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The complexity of amphibian population declines: understanding the role of cofactors in driving amphibian losses

Andrew R. Blaustein,¹ Barbara A. Han,² Rick A. Relyea,³ Pieter T.J. Johnson,⁴ Julia C. Buck,¹ Stephanie S. Gervasi,¹ and Lee B. Kats⁵

¹Department of Zoology, Oregon State University, Corvallis, Oregon. ²Odum School of Ecology, University of Georgia, Athens, Georgia. ³Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania. ⁴Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado. ⁵Natural Science Division, Pepperdine University, Malibu, California

Address for correspondence: Andrew R. Blaustein, Department of Zoology, 3029 Cordley Hall, Oregon State University, Corvallis, OR 97331-2914. blaustea@science.oregonstate.edu

Population losses and extinctions of species are occurring at unprecedented rates, as exemplified by declines and extinctions of amphibians worldwide. However, studies of amphibian population declines generally do not address the complexity of the phenomenon or its implications for ecological communities, focusing instead on single factors affecting particular amphibian species. We argue that the causes for amphibian population declines are complex; may differ among species, populations, and life stages within a population; and are context dependent with multiple stressors interacting to drive declines. Because amphibians are key components of communities, we emphasize the importance of investigating amphibian declines at the community level. Selection pressures over evolutionary time have molded amphibian life history characteristics, such that they may remain static even in the face of strong, recent human-induced selection pressures.

Keywords: amphibian population declines; *Batrachochytrium*; biodiversity; pathogens; parasites; invasive species; evolutionary trap

Introduction

The loss of populations and extinctions of species are occurring at unprecedented rates.¹ Some scientists believe that we are observing a major extinction episode mirroring the five mass extinction events that have occurred during the Earth's history.² Despite widespread interest in understanding extinctions and the recognition that population declines may be complex phenomena, research efforts directed at understanding species losses typically focus on the direct effects of single factors. This is illustrated by attempts to understand the global decline of amphibian populations.^{3,4} One estimate suggests that the extinction rates of amphibians may be 211 times the background rate of extinction.⁵ According to International Union for Conservation of Nature (IUCN) criteria, a higher percentage of amphib-

ians are threatened than birds or mammals, with many amphibians on the brink of extinction.⁶ Stuart *et al.*⁶ classified 435 species as "rapidly declining" that qualified for listing in IUCN categories of higher threat than they would have in 1980. These are further divided into groups based on potential causes for their declines, with a large number of species listed as "enigmatic declines"—population declines for reasons not fully understood.

The causes for amphibian population declines have been reviewed.^{3–8} These include habitat destruction, the most significant factor contributing to amphibian population declines and extinctions, pollution, introduced exotic species, disease, climate change and associated atmospheric processes, and overexploitation, including collecting for the pet and food industry. All these causes may have interacting cofactors. Moreover, causes for population

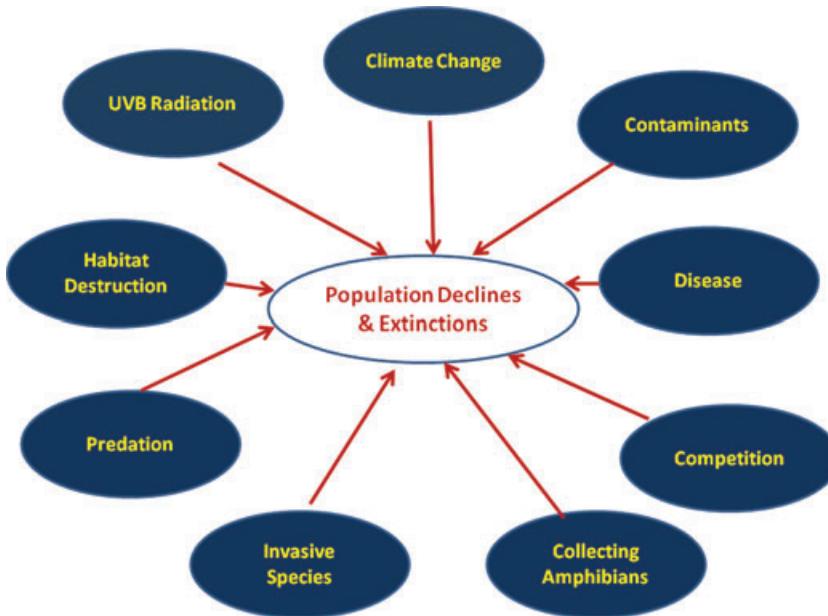


Figure 1. Multiple stressors affect amphibians.

declines may differ from region to region and even in different populations of the same species. There may be interspecific differences and even differences between life stages in how amphibians react to stressors. Amphibians are continuously bombarded with numerous stressors that may affect them directly and indirectly (Fig. 1). Natural stress associated with competition, predation, resource availability, reproduction, and disease may be compounded by human-induced stresses such as habitat destruction, environmental contamination, invasive species, and climate change. These stressors affect amphibians at the molecular, physiological, individual, population, and community levels.

Given that many stressors are acting simultaneously on amphibians, we suggest that single-factor explanations for amphibian population declines are likely the exception rather than the rule. Certainly, in specific regions, one factor may be more devastating than others. However, it is becoming increasingly clear that many of the factors proposed to explain population declines in amphibians and other threatened taxa exhibit a high degree of temporal and spatial variation. Thus, the ways in which various factors contribute to population declines may also vary and will probably be manifested as a series of complicated local interactions.^{4,8} This review focuses primarily on stressors affecting am-

phibians above the level of the individual. We provide some emphasis on pathogens and the diseases they cause because many declines are associated with disease. We suggest that (1) studies focused on single causes for a population decline may miss complex interrelationships involving multiple factors and indirect effects; (2) efforts focused solely at the population level may fail to detect effects at the community level following amphibian losses; (3) modern selection pressures, especially those that are human induced, may occur too quickly and strongly to allow amphibians adequate time to evolve adaptations to overcome them; and (4) there is a continued need for long-term field data to assess the status of a population. Clearly, amphibian population decline research needs to develop approaches in which to manage the context dependency that is prevalent in ecological systems, which could provide a valuable model for conservation efforts in general.

The value of long-term studies and the need to standardize criteria for determining population declines

Stuart *et al.*⁶ suggested that extensive field work is necessary to obtain a precise estimate of the number and rate of amphibian extinctions. Amphibian populations fluctuate, and metapopulation dynamics can result in local extinctions and

colonizations that are difficult to document and predict.^{9,10} Amphibian populations are often described as having “crashed” or undergone “sudden declines,” “rapid declines,” or “significant declines,” frequently without precisely defining the criteria used to describe the declines.^{11–13}

Stuart *et al.*⁶ provided criteria for categorizing amphibian population declines and extinctions, but standardization of the criteria used for listing a population as “declining” or “extinct” has not been accomplished. Yet, quantifying declines and standardizing criteria are necessary for assessing whether or not a population is in decline. To predict with confidence the probability that a given population will persist requires sufficient demographic data to project the future trajectory of a population’s capacity to increase from low numbers.¹⁴ Since age/stage distributions, birth and death rates, and rates of migration are seldom stable, accurate projections can only be made on a “real-time” basis from year to year.¹⁴ Furthermore, populations may naturally have multiple years of small declines followed by years of large recruitment. The spatial scale at which demographic data are collected is also critical. Populations, especially metapopulations, must be monitored and managed on a landscape scale, with distinct demographic measurements being collected from all significant phases of the habitat, both aquatic and terrestrial. This is especially critical for amphibians whose life histories include both aquatic and terrestrial phases.

Long-term records of a variety of amphibian species, populations, habitats, and geographic areas will help us evaluate (1) which species, on average, have more variable populations per turnover; (2) the average probability of local extinction per turnover; (3) the recovery rates after local population extinction; and (4) the spatial scale of local extinctions. Only with long-term data can we assess unambiguously whether an amphibian population is suffering an unusual decline.

Recent studies by Briggs *et al.*¹⁵ and Vredenburg *et al.*¹⁶ convey the value of long-term field data. Instead of simply recording the presence or absence of the fungal pathogen *Batrachochytrium dendrobatidis* (Bd), they identified a “lethal threshold” of Bd intensity and its spread in yellow-legged frogs in California. Despite intensive sampling of 48 populations over a seven-year period, Vredenburg *et al.*¹⁶ could not detect Bd in frog populations until just be-

fore die-offs began. Within three years of its detection, Bd spread in a “wave-like” pattern among lakes until nearly all populations were infected. However, amphibian populations did not collapse until a lethal threshold of Bd intensity was reached. Previous studies did not consider the role of Bd intensity (amount of infection per individual) in controlling host population losses. The existence of an intensity threshold may help to explain how Bd causes near-complete losses of amphibian hosts in some systems. Because this threshold creates a time lag between exposure and mortality, the pathogen can spread through much of the amphibian population before disease-driven declines in host density negatively affect Bd transmission. Briggs *et al.*¹⁵ combined long-term field data with models to examine how some populations of amphibians persist with Bd. Intensive mark-recapture data revealed that infected yellow-legged frogs in persistent populations had fungal loads well below the lethal intensity and lost and regained Bd infection for years with no effect on survival. These papers increase our understanding of a disease affecting many amphibian populations and were based on long-term, extensive field data.¹⁷

Complex interactions involving pathogens

The complexity of amphibian population declines and the often difficult task of interpreting data on the phenomenon can be exemplified with studies involving amphibian pathogens. Pathogens, especially *Batrachochytrium*, have received much recent attention for their role in causing population declines (Fig. 2). Growing evidence indicates that *Batrachochytrium* has devastated numerous amphibian populations.^{18,19} Losses in Panama and surrounding regions are especially well documented.¹⁹ However, in a general sense, the complex interrelationships between amphibian hosts and their pathogens have not been an area of focus, leaving our understanding of the environmental factors that influence infection and pathology rather limited. Although there is little doubt that Bd has been a major factor in amphibian population declines and extinctions in certain regions, it cannot be the sole cause for all amphibian population declines because declines can occur in the absence of Bd and populations may persist with Bd without causing local extinctions.^{20,21} These observations indicate that additional but unidentified

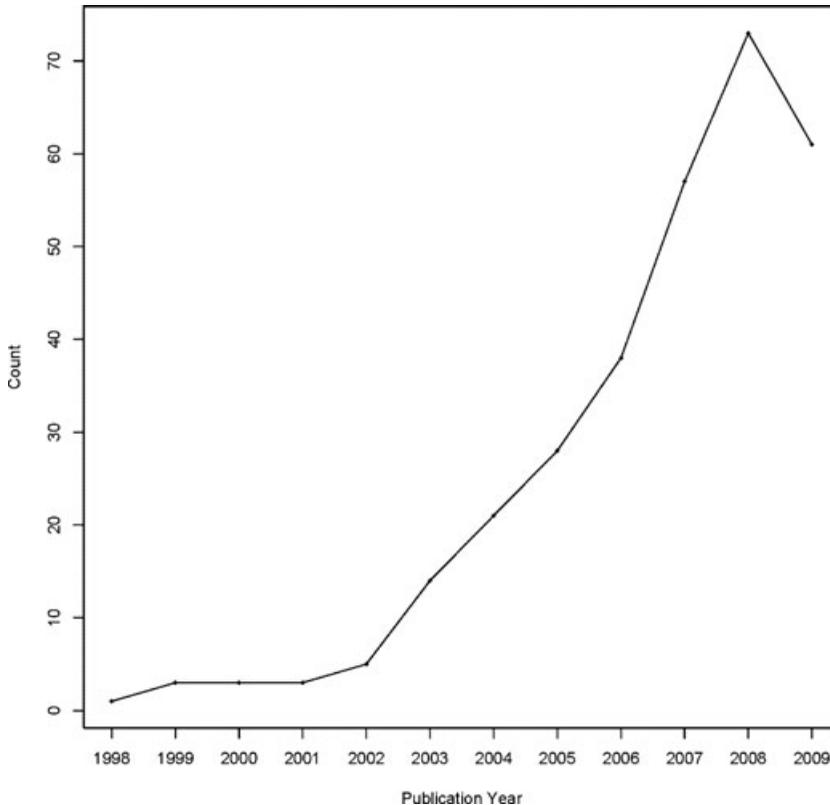


Figure 2. Total number of articles published on *Batrachochytrium dendrobatidis* in the primary literature yearly from 1998 to 2009. Articles were compiled using the search strings *Batrachochytrium dendrobatidis* and *amphibian* in three databases: Web of Science (221 hits), BIOSIS (248 hits), and Zoological Record (185 hits), from which duplicates and articles from nonprimary literature were removed for a total of 307 articles.

factors can mediate the severity of disease-driven declines, as is often the case for emerging infections.²²

Over 80% of pathogens infect more than one host species,²³ and hosts are often burdened by more than one pathogenic species concurrently. Yet most studies of amphibian diseases focus on the effects of single pathogens on single hosts. The parasite community within a single amphibian can be extremely diverse, sometimes numbering 10,000 individuals of 15 or more parasite groups.²⁴ Moreover, each pathogen can have different effects on hosts. For example, Bd disrupts electrolyte balance;²⁵ the trematode *Ribeiroia ondatrae* can increase the frequency of severe limb malformations;²⁶ while the trematode *Echinostoma trivolvis* can cause kidney damage.²⁷

Within a host, pathogens can interact in a synergistic, additive, or less-than-additive fashion as exemplified in several scenarios by three potentially cooccurring pathogens—Bd, the water mold

Saprolegnia, and the trematode *Ribeiroia*. For example, pathogens that produce zoospores, such as Bd and *Saprolegnia*, could potentially compete with zoospores of other pathogenic species if colonization sites are limited. Alternatively, skin damage in a host caused by the zoospores of one pathogen could facilitate invasion of zoospores from another pathogen. Infection by water molds may be aided by pathogens such as *Ribeiroia*, which damage the host epidermis. Coinfection of *Saprolegnia* and Bd may even enhance the effects of *Ribeiroia* by damaging the skin and reducing the host's ability to defend against *Ribeiroia* parasite infection, leading to higher prevalence of deformities.²⁸ Alternatively, water molds may attack encysting trematodes and preventing them from causing deformities. This speculative exercise illustrates the diversity of potential interactions among a small number of amphibian pathogens; thus far, few

multiparasite experiments have been conducted in amphibians or other wildlife hosts. In nature, however, coinfection of hosts by infectious organisms is likely to be the rule rather than the exception, but research examining the combined effects of multiple infectious agents is lacking.²⁹

Hypotheses related to the origins of disease-mediated amphibian population declines have been placed into two broad categories: (1) those suggesting that pathogens are novel and (2) those suggesting that other factors, including those related to environmental change, may trigger changes in an existing disease.^{4,30} Realistically, even this dichotomy is grossly oversimplified, as novel pathogens can still be influenced by a variety of host and environmental factors, the most obvious of which are the conditions that led to their emergence (e.g., introduction events or novel species interactions). Yet the hypotheses on the origin of disease-mediated population declines are often difficult to disentangle, and the interrelationships among diseases and their cofactors are often complex, as exemplified below.

Parasite infection and nutrient pollution

Although the relationship between amphibian malformations (e.g., frogs with missing, extra, or abnormal limbs) and population declines remains unclear, the amphibian malformation phenomenon is ideal to illustrate the role of cofactors in the spread of a pathogen. Parasite infection and pollution, for example, can interact through multiple pathways. Eutrophication caused by excess inputs of nitrogen and phosphorus into wetland habitats can increase the abundance of *R. ondatrae* trematodes.³¹ Eutrophication increases algal growth (periphyton), which is the primary food source for herbivorous snails (*Helisoma trivolvis*) that function as the first intermediate hosts for *Ribeiroia*.³¹ More snails can increase the success of parasites in finding a suitable host, thereby increasing snail infection prevalence. Higher nutrient enrichment can also increase the number of infectious parasites produced per snail, which is a direct predictor of malformation risk in amphibians. Thus, the combination of more infected snails and more parasites produced per snail jointly drive the link between eutrophication and *Ribeiroia* infection. Other studies have illustrated the potential linkage between pesticide contamination and increased infections by trematode parasites, demonstrating an additional, often concurrent

mechanism through which cofactors can influence disease.³²

Ultraviolet-B radiation, climate change, non-native species, and disease

Synergistic interactions among multiple stressors can exacerbate the effects of single stressors acting alone. Kiesecker *et al.*³³ illustrated the complex interrelationships among climate change, atmospheric effects, and an infectious pathogen (Fig. 3). They reported that periodic mass mortality of toad embryos in Oregon resulted from a synergism between UV-B radiation, which by itself can be harmful to amphibians,³⁴ and the pathogenic water mold *Saprolegnia ferax*, which often infects amphibian embryos.³⁵ UV-B exposure was in large part determined by water depth at oviposition sites. Kiesecker *et al.*³³ linked El Niño Southern Oscillation (ENSO) events with decreased winter precipitation in the Oregon Cascade Range. They suggested that less winter snow pack resulted in lower water levels when western toads breed in early spring. Toad embryos developing in shallower water were exposed to higher levels of UV-B radiation, resulting in increased infection and mortality from *Saprolegnia*, thus demonstrating that global events clearly affect local populations. This complexity is compounded because *Saprolegnia* is routinely introduced to amphibian habitats through stocked fishes.³⁶ Amphibian embryos experimentally exposed to infected fish were more likely to develop *Saprolegnia* infections and had higher mortality rates compared to embryos exposed to control conditions.³⁶

Climate change and *Batrachochytrium*

Although Bd may spread directly³⁷ in some regions, cofactors may be involved in other cases. For example, Bd and its hosts are sensitive to changes in temperature,^{38,39} suggesting that climate change has the potential to affect the spread of Bd.^{40–42} While controversial, Pounds *et al.*⁴³ presented a mechanistic explanation for how climate change could influence outbreaks of Bd by modifying conditions in montane areas of tropical America where nighttime temperatures are shifting closer to the thermal optimum for the pathogen, while increased daytime cloudiness prevents frogs from finding thermal refuges from Bd. Others have suggested that changes in El Niño events and temperature variability—rather than mean conditions—are a more likely

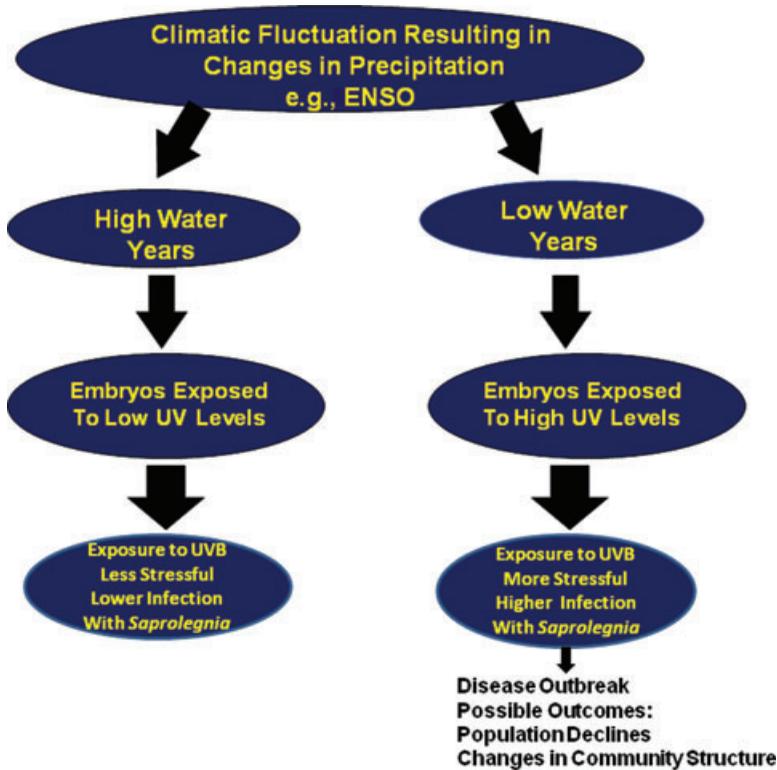


Figure 3. Complex interactions among climate change, ultraviolet-B radiation, and an amphibian pathogen. Modified from Ref. 33.

explanation for changes in infection.⁴⁴ Parmesan and Singer⁴⁵ suggested that both the “direct spread hypothesis” and the “environmental cofactor hypothesis” likely influence the spread of Bd. Neither of these hypotheses are mutually exclusive, and there is potential for interactions between them. If Bd is an invasive pathogen spreading among naive host populations, for example, the future pathology of this disease within its new range will probably be influenced by environmental factors, including climate and host demography, indicating that management efforts will need to be cognizant of the potential roles of cofactors.

Community and ecosystem effects of amphibian declines

The effects of amphibian population declines on ecological communities have received little attention. Amphibians are important both as consumers and as prey in aquatic and terrestrial food webs, and can change the chemical and physical habitat where they live.^{46,47} Amphibians may make up a

large portion of the vertebrate biomass in some ecosystems.^{48,49} They can have significant effects on organic matter and sediment dynamics, primary productivity, algal community composition, invertebrate grazers, and predators. For example, reduced abundance of larval amphibians was associated with greater levels of chlorophyll-a, increased mean algal cell biovolume, increased dry mass of periphyton, and a shift in algal species composition.^{50–52} With increased availability of algal resources, herbivorous macroinvertebrates are released from competition with tadpoles and increase in abundance.⁵³ Collectively, these observations underscore the importance of identifying the role of amphibians in communities and the ecological consequences of their declines.

Communities and disease

Recent experiments reveal how pathogens can influence community structure by impacting the interactions between species. For example, the outcome of competitive interactions between two

larval amphibian species was reversed in the presence of the pathogenic oomycete *S. ferax*.⁵⁴ The presence of competitors and predators can affect growth, susceptibility, and survival of larval amphibians exposed to Bd.^{55,56} Sublethal consequences of Bd infection can alter host behaviors with consequences for disease dynamics. For example, Bd-induced changes in aggregation behavior among schooling larvae⁵⁷ and natural contact patterns between hosts⁵⁸ may increase Bd transmission probability. These few studies highlight the importance of considering the impacts of host behavioral responses to Bd infection on species interactions and infection dynamics at the population and community level.

As Bd infection and amphibian declines occur in some of the world's most biodiverse communities, examining Bd-induced changes in community structure is of considerable value. For example, high amphibian species richness could underlie long-term, low-level persistence of chytridiomycosis through reservoir species.⁵⁹ Conversely, the invasion of exotic reservoir hosts could dramatically increase the Bd exposure in native hosts whose susceptibility to infection is unknown.^{60,61} The influence of host species diversity on infection dynamics remains a pervasive topic in disease ecology for which the amphibian–chytridiomycosis system may provide an opportune and tractable test.

Recent studies have shown that chytridiomycosis also has consequences at the ecosystem level. Through experimental exclusions of tadpoles from pre- and postdecline streams, Connelly *et al.*⁵² found dramatic increases in inorganic sediments, increases in stream algae biomass, and changes in algal community composition immediately following larval amphibian extirpations. Ecosystem-level consequences of such extensive biodiversity loss are likely to be complex and long-lasting, encompassing concurrent changes in primary productivity, energy transfer between aquatic and terrestrial habitats, and the composition and interactions among organisms found at multiple trophic levels.

Communities and contaminants

Synergistic and indirect effects of contaminants applied to amphibian habitats may result in profound effects in a community context. For example, several different classes of pesticides become more lethal if tadpoles simultaneously experience

the stress of predators in the water. Aquatic predators emit water-borne cues that diffuse through the water and induce a range of antipredator behavior, morphology, and life history changes in prey.⁶²

Contaminants can cause sublethal effects including changes in behavior⁶³ such as reduced locomotion. The effects of contaminant-induced behavioral changes on amphibian populations are difficult to predict. For example, lowered amphibian activity might cause reduced feeding and growth, but it could also reduce risks from predators (depending on how the predator's behavior is affected by the contaminant). Sublethal concentrations can also affect the endocrine system. For example, atrazine can cause genetically male frogs to become either hermaphrodites or fully feminized.⁶⁴ In terms of population predictions, the extrapolation of this effect is that there will be fewer males that are functionally male (and attractive to females) and that this outcome could lead to population declines with profound implications for communities.

Contaminants can also impact amphibians indirectly through food web changes (Fig. 4). A contaminant that may not be lethal to an amphibian can cause a cascade through the food web through its lethal effects on another taxon within the food web.⁶³ As an example, low concentrations of malathion, a widely applied insecticide used to control crop pests, are not directly lethal to tadpoles but are highly lethal to zooplankton.⁶⁵ In a wetland community, low concentrations of malathion nearly eliminate the zooplankton, which in turn allow the phytoplankton to bloom and shade the underlying periphyton (i.e., the food of tadpoles). This causes insufficient food for many tadpoles to grow and develop before the pond dries. In the case of leopard frogs, researchers found that 43% of tadpoles died due to this indirect effect.⁶⁵

Thus, even sublethal concentrations of contaminants can have lethal effects on amphibians.

Evolutionary considerations

Behaviors and ecological attributes of amphibians have been molded over evolutionary time under selection pressures that acted on amphibians in a variety of ways. We suggest that ecological processes associated with amphibian population declines be considered in light of key evolutionary principles (Fig. 5).⁶⁶ evolution is limited by historical constraints; not all evolution is adaptive; adaptations

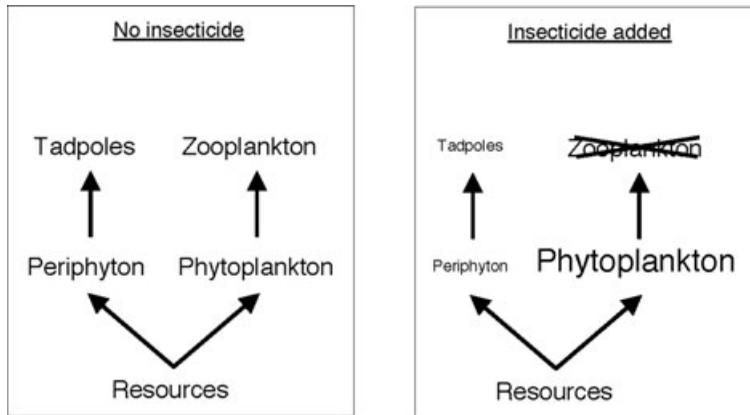


Figure 4. Effects of insecticides on a simplified wetland community. At very low concentrations, most insecticides cannot directly kill tadpoles. However, zooplankton are highly sensitive and can be eliminated, allowing the phytoplankton to bloom throughout the water column, thereby shading the underlying periphyton and causing tadpoles to experience reduced growth and slower development. Should the wetland dry, the slower developing tadpoles cannot metamorphose in time and will die. Arrows indicate the direction of energy flow in the community and changes in font size of each trophic group represent relative changes in abundance.

are often compromises; evolution can only alter existing variations; and evolution takes time.

Limited by historical constraints, many amphibians must lay their eggs in water. This exposes eggs to aquatic predators and competitors and to a variety of abiotic factors, both natural and human induced, that may be especially harmful to them, such as today’s increasingly contaminated habitats. Such contamination can be measured in hundreds of years—a rapid change, given that amphibians have been laying their eggs in less-contaminated water for millions of years.

Over evolutionary time there have probably been numerous benefits for animals to lay their eggs communally or to join groups. Yet the reproductive habits and social behavior of many extant species may be placing amphibians in danger of acquiring infectious diseases. Eggs of amphibians that are laid in communal masses are especially at risk of acquiring infectious pathogens such as *Saprolegnia*.³⁵ Similarly, schooling larvae may be especially prone to Bd infection.⁶⁷ Larvae that can persist for long periods with Bd may be a key to transmitting the pathogen to more sensitive hosts.¹⁵ Even after metamorphosis, juvenile frogs and adults may congregate in large numbers, metamorphose synchronously, and remain in large aggregations.⁴⁷ Adults of many amphibian species congregate to breed.⁴⁷ These aggregations may enhance the probability of pathogen transmission. Yet these social behaviors have persisted for millions of years.

Many selection pressures, especially those that are human induced, such as environmental contamination, changes in the atmosphere, or the introduction of exotic species, may be too intense and may have arisen too rapidly for amphibians to evolve adaptations to overcome them.⁶⁶ These human-induced changes can interact with one another in complex ways and trigger unpredictable dynamics, including the emergence of infectious diseases.

Ozone depletion is an example of a recent anthropogenic change impacting stratospheric chemistry.⁶⁸ Stratospheric ozone has historically protected living organisms from the harmful effects of Ultraviolet-B (UVB) radiation. However, due to ozone depletion, living organisms have been bombarded with constantly rising levels of harmful UVB radiation only for the past several decades. Increasing UVB radiation is therefore a relatively new selection pressure. For some species, populations may be adversely affected before behaviors limiting amphibian exposure to sunlight, and other defenses can overcome strong established selection pressures for seeking warmth.⁶⁹ It is likely that some species will continue to seek sunlight, and those species without effective defense mechanisms against the damage from UVB radiation will be harmed or die when exposed to UVB.⁶⁹

Like most native species, amphibians often lack the evolutionary history to respond to invasive species.⁷⁰ For example, one well-studied invader that negatively impacts amphibian populations is

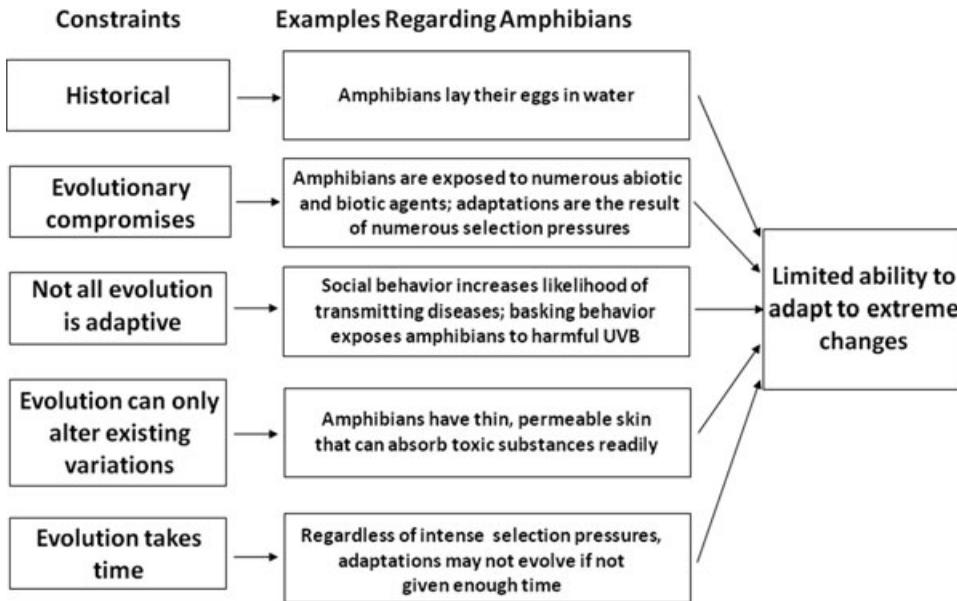


Figure 5. Evolutionary constraints molding amphibian behaviors and life history characteristics in light of amphibian population declines. Modified from Ref. 66.

the red swamp crayfish (*Procambarus clarkii*). Amphibian populations that suddenly must cope with red swamp crayfish often perform poorly, in part because these same amphibian species have likely never had to deal with voracious aquatic omnivores like the crayfish.⁷¹ Native crayfishes have very small geographic ranges;⁷² thus, many species of amphibians have no evolutionary history with crayfish. In some instances, even when amphibians have history with a functionally similar predator, they cannot recognize the invading species and do not avoid it.⁷³ In the few examples where amphibians coexist with introduced predators, it appears that those amphibians benefit from a genetic propensity for inducible defenses that facilitated coexistence with the nonnative predator.⁷⁴

We do expect and observe variation in how amphibians cope with various selection pressures—both natural and human induced. However, constraints imposed by a long evolutionary history may limit the variation necessary to mold “the perfect amphibian” in time to survive the mounting threats of modern selection pressures. Complete removal or mitigation of the challenges confronting amphibians is neither feasible nor desirable; however, given adequate genetic diversity and the potential for rapid adaptation, individuals with characteris-

tics that allow them to cope with anthropogenic environmental changes, emerging infectious diseases, and other stressors will produce more offspring than individuals lacking those characteristics. Possibly, populations with individuals containing such attributes will persist for million more years, particularly if conservation approaches can be used to allow amphibians adequate time to respond to such threats.

Conclusions

We suggest that the amphibian population decline phenomenon is complex in origin and multifactorial in etiology. Multiple stressors from natural and anthropogenic sources affect amphibians from the molecular to the community level. The ways in which stressors contribute to amphibian population declines will vary and often appear as a series of complicated, local interactions. Therefore, controlling the problem will be challenging, particularly if management strategies fail to consider to the role of cofactors in affecting amphibian populations.

Environmental problems such as global warming, ozone depletion, and airborne contaminants cross international boundaries and are difficult but not impossible to control. The Montreal

Protocol is an example of a successful international treaty that limits anthropogenic ozone-destroying substances. Treaties that limit gases contributing to global warming and those that limit the use of toxic substances have been less successful thus far. These types of treaties are imperative to save wildlife, including amphibians.

Preliminary efforts to control amphibian pathogens have been initiated, offering hope that the effects of disease can be managed or prevented. These efforts have included captive-breeding efforts as well as interventions designed to prevent *Batrachochytrium* infection from reaching the lethal-intensity threshold. Because it is unlikely that Bd will ever be completely eradicated or controlled, one strategy is to manage sensitive amphibian populations by shifting the disease toward an endemic rather than epidemic state of infection. This could involve reducing the density of susceptible frogs by capturing them before the infection wave, or by treating a subset of individuals with an anti-fungal agent, thereby reducing the transmission of Bd and prevent infection intensities from becoming lethal.^{15–17,75} Furthermore, the use of probiotics that incorporate beneficial bacteria and their natural products to prevent or treat amphibian diseases such as Bd are exciting and promising approaches.⁷⁶

We emphasize, however, that conventional efforts focused on single causes and single populations under decline may obscure important interrelationships among multiple factors and obscure indirect effects underlying observed declines, especially at the community level. The occurrence of biological and environmental reservoirs, for example, could confound efforts to control or treat infections in natural populations, as could failures to identify the pathway through which pathogens are introduced to host populations in the first place. In some cases, elimination of particular pathogens or environmental threats could release or exacerbate other co-occurring agents of decline. Rapid pathogen evolution in response to initiated control measures could also select for heightened virulence. Finally, our perspectives on alleviating amphibian population declines must be informed by an understanding of amphibian evolutionary history, bearing in mind that modern selection pressures, especially those associated with human activity, may be too severe and may have arisen too rapidly for amphibians to evolve adaptations to overcome them. Future research to

inform conservation and management efforts will require shifting to more holistic investigations of the complexity underlying the global amphibian decline phenomenon.

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Conflicts of interest

The authors declare no conflicts of interest.

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