is often observed when a widespread species hybridizes with a rare, geographically restricted congener. For instance, hybridization between the Florida bog frog (*Lithobates okaloosae*) and the green frog (*L. clamitans*) puts into question the distinctiveness of the former (Austin, Gorman, Bishop, & Moler, 2011). Genetic swamping through human-mediated introgressive hybridization between local species and exotic relatives is an important aspect of biological invasions. Hybridization between invasive barred tiger salamander *Ambystoma mavortium* and California tiger salamander *A. californiense* threatens the latter due to higher hybrid survival rates (McCartney-Melstad & Shaffer, 2015). In Switzerland and the Netherlands, massive introgression from invasive *Triturus carnifex* resulted in local pollution of the genome of threatened *T. cristatus* (Dufresnes et al., 2016; Meilink, Arntzen, van Delft, & Wielstra, 2015). In extreme cases, hybridization can result in the formation of a population comprised entirely of hybrids (hybrid swarm) and, thus, the loss of a pure parental species—this appears to be the fate of most Swiss populations of the pool frog *Pelophylax lessonae* following invasion by the Italian pool frog (*P. bergeri*) (Dufresnes et al., 2017). *Pelophylax* frogs seem to be particularly prone to lineage fusion after introduction: Molecular sequence analysis has revealed numerous cases of cryptic translocations of several exotic lineages in Europe. The extent and consequences of the resulting introgression events are unclear, but may dramatically affect the viability of native hybridogenetic populations through demographic or genetic swamping (Dufresnes & Dubey, 2020).

From a broader perspective, hybrids can also negatively impact other amphibian species. For example, hybrid tiger salamander larvae dramatically reduced the survival of two native amphibians (Ryan, Johnson, & Fitzpatrick, 2009). Hybridization and subsequent recombination between strains can generate new, highly virulent pathogen genotypes, as in the case of two *Bd* lineages in Brazil's Atlantic Forest. The virulence of the new hybrid lineage exceeded that of both parents in some host species, suggesting that novelty arising from hybridization between *Bd* strains is of conservation concern (Greenspan et al., 2018).

5.2 | Hybridization as an opportunity for conservation

Hybridization may also facilitate conservation (Hamilton & Miller, 2016). First, hybridizing species may have access to a larger pool of genetic variation than species evolving independently (Hedrick, 2013), which may increase their adaptive potential. Introgressive hybridization from the Mexican spadefoot toads (*Spea multiplicata*) may have facilitated the expansion of plains spadefoot toads into novel habitat in the southwestern United States (Pierce et al., 2017). Beneficial alleles can cross species barriers relatively easily even at advanced stages of speciation, when selection against hybrids is strong and the risk of genetic swamping is low. For example, the highly diverged newts *Lissotriton vulgaris* and *L. montandoni* demonstrate massive, most likely adaptive introgression of MHC (Dudek, Gaczorek, Zieliński, & Babik, 2019) and possibly other immune genes (Fijarczyk et al., 2018).

Second, extensive and asymmetric mtDNA introgression may involve the replacement of mutationally loaded mtDNA by molecules of lesser load, preventing mutational meltdown in the recipient species (Hill, 2019). Newts from the *L. vulgaris* complex (Pabijan et al., 2017) are a possible example. However, interspecific crosses are rarely used for genetic rescue due to concerns about outbreeding depression (Kovach, Luikart, Lowe, Boyer, & Muhlfeld, 2016). Nevertheless, in cases of severe inbreeding depression, human-assisted hybridization should be seriously considered as a last-ditch resort for genetic rescue, even though such interventions are reaching the limits of what conservation is.

Finally, hybridization may lead to reinforcement of prezygotic isolation. In the hybrid zone between North American upland chorus frog (*Pseudacris feriarum*) and southern chorus frog (*P. nigrita*), reinforcement has led to the evolution of both female preferences and male signals, resulting in increased prezygotic isolation countering maladaptive hybridization (Lemmon & Lemmon, 2010).

5.2.1 | Implications for conservation

Hybridization is of conservation concern because of the risk of demographic and genetic swamping; however, it is also a potential source of adaptive genetic variation. Predicting which is more likely

following secondary contact has management value. Although the negative effects of hybridization have been emphasized, only a few studies have assessed the fitness effects of introgressed alleles. This information is crucial for an understanding of the consequences of hybridization in maintaining species distinctiveness and adaptive potential (Kovach et al., 2016), and also its effectiveness as a tool used in conservation interventions.

Growing trade and climate change will likely cause further amphibian range shifts and invasions. Therefore, a global increase in hybridization frequency is expected. However, the legal status of genetically admixed individuals remains largely unresolved. Hence, coherent policy on hybrids and hybridization is urgently needed. In our opinion, naturally occurring hybrids are part of the evolutionary process and as repositories of their parental genomes should be subject to the same conservation policy as parental species. Regarding the protection status of hybrids resulting from human-mediated hybridization, we argue that decisions should be made on a case-to-case basis to maximize the retention of genetic diversity, distinctiveness, and fitness of species involved (Wayne & Shaffer, 2016). Hybridization is still an underexplored and underappreciated source of genetic variation which can be utilized for genetic rescue of species when there is no possibility of intra-specific population crosses. As the amphibian conservation crisis worsens, the propagation of genetic variation via human-mediated hybridization may become a valuable part of the amphibian conservationist toolbox.

6 | EVOLUTIONARY EFFECTS OF INVASIVE AMPHIBIANS

The intentional or inadvertent introduction of alien amphibian species has occurred hundreds of times across the globe (Kraus, 2008). Of the dozens of species that have established populations far outside of their native ranges, seven (in descending impact: *Rhinella marina*, *Xenopus laevis*, *Duttaphrynus melanostictus*, *Ambystoma tigrinum*, *Lithobates catesbeianus*, *Eleutherodactylus coqui*, and *Osteopilus septentrionalis*) have undisputed and significant ecological impacts and have generated the most scientific interest (Measey et al., 2016). Some of the world's most highly invasive amphibian species (e.g., *Xenopus laevis*, *Rhinella marina*, and *Lithobates catesbeianus*) are also subclinical carriers of deadly amphibian pathogens and aid in their spread and maintenance in the environment (Fisher & Garner, 2007). The consequences of amphibian introductions include increased predation, competition, hybridization (see Section 5), and others, as well as socio-economic impacts to human well-being and food production (Kraus, 2008, 2015; Measey et al., 2016). Many of these changes may have evolutionary consequences in both the invading species and the impacted native species (Shine, 2012).

One common finding is that successful establishment of invasive amphibians is not contingent on the genetic variation present in the founding population: Most amphibian invaders have low genetic diversity yet exhibit spatial and demographic growth (e.g., Peacock,

Beard, O'Neill, Kirchoff, & Peters, 2009). Moreover, introduced populations may themselves be sources of secondary introductions (Heinicke, Diaz, & Hedges, 2011).

Much of the information on evolutionary repercussions in invading species comes from comprehensive analyses of the cane toad (*Rhinella marina*), the natural range of which encompasses Central and tropical South America. This species has been intentionally introduced into other tropical regions, most notably into northern Australia and many Pacific islands. All life stages of this toad produce toxic substances, and lethal ingestion is the primary pathway of direct impact on native species. In Australia, the range of this species has expanded rapidly over the last eight decades (Urban, Phillips, Skelly, & Shine, 2008). A reduction in genetic diversity after the introduction does not seem to have affected ecologically relevant traits in cane toads (Selechnik et al., 2019); instead, the up-regulation of a suite of genes related to metabolism, energetics, and immune function may hold the key to increased invasiveness in this species (Rollins, Richardson, & Shine, 2015). The spread of toads in Australia has resulted in the appearance of a range-expansion phenotype manifested in dispersal-prone behavior, faster growth rates, longer leg lengths, and greater stamina in toads at the invasion front (Lindström, Brown, Sisson, Phillips, & Shine, 2013; Phillips, Brown, Webb, & Shine, 2006). Common-garden experiments suggest that many of these traits have a genetic basis and are potentially adaptive (Gruber, Brown, Whiting, & Shine, 2017; Phillips, Brown, & Shine, 2010). However, there is also evidence that faster dispersal in toads at the invasion front is a result of the spatial sorting of alleles determining higher mobility: Such alleles will inevitably accumulate at the range margin leading to assortative mating by dispersal in toads (Phillips et al., 2006; Shine, Brown, & Phillips, 2011). Thus, adaptive evolution in both life-history and dispersal traits, spatial sorting due to nonequilibrium demographics, and epigenetic mechanisms have all contributed to the invasiveness of this species (Perkins, Phillips, Baskett, & Hastings, 2013). In line with the cane toad example, a recent study documented longer limbs and greater stamina in peripheral populations of the invasive African clawed frog (*Xenopus laevis*) in France (Louppe, Courant, & Herrel, 2017), albeit at a much smaller spatial scale.

In another toad example (Vimercati et al., 2018; Vimercati, Davies, & Measey, 2019), an invasive population of the guttural toad (*Sclerophrys gutturalis*) in South Africa has evolved a suite of behavioral, phenotypic, and reproductive traits that allow it to better cope with the drier conditions in its new range. However, it is not yet possible to distinguish whether these shifts represent local adaptation or phenotypic plasticity and thus should be viewed as responses lowering phenotypic mismatches between invasive species and their novel environments.

A recent meta-analysis found that alien species of a wide range of taxonomic groups (but especially fish and crayfish) have detrimental effects on native amphibian species (Nunes et al., 2019). However, native amphibian populations may also respond adaptively, reducing the invaders' impact or exploiting the novel opportunity it provides (reviewed in Shine, 2012 and Table 1).

6.1 | Implications for conservation

Identifying the provenance of extralimital amphibian populations is important for prioritizing conservation actions (do we eradicate or protect?) but can be tricky. Importantly, the contrasting population genetic hallmarks of expansions in human-mediated versus landscape- or climate-mediated range expansions can be put to work for this purpose. For instance, Tolley, Davies, and Chown (2008) pitted jump dispersal versus diffusion population genetic signatures to resolve the status of extralimital populations of the painted reed frog (*Hyperolius marmoratus*) in southern South Africa, finding that all new populations were most likely the result of human transport and thus should be considered alien and potentially invasive.

Research on several species showed that the phenotypes of invasive amphibians may undergo rapid optimization in their new habitats which, coupled with increased dispersal ability, may render invasive populations unmanageable. Unfortunately, after establishment, alien-species naturalizations are usually irreversible. Novel evolutionary measures against invasive amphibian populations have been proposed. One as yet untested idea to counter the hyperdispersive toads leading the cane toad expansion in northwestern Australia is to introduce individuals of lower dispersal capacity (from established populations) to the invasion front. It is thought that this "genetic backburning" strategy (Tingley et al., 2017) could stop the toads from dispersing across dry terrain and curb the colonization of areas of more amiable climate. Another idea is to facilitate the spread of natives adapted to invasion. Rapid adaptation in the form of behavioral avoidance of toads as prey suggests the use of targeted gene flow (Kelly & Phillips, 2016) to introduce toad avoidance into toad naïve populations of would-be predators.

7 | COEVOLUTION WITH PATHOGENS

Pathogens and hosts with shared evolutionary history have often coevolved to stable coexistence. Environmental stressors, such as climate change, pollution, and alien species, can tip the balance in favor of pathogens or introduce new pathogens to naïve hosts (Box 1; Blaustein & Kiesecker, 2002; Blaustein et al., 2018). Furthermore, the presence of multiple stressors interacting with amphibian diseases complicates the identification of disease-specific effects and predictions relevant for conservation. In this section, we review evolutionary aspects of amphibian diseases: susceptibility, evolutionary consequences, coinfections, and management strategies.

7.1 | Susceptibility to disease: the sum of elements

Many aspects of life and evolutionary histories of hosts and pathogens shape the evolution of susceptibility to disease, leading to enormous variation among individuals, populations, and species (Gervasi et al., 2017; Lips, 2016). Different strains of pathogens can differ

in virulence, as described for ranavirus (Duffus et al., 2015) and *Bd* (O'Hanlon et al., 2018). Regarding hosts, three aspects should be considered. First, microbiota play an important role, since they may impede or facilitate pathogen infection (Jiménez & Sommer, 2017). Second, amphibian life-history traits and behaviors may coevolve with pathogens. Genetic and phenotypic correlations were detected between larval period length and *Bd* load (Palomar et al., 2016) and body size affects the rate of ion loss and energetic demand during chytridiomycosis, making smaller individuals more vulnerable (Wu, Cramp, & Franklin, 2018). Likewise, elevated body temperatures decrease *Bd* infection probability and help to overcome *Bd* and ranavirus in some species (Rowley & Alford, 2013; Sauer et al., 2018; Sauer, Trejo, Hoverman, & Rohr, 2019). Hence, thermoregulatory behaviors as well as other behaviors mitigating infection risk or fitness cost may be subject to selection (Kelleher, Silla, & Byrne, 2018; Koprivnikar, Gibson, & Redfern, 2012). Finally, host immune response genes are major drivers of host–pathogen coevolution. Some MHC alleles participate in amphibian resistance against several bacteria, fungi, and viruses (see Section 4, Barribeau, Villinger, & Waldman, 2008; Bataille et al., 2015; Teacher, Garner, & Nichols, 2009a), and higher overall genetic diversity increases survival at the population level (e.g., Pearman & Garner, 2005). The dynamics of chytridiomycosis could be driven largely by host capacity for rapid adaptation, as there is little evidence of *Bd* evolving to reduce its virulence in the short term (Voyles et al., 2018)—if so, conservation management should focus on host adaptation. Environment also influences coevolution between hosts and pathogens. For instance, ephemeral aquatic environments have been linked to high susceptibility of some species to *Bd* (Gervasi et al., 2017), while permanent, lotic environments seem to increase infection prevalence and intensity for other species (Kriger & Hero, 2007). Furthermore, temperature-dependent immunity in amphibians (e.g., Raffel, Rohr, Kiesecker, & Hudson, 2006) may promote the evolution of pathogen life-history strategies that exploit periods of increased host susceptibility (Woodhams, Alford, Briggs, Johnson, & Rollins-Smith, 2008). In sum, multiple factors affect the evolution of susceptibility, but an understanding of their individual contributions and, in particular, of their interactions is far from complete.

7.2 | Evolutionary consequences of disease

Infectious disease can profoundly affect host evolution. Responses to other stressors, such as predation risk, might be compromised in infected individuals (Rae & Murray, 2019). Furthermore, genotype-dependent fitness differences rapidly change the genetic composition of populations (reviewed in McKnight, Schwarzkopf, Alford, Bower, & Zenger, 2017): Diversity may decrease both overall, due to population crashes, and around genomic targets of selection. Selection imposed by disease prompts two nonexclusive responses: resistance defense, limiting pathogen burden, and tolerance strategy, reducing the fitness costs. These responses are expected to have different evolutionary consequences. Alleles conferring tolerance tend to fix if disease

prevalence remains high, because they provide universal advantage in the presence of the pathogen and the allele is permanently beneficial. In contrast, loci conferring resistance are usually polymorphic because the selective advantage of particular resistance alleles tends to deteriorate under decreasing prevalence (Roy & Kirchner, 2000). For instance, many studies have documented how diseases drive the evolution and maintenance of MHC variation (reviewed in Spurgin & Richardson, 2010). These evolutionary consequences apply not only to alleles but also to behaviors, microbiota composition, life-history traits, and other factors under selection by the disease. Which defense strategy is selected for by disease is context-dependent. On the one hand, if selection favors a strategy that allows a host genotype to outperform competitors by creating a harsh parasitic environment, by maintaining the pathogen reservoir, then high tolerance and low resistance may evolve (Restif & Koella, 2004; Venesky, Raffel, McMahon, & Rohr, 2014). On the other hand, low rates of pathogen exposure and high pathogen virulence should favor resistance over tolerance (Restif & Koella, 2004). Interestingly, the strategy can even depend on amphibian host age and developmental stage. For instance, Pacific chorus frogs (*Pseudacris regilla*) are tolerant to trematode infection during larval development and resistant after metamorphosis (Johnson, Kellermanns, & Bowerman, 2011). Understanding the relative importance of host tolerance/resistance can have relevant connotations for amphibian conservation (Venesky et al., 2014) as *Bd*-induced extinction dynamics are more sensitive to host resistance/tolerance than to *Bd* transmission (Wilber, Knapp, Toothman, & Briggs, 2017).

Gene flow patterns will also be modified by diseases due to changes in behavior or dispersal (Teacher, Garner, & Nichols, 2009b) and the reduction of population size, increasing fragmentation, and disconnection between patches (see Section 3). Population dynamics will be altered if mortality due to disease is conditional on life stage or sex, leading to biased age structure or sex ratio (Rosa et al., 2019; Scheele et al., 2019). Implications include destabilization of the population networks, decrease in population resilience, strong selection on some life-history traits, and dependence on consistent and high recruitment (Scheele et al., 2019). Some species or populations will simply not be able to adapt because of limited genetic variation, trade-offs, or physiological constraints, which may lead to extinction (see Sections 2 and 4). Finally, it is important to emphasize that host–pathogen dynamics are contingent on environmental factors (James et al., 2015; Savage et al., 2015).

7.3 | Coinfection, the great unknown

Coinfection by two or more pathogens is commonly reported in amphibians (Olori et al., 2018; Warne, LaBumbard, LaGrange, Vredenburg, & Catenazzi, 2016), but its consequences for host–pathogen coevolution are poorly known. Correlations between some infections have been detected (Stutz et al., 2018), and hybridization between different pathogen lineages has been demonstrated (see Section 5). Coinfections may have diverse outcomes for host fitness. Some pathogens attenuate host immune response, opening

the door to other pathogens. For instance, *Bd* produces toxins that impair lymphocyte proliferation and induce apoptosis in the amphibian skin (Fites et al., 2013) and in consequence may facilitate infection of the skin by the ectoparasite *Gyrodactylus jennyae* (Paetow, McLaughlin, Pauli, & Marcogliese, 2013). In contrast, cross-reactive immunity or competence may reduce the effect of a second pathogen (Hoverman, Hoyer, & Johnson, 2013). For example, prior infection with trematode parasites reduced ranavirus loads and increased survival (Wuerthner, Hua, & Hoverman, 2017). Unfortunately, this was not the case when animals that cleared *Bd* infection were infected with *Bsal* (Longo, Fleischer, & Lips, 2019). The understanding of processes such as competition between pathogens, cross-reactive immunity, and immune suppression in amphibians would help to develop new conservation measures.

7.4 | Implications for conservation

From antivirals, antifungals, and salt treatment to exposure to dead pathogens or high temperatures (Jiménez & Sommer, 2017; McMahon et al., 2014; Woodhams et al., 2011), conservation strategies have attempted to minimize the mismatch between host phenotype and fitness optimum, and therefore can be considered evolutionary in a broad sense. However, there are few examples of strategies explicitly considering evolutionary principles of pathogen–host coevolution and effective mitigation strategies in situ are still lacking. Although there is no general recipe, some interventions could be applied in the short term to prevent immediate population collapse, increasing the opportunity for adaptation. Some reports suggest that chytridiomycosis might be alleviated by bioaugmentation of locally occurring protective bacteria (Jiménez & Sommer, 2017; Woodhams et al., 2011) although the practical utility of this measure still needs to be demonstrated. Management approaches manipulating the environment to create climatic refuges from disease may be an option (Richards-Zawacki, 2009; Scheele et al., 2019), for example, by reducing canopy cover within an aquatic environment to create warm sites above the tolerance limit of *Bd*, facilitating clearance in amphibian hosts native to warm environments (Hettley et al., 2019), or increasing canopy cover creating cooler sites for clearance of amphibians adapted to cold environments (Sauer et al., 2019). Identification of the loci involved in resistance/tolerance could be a breakthrough in amphibian conservation. Assessment of susceptibility based on molecular markers could prioritize and focus conservation efforts (Bataille et al., 2015; Woodhams et al., 2011), and integration of genetic and environmental data may help in understanding the evolutionary response to disease (Horner, Hoffman, Tye, Hether, & Savage, 2017; Savage et al., 2015). Furthermore, the introduction of resistant or tolerant individuals into populations threatened by disease or as new population foci (the “recovery engine strategy” for *Bd* (Mendelson, Whitfield, & Sredl, 2019)) could facilitate adaptation and drive the re-establishment of extirpated populations. This explicitly evolutionary approach is in urgent need of assessment—Joseph and Knapp (2018) provide one successful

example in a high-altitude population of *R. sierra*, while anecdotal data suggest that the method may work in tropical latitudes as well. Another as of yet untested approach entails the release of numerous surplus amphibians (e.g., at the tadpole stage) from CBP into suitable habitat in which *Bd* is present with the expectation that natural selection will eventually generate a tolerant or resistant variant (Lewis et al., 2019). Amphibian farming and trade are major contributors to the spread of chytridiomycosis and ranavirosis (Picco & Collins, 2008; Ribeiro et al., 2019). Hence, conservation efforts eradicating introduced species would help amphibian communities by reducing the probability of infection via decreasing reservoirs.

8 | CONSERVATION OF MACROEVOLUTIONARY PROCESSES: MAINTAINING PHYLOGENETIC AND FUNCTIONAL DIVERSITY IN AMPHIBIAN COMMUNITIES

The in situ conservation of amphibians relies on the establishment of protected areas. For many species, site-based protection may be the primary strategy to ensure their survival. With a limited budget and continuing habitat conversion across the globe, decisions on where to place new protected areas or expand existing ones are not a trivial matter. Nearly a quarter of amphibian species are not encompassed by any kind of protected area, despite a global increase in their extent (Nori et al., 2015). New research emphasizes that an evolutionary perspective is essential in the planning of protected areas for the preservation of amphibian biodiversity. Instead of using traditional measures such as species counts based on taxonomic categorization, conservationists are increasingly turning to phylogenetic measures (e.g., phylogenetic diversity and evolutionary distinctiveness) as standards used in conservation planning. These measures are based on the phylogenetic relationships of organisms and have two main advantages over traditional measures: They bypass the problem of defining species and can be used as a surrogate for evolutionary potential. The second is particularly crucial in conservation science since a loss of evolutionary potential may be more important than a loss of species per se. One such measure is evolutionary or genetic distinctiveness (Redding & Mooers, 2006) which gives greater value to species whose evolutionary history is not shared with many other species. Combined with an assessment of the level of threat of a species (typically IUCN categories), evolutionary distinctiveness can help to prioritize areas for protection and target species of special concern (Isaac, Redding, Meredith, & Safi, 2012). For instance, old lineages contribute more phylogenetic diversity than younger lineages and many are at risk of extinction, the top five most in need of conservation action being *Leiopelma*, *Andrias*, *Boulengerula*, *Nasikabatrachus*, and *Telmatobufo* (Isaac et al., 2012). Greenberg, Palen, Chan, Jetz, and Mooers (2018) used evolutionary distinctiveness to compare natural and disturbed habitats across the globe and showed that intact (tropical) forests “span the diversification continuum” in amphibians, encompassing both evolutionarily distinct lineages and clades that have undergone rapid diversification. These

results emphasize that losing tropical forest will entail the loss of a substantial amount of amphibian evolutionary history, and thus provide one more reason why in situ conservation efforts should prioritize what remains of the world's tropical forests.

Another study that used phylogenetic diversity measures as a basis for conservation guidelines (Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018) showed that closely related amphibian species (at the level of genera or families) respond similarly to human-induced habitat change. Most amphibians (ca. 80%), especially clades associated with pristine tropical rainforest such as *Pseudophilautus* (Rhacophoridae), *Craugastor* (Craugastoridae), *Pristimantis* (Strabomantidae), and the Neotropical salamanders *Bolitoglossa* (Plethodontidae), are being disproportionately affected by habitat conversion. These lineages are typically species-rich and share some life-history and ecological traits; for instance, many species have lost the free-swimming larval stage, have small body sizes, and inhabit pristine rainforest. Their survival hinges on the protection of large swathes of rainforest in countries that are undergoing human population expansion and rapid development. Nowakowski et al. (2018) found that other clades (about 20% of amphibian species) seem pre-adapted to novel conditions after habitat conversion and may even thrive; some notable examples include Asian grass frogs of the genus *Fejervarya* (Dicroglossidae) that inhabit rice paddies, *Dendropsophus* treefrogs (Hylidae) that live in deforested areas of the Neotropics, and some members of the large families Leptodactylidae, Ranidae, and Bufonidae.

Another area-based conservation parameter is a community's functional diversity (Cadotte, Carscadden, & Mirotnick, 2011). This approach assumes that the diversity of species traits in an assemblage in a predefined area is representative of species niche diversity. Functional diversity is thought to underlie a number of important ecosystem properties such as stability and resilience (Loreau & De Mazancourt, 2013) and therefore should be included in conservation planning. Functional diversity has been used in conjunction with phylogenetic and taxonomic diversity in an effort to optimize the planning of protected habitat for amphibians in the Brazilian Atlantic forest hotspot (e.g., Campos, Lourenço-de-Moraes, Llorente, & Solé, 2017). Habitat loss alters the functional diversity of amphibian communities by changing or reducing their functional complexity (Almeida-Gomes, Vieira, Rocha, & Melo, 2019; Riemann, Ndriantsoa, Rödel, & Glos, 2017). Joint consideration of functional and phylogenetic diversity is essential, because it remains unclear to what extent phylogenetic relatedness determines similarity in the roles species play in ecosystems (Webb, Ackerly, McPeck, & Donoghue, 2002). Including these two measures of diversity allows combining ecological and evolutionary approaches into conservation decision-making (Lourenço-de-Moraes et al., 2019).

8.1 | Implications for conservation

These studies have several ramifications for amphibian conservation. First, expanding current protected areas, especially in tropical

countries, is necessary if we want to preserve a large part of amphibian evolutionary history. Policymakers should target remnant forests as these will tend to encompass both evolutionarily distinct lineages and closely related species that have recently diversified. Phylogenetic distinctiveness and level of threat form the basis for constructing Evolutionarily Distinct and Globally Endangered species lists (EDGE lists), and one is now available for amphibians (Isaac et al., 2012). Second, since a large proportion of amphibian clades are present outside of protected areas, maintaining extensive agricultural management practices that provide ecological diversity can help maximize amphibian phylogenetic (and species) diversity in a human-dominated landscape. Third, human-induced changes in the environment have increased available habitat (and/or decreased competition) for some species (Nowakowski et al., 2018).

Can habitat restoration (the design of secondary communities) revive threatened amphibians, especially the evolutionary unique, specialist species? There is some evidence that this indeed may be the case. In a study examining the effects of habitat restoration in southern Mexico, Díaz-García, Pineda, López-Barrera, and Moreno (2017) showed that after 7 years, restoration areas adjacent to forest fragments contained a combination of cloud forest specialist as well as generalist species that came close to pristine sites in terms of species and functional diversity. Unfortunately, habitat restoration does not afford protection from threats such as climate change or infectious diseases. Ideally, protected areas should be large enough to sustain populations of target species and to act as sources of colonizers for smaller habitat patches in the landscape and should also envelope as much phylogenetic and functional diversity as possible.

9 | CONCLUSIONS: AN EVOLUTIONARY PERSPECTIVE ON MANAGING ECOSYSTEMS FOR AMPHIBIANS

It is abundantly clear from our review that amphibian populations can evolve to accommodate new environmental situations. However, the evolutionary response may not be rapid enough to cope with the pace of current global change. Collectively, the field has amassed a substantial amount of information on evolutionary processes in amphibians and we have a reasonable idea of what to protect and how to prioritize protection in the case of limited resources. However, there is a dearth of studies that have attempted to implement evolutionary principles in or that are directly informative for amphibian conservation. Table 2 lists some fundamental research questions that could be pursued in this respect. Ideally, baseline information for each species on a conservationist's agenda could be obtained through detailed and time-consuming studies. Under the current circumstances, however, a common sense ("quick and dirty") approach may be a legitimate alternative. For instance, predictive frameworks linking genetic cohesion to functional traits of the amphibian community will probably succeed in determining the extent of necessary habitat restoration in a given area, without the need of conducting landscape genetic studies of each constituent species.

TABLE 2 In need of further study—evolutionary research questions of fundamental importance for amphibian conservation

Drift and inbreeding
<ul style="list-style-type: none"> Information on the effectiveness of genetic rescue More data on N_e of local populations and the mechanisms supporting relatively high N_e/N ratios
Migration
<ul style="list-style-type: none"> Landscape genetic studies aimed at evaluating the effectiveness of habitat restoration on population genetic cohesion Fragmentation and management of gene flow among captive colonies as a tool for minimizing adaptation to captivity and loss of variation.
Selection
<ul style="list-style-type: none"> Does adaptation to captivity affect translocation success? What are the short- and long-term costs of diluting local adaptation through translocation?
Hybridization
<ul style="list-style-type: none"> Do the benefits of hybridization as a source of adaptive genetic variation typically exceed risks?
Evolutionary effects of invasive amphibians
<ul style="list-style-type: none"> Adaptation versus phenotypic plasticity versus spatial sorting—more experimental data needed to verify potential adaptive scenarios Can manipulation of phenotypes/genotypes at the expansion front impede the spread of invasive species?
Coevolution with pathogens
<ul style="list-style-type: none"> Identification of loci involved in resistance/tolerance Can the introduction of resistant or tolerant individuals into populations threatened by disease facilitate adaptation?
Conservation of macroevolutionary processes
<ul style="list-style-type: none"> Can habitat restoration revive threatened amphibians, especially the evolutionary unique, specialist species?

Can evolutionary principles aid in halting amphibian declines? Yes, by securing the adaptive potential of (declining) amphibian species, by optimizing habitat management to ensure landscape-scale population dynamics, by reducing phenotype–environment mismatch, and by recognizing and spreading fitness-increasing variants. A number of conservation tools have been proposed, including evolutionary approaches to captive breeding aimed at increasing N_e and minimizing unwanted adaptation, selective breeding, and targeted gene flow for specific traits or adaptive variants (e.g., disease resistance), translocations of more fit individuals to populations experiencing fitness declines, and interspecific hybridization as a source of adaptive variation. Few of these tools have actually been implemented in amphibian conservation, and all are in need of evaluation. We also raise awareness of the possibility that the implementation of evolutionary solutions to amphibian conservation may have ecological implications for the local communities. Most obviously, actions that directly modify habitat such as breeding site restoration (aimed at securing population connectivity) or establishment of thermal refugia (to mitigate disease) will likewise affect the local ecology. However, translocations of individuals or genes may also seriously and

unpredictably alter local associations. Ideally, the potential conflict between an evolutionary solution for an imperiled amphibian species and the ecological outcome of the action should be acknowledged and factored into a conservation strategy.

Protecting the existing primary habitat patches and increasing their quality or extent is a direct conservation measure of immediate effect and is essential for many nongeneralist species. However, as we watch most pristine ecosystems, especially tropical forests, disappear, secondary habitat in disturbed areas or restored forest is becoming increasingly important for many amphibian species. An evolutionary perspective incorporating phylogenetic and functional diversity is essential in the planning of the secondary habitat, and management approaches manipulating the environment to create climatic refuges from disease could become valid approaches in a more homogenous landscape.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY STATEMENT

This article does not contain data.

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