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SPECIAL ISSUE: AMPHIBIAN DECLINES

Global amphibian declines: sorting the hypotheses

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Abstract. Reports of malformed amphibians and global amphibian declines have led to public concern, particularly because amphibians are thought to be indicator species of overall environmental health. The topic also draws scientific attention because there is no obvious, simple answer to the question of what is causing amphibian declines? Complex interactions of several anthropogenic factors are probably at work, and understanding amphibian declines may thus serve as a model for understanding species declines in general. While we have fewer answers than we would like, there are six leading hypotheses that we sort into two classes. For class I hypotheses, alien species, over-exploitation and land use change, we have a good understanding of the ecological mechanisms underlying declines; these causes have affected amphibian populations negatively for more than a century. However, the question remains as to whether the magnitude of these negative effects increased in the 1980s, as scientists began to notice a global decline of amphibians. Further, remedies for these problems are not simple. For class II hypotheses, global change (including UV radiation and global climate change), contaminants and emerging infectious diseases we have a poor, but improving understanding of how each might cause declines. Class II factors involve complex and subtle mechanistic underpinnings, with probable interactions among multiple ecological and evolutionary variables. They may also interact with class I hypotheses. Suspected mechanisms associated with class II hypotheses are relatively recent, dating from at least the middle of the 20th century. Did these causes act independently or in concert with pre-existing negative forces of class I hypotheses to increase the rate of amphibian declines to a level that drew global attention? We need more studies that connect the suspected mechanisms underlying both classes of hypotheses with quantitative changes in amphibian population sizes and species numbers. An important step forward in this task is clarifying the hypotheses and conditions under which the various causes operate alone or together.

Key words. Amphibian declines, complexity, sorting hypotheses, time scale.

INTRODUCTION

Beginning in the 1980s herpetologists increasingly described amphibian declines and extinctions at former field sites. At the First World Congress of Herpetology in 1989, scientists from around the world exchanged anecdotal reports that led to concern about the possibility of a global pattern of amphibian decline. A U.S. National Research Council Workshop in 1990 followed with the first systematic examination of amphibian population declines (Barinaga, 1990; Wake, 1991). Participants agreed that there was empirical support for amphibian declines, but there was no consensus regarding a cause; in fact, it was suspected that several causes could be interacting. Since the workshop reports documented declining populations and extinction of species of frogs and salamanders in the Neotropics (Pounds *et al*., 1997; Lips, 1998, 1999), the U.S. (Stebbins & Cohen, 1995) and Australia (Richards *et al*., 1993; Laurance *et al*., 1996),

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although two U.S. studies showed no declines (Pechmann *et al.*, 1991; Hairston & Wiley, 1993). There is insufficient information to reach a conclusion regarding changes in amphibian populations in Africa and Asia. Reports of declining populations persisted at the Third World Congress of Herpetology in 1997, engendering a call for research focused on the question: is the threat of extinction increasing for amphibians (Wake, 1998; Storfer, 2000; Collins *et al.*, 2003b)? Over the last 5 years, workshops, conferences, symposia and new research findings have greatly improved our capacity to answer this question.

Biodiversity is declining worldwide, and amphibians are representative of the general loss of populations and species (Houlahan *et al.*, 2000; Alford *et al.*, 2001; Wilson, 2002). None the less, since the early 1990s declining amphibian populations have drawn special attention because of three distinctive features: (1) recent (since the 1980s) increases in reports of population declines and species' extinctions; (2) cause(s) seemed to be occurring simultaneously and over great distances; and (3) amphibian populations in protected, natural areas were declining. The latter was alarming because it meant that habitat protection, perhaps the best way to ensure a species' survival, was failing in the case of some amphibians.

No single explanation currently accounts for these three distinguishing characteristics. Understanding the causes of declines is important in order to explain why amphibians are at risk. Amphibians are also thought to be indicators of general environmental health and, thus, causes of declines might also threaten other species. In the case of aquatic breeding amphibians that are noticeable due to large breeding aggregations and calling choruses, declines may also be more visible than for species that do not generally aggregate, such as reptiles. However, most amphibian populations fluctuate annually in size, sometimes by orders of magnitude, from the interaction of causes such as drought, extreme temperatures and predation. Therefore, it is challenging to distinguish between typical, annual changes in population size and a systematic decline preceding extinction (Pechmann *et al.*, 1991). A key step in understanding and perhaps slowing amphibian declines will be sorting among the potential causes and clarifying the circumstances when each is operating alone or in combination. Our goal here is placing the general problem in perspective. To do so, we will review briefly several hypotheses (four of which are reviewed in this issue) that address different facets of the question: what is causing amphibian declines?

SIX HYPOTHESES

There are six leading hypotheses thought to underlie amphibian declines. The first three, alien species, over-exploitation and land use change, are known for their negative affects on biodiversity of native communities. A fourth hypothesis is global change, which includes increased ultraviolet radiation and global warming. The fifth hypothesis is increased use of pesticides and other toxic chemicals, and the sixth is emerging infectious diseases.

We sort these hypotheses into two classes. For class I hypotheses, alien species, over-exploitation and land use change, we have a good understanding of the basic ecological mechanisms underlying declines, in part because of their long history. The direct effects of these processes have negatively affected amphibian populations for at least 100 years. For class II hypotheses, global change, chemicals and emerging infectious diseases, we have a poor but improving understanding of how each might cause declines. These factors involve complex and subtle mechanistic underpinnings, with probable interactions among multiple ecological and evolutionary variables. With one exception that we will discuss, suspected mechanisms associated with class II hypotheses are relatively recent, with their greatest influence dating from at least the middle of the last century. We need more studies connecting suspected mechanisms underlying hypotheses in both classes with quantitative changes in amphibian population sizes, species' range reductions, and losses of species.

Class I hypotheses

Alien species

The direct effect of this mechanism is straightforward: alien species often cause declines and even extinctions of native amphibian populations. Multiple mechanisms may act alone or together, including predation by alien species on natives,

competition between one or more life stages, introduction of pathogens by non-natives and hybridization. An example is provided by effects of non-native fish on mountain yellow-legged frogs (*Rana muscosa*). Our summary follows David Bradford's review in Carey *et al*. (2003).

In the early 1900s, *R. muscosa* was common and widespread above 1500 m in the Sierra Nevada Mountains of California and Nevada (U.S.A.). By 1910, yellow-legged frog populations declined or disappeared from lakes where non-native trout had been stocked since the 1800s. Predation by trout was a direct mechanism causing frog declines, although hatchery-reared fish may also transmit disease (Knapp *et al*., 2001; Carey *et al*., 2002). Ongoing research shows that effects of trout extend throughout a food web, and possibly to fishless lakes by disrupting amphibian metapopulation structure (Pilliod & Peterson, 2001). Yellow-legged frogs continue to decline to the present, but the severity of the declines was not apparent until the 1980s and 1990s.

The *R. muscosa* case illustrates two key points. First, frog populations did not begin declining in the 1980s and 1990s when global amphibian declines were reported. Rather, declines were evident throughout the 20th century, but their scope was unappreciated until the 1980s. As part of the general declining amphibian problem, we need to distinguish between three alternatives: (1) rate of loss of amphibian populations increased during the end of the 20th century, possibly due to a threshold effect; (2) loss rate was constant and the severity of the declines only became evident in the 1980s and 1990s; or (3) there was a time lag between fish introductions and appreciable declines. Secondly, intentional introduction of non-native species is a policy issue that must balance conflicting demands of humans and native amphibian populations. Multiple lines of evidence support the hypothesis that non-native salmonids, introduced for recreational fishing, are the leading cause of amphibian declines in protected areas throughout the Sierra Nevada Mountains (Knapp *et al*., 2001). Policies endorsing introduction of alien fish in these areas reflect primarily economic and recreational goals, with less attention to ecosystem and landscape processes needed to support amphibian biodiversity. Knapp *et al*. (2001) make the important point that 'These results pose a difficult challenge for fisheries and wildlife managers interested in better balancing the conflicting goals of maintaining non-native fisheries in wilderness areas while also minimizing the effects of these fisheries on natural processes' (p. 277).

In this issue, Kats & Ferrer show that the *R. muscosa* case is one example of many where a non-native species has led to the decline of native amphibians. It is often a policy issue as to whether or not aliens are introduced in the first place (Knapp *et al*., 2001; Kats & Ferrer, 2003). Although the mechanism by which aliens can cause amphibian declines or extinctions is relatively straightforward, dealing with aliens once they are introduced is difficult. In addition, aliens can interact with other factors, such as acting as vectors for emerging infectious diseases, resulting in complex indirect effects.

Over-exploitation

The effect of harvesting on amphibian populations is poorly known, but there is evidence that it can be significant. Emmons (1973) noted that 'As early as 1918, tons of frogs were moved by Railway Express out of the tri-state area of North and South Dakota and Minneapolis …' (p. 91) for use as fresh frog legs. He then added, 'It is not uncommon [in 1973] for some [amphibian supply] houses to voluntarily eliminate certain species of turtles and amphibians from their current list of offerings in efforts to protect diminishing supplies in nature' (p. 91). So, three decades ago, a connection was evident between harvesting and declining amphibian populations, but frogs had been harvested in large numbers from much earlier in the late 19th and early 20th centuries (Jennings & Hayes, 1985). Lannoo *et al*. (1994) estimated that between 1920 and 1992 amphibian populations in one Iowa county declined from at least 20 million frogs to 50 000; at least one-third of this decline can be attributed to harvesting with the rest due to wetland drainage.

Land use/land cover change

This hypothesis is also straightforward mechanistically: land use change can facilitate local and eventually regional extinction of populations and species by killing organisms, removing habitat or preventing access of animals to breeding sites. Land use change involves altering the way humans use land, while land cover change is

alteration of the physical or biotic nature of a site (e.g. converting a forest to grassland) (Meyer & Turner, 1992). They occur together or separately, and like Vitousek (1994), we will label both 'land use change'.

Starting in 1992, Stephen Hecnar began studying the variables controlling temperate zone amphibian communities across 42 962 km^2 in south-western Ontario, Canada (Hecnar, 1997). Wetlands covered 69% of the southern and 23% of the northern part of the study area in presettlement times. Drainage of wetlands for agriculture began in the 1800s, and wetlands (often artificial agricultural ponds) now cover 3% of the south and 10% of the north. Heading from south to north, forest cover now increases, human population density decreases and amphibian species richness increases. Hecnar concluded: 'The most important factor that has affected amphibian diversity in south-western Ontario has occurred historically. The massive deforestation and wetland drainage of the 1800s destroyed most amphibian habitat. While the building of artificial ponds may have been beneficial (those not stocked with fish), the magnitude of habitat loss and change resulted in less diverse communities' (Hecnar, 1997: 13). Amount of regional woodlands, predation by fish, habitat isolation and perhaps agricultural chemical use interact at local and regional scales to control amphibian diversity (Hecnar & M'Closkey, 1996). Overall, however, 'The primary process affecting local amphibian richness in south-western Ontario appears to be historic habitat loss … Continued deforestation in the more northern regions of south-western Ontario will likely result in less diverse amphibian communities consisting mainly of green frogs [*Rana clamitans*], leopard frogs [*Rana pipiens*], and American toads [*Bufo americanus*]' (Hecnar & M'Closkey, 1998: 770). Historically, this region supported 13 species of frogs and salamanders, leading to the more general concern that land use change that eliminates native woodlands and wetlands selects against endemic amphibian taxa, favouring species that can adapt to less complex, human-dominated landscapes.

Similar to aliens in the Sierra Nevada Mountains, the negative effects of land use change on amphibian populations were at work in Ontario before the 1980s, and there are other examples worldwide. Habitat conversion over more than a century diminished amphibian biodiversity in south-western Ontario across some 43 000 km^2; by comparison, between 1990 and 1997 an average of about 60 000 km^2 of humid tropical forest were converted to agricultural landscapes each year, and an average of about 23 000 km^2 were degraded (Achard *et al.*, 2002).

Land use change is a major cause of reduced biodiversity globally, and amphibians are no exception. Similar to questions related to alien species, we can ask: was the rate of land use change and consequent loss of amphibian populations constant throughout the 19th and 20th centuries? Or did the rate change significantly in the last decades of the 20th century? The next section addresses how amphibians may have become more susceptible to habitat modification as environmental degradation increases due to anthropogenic forces.

Class II hypotheses

Testing class II hypotheses is difficult because there are complex and often subtle interactions that connect global change or emerging infectious diseases with amphibian population trends. Population changes depend on many variables interacting locally (Blaustein & Kiesecker, 2002; Blaustein *et al.*, 2003), but can also be influenced by changes in other variables far from the target population (Kiesecker *et al.*, 2001).

Global change (including UV and chemicals)

Examples of global change include increasing concentrations of carbon dioxide in the atmosphere, increased nitrogen fixation, increased atmospheric concentrations of gaseous nitrous oxide, widespread distribution of synthetic organic compounds, altered biogeochemistry of global element cycles, harvesting of natural populations by humans, land use/land cover change and biological invasions by non-native species (Vitousek, 1994). We have already discussed the last three components, so we will not include them here.

Global change hypotheses receiving the most attention are those where human actions might cause amphibian declines from global warming, increased levels of UV-B radiation, exposure to contaminants (e.g. from widespread use of synthetic organic compounds such as DDT, PCBs or

CFCs) or increased susceptibility to pathogens. The mechanisms underlying these hypotheses are more complex and more difficult to understand than class I hypotheses.

Global change may affect a region directly, or change in one region may initiate a string of events that alters habitats far from the source (Stenseth *et al*., 2002). Global change hypotheses are inherently complex, impacting individuals and populations either directly or indirectly, and perhaps taking years or decades to be manifest (Walther *et al*., 2002). Because of the complexity involved in climate change models, Carey & Alexander (2003) argue that the role of climate change in amphibian declines has received limited attention. They conclude that, based on current data, there is only a tenuous link between changes in global temperature and moisture patterns and amphibian declines. Global temperatures fluctuated in the past, throughout the evolutionary history of amphibians. However, the speed with which temperatures and moisture patterns are predicted to change is unprecedented, and amphibians may not be able to track predicted habitat shifts due to characteristically limited dispersal abilities. Carey & Alexander note that future changes of the magnitude predicted would pose challenges for surviving populations, as well as recovery of those already declining.

Blaustein *et al*. (2003) review the effects of UV and toxic chemicals on amphibian declines. Several studies have shown detrimental effects of UV radiation and toxic chemicals on amphibians, while others do not (Palen *et al.*, 2002; Corn & Muths, 2002). An increasing number of studies have investigated synergistic effects of multiple factors. Blaustein *et al*. suggest that these interactions should be explored further because amphibians are probably exposed to several environmental stressors simultaneously. Storfer (2003) highlights the need for multifactorial studies in investigations of class II hypotheses.

Emerging infectious diseases

Emerging infectious diseases are diseases that are newly recognized, newly appeared in a population or rapidly increasing in incidence, virulence or geographical range (Daszak *et al*., 2000, 2003). The hypothesis is that emerging pathogens can cause the decline and even extinction of amphibian populations. The two major suspected pathogens are a chytrid fungus and iridoviruses (Carey *et al*., 2003; Collins *et al*., 2003b).

The distinctive biology of the chytrid fungus, *Batrachochytrium dendrobatidis*, is highlighted by evidence that, unlike most chytrids, *B. dendrobatidis* is diploid and the first described vertebrate pathogen in the phylum Chytridiomycota (Berger *et al*., 1998). Multilocus sequence typing showed only five variable nucleotides of 5918 total bases at 10 loci among 32 globally distributed chytrid strains and therefore has likely spread recently, supporting the argument that amphibian chytridiomycosis is an emerging disease (Daszak *et al*., 1999, 2000; Morehouse *et al*., 2003).

The fungus is associated with anuran declines and extinctions in Australia, Central America and North America, but co-exists with non-declining species in the same areas (http://www.jcu.edu.au/school/phtm/PHTM/frogs/chyglob.htm). This is important for two reasons: all wild amphibians are potential pathogen reservoirs, and species-specific differences in susceptibility and life history affect host survivorship and thus reservoir size. Declines due to chytrid epizootics are most common at higher elevations in the tropics (Alford *et al*., 2001; Young *et al*., 2001). The most susceptible species have restricted elevational ranges, large body sizes and breed in streams (Lips *et al*., 2002, in review).

B. dendrobatidis infects 46 Australian frog species analysed to date; 13 species appear to have declined, three are extinct, and many of these occurred at high elevation. Three-quarters of frog species surveyed in Costa Rica and Panama have declined (Lips *et al*., 2003; Lips, 1999; Young *et al*., 2001); chytrids are associated in almost every instance. Chytrids are implicated in precipitous declines of the Wyoming toad, *Bufo baxteri* (Daszak, unpublished; Pessier, unpublished) and the boreal toad (*B. boreas*); infections were found in preserved specimens of the threatened Yosemite toad (*B. canorus*) dating back to at least the 1970s (Green & Sherman, 2001). Chytrid infections were also detected in several frog species at the Savannah River Ecology Laboratory site in the United States, but no declines are reported.

Ranaviruses are important pathogens of amphibians worldwide (Collins *et al*., 2003b), and studies in North America are illuminating the details of epizootics. Two ranaviruses were isolated independently from tiger salamander

epizootics: *Ambystoma tigrinum* virus from Arizona (Jancovich *et al*., 1997) and Regina ranavirus from Saskatchewan, Canada (Bollinger *et al*., 1999). Genetic analyses of ranaviruses isolated and characterized from tiger salamander epizootics in six states and two provinces in western North America revealed low DNA sequence divergence in all genetic markers studied, suggesting recent spread (Jancovich *et al*., 2002a, in prep.). Enhanced viral spread due to human actions may have caused this phylogenetic similarity over large geographical areas (Jancovich *et al*., 2002a; in prep., Jancovich *et al*., 2002b, in prep.). However, a co-evolutionary history between salamanders and viruses is supported by field data and laboratory experiments. Salamander populations most often recover 1–2 years after a die-off, suggesting evolved resistance (Brunner *et al*., in review). In addition, disease selects against cannibalistic morph salamanders because it is transmitted easily by eating conspecifics (Pfennig *et al*., 1991; Jancovich *et al*., 2001). Accordingly, there is a negative correlation between frequency of disease and frequency of cannibalistic salamanders throughout Arizona (Pfennig *et al*., 1991).

In contrast to chytrids that characteristically cause declines, long-term studies of Arizona tiger salamander populations suggest that iridoviruses cause population fluctuations (Collins *et al*., 1988). Partially because of the different roles they apparently play in amphibian population dynamics, it was hypothesized initially that ranaviruses have an older relationship with amphibians, but that chytrids have recently evolved pathogenicity or are newly introduced. These predictions are supported by current data, but ranavirus and chytrid phylogeographical analyses both suggest possible anthropogenic spread. Thus, *Ambystoma tigrinum* virus and *B. dendrobatidis* are considered emerging amphibian pathogens.

Daszak *et al*. (2003) discuss the role of pathogens in amphibian declines. They suggest that chytrid fungi are the best supported pathogen related to amphibian declines, and consequently much of their paper focuses on this pathogen. They speculate on potential modes of anthropogenic spread, and propose that chytrid fungi are a model for studying emerging infectious diseases in general.

DISCUSSION

Understanding and perhaps reversing amphibian declines requires a clear awareness of the possible causes and how they might be interacting. Our brief overview highlights what we know and the areas that require further research.

Habitats change over time and amphibian populations and species move among sites (Skelly *et al*., 1999); neither is a new ecological mechanism affecting the distribution and abundance of species (Flannery, 2001). Alien species, overexploitation and land use change have affected amphibians negatively since the 19th century, and probably longer. Have amphibians been declining at a constant rate for more than a century because of these causes? Or did the rate of loss of species and populations attributable to land use change and alien species increase in the latter part of the 20th century? If the rate of loss increased, was it because environmental degradation reached a threshold ('tipping point') beyond which amphibian susceptibility to all factors increased?

Houlahan *et al*. (2000) argued that amphibian populations declined rapidly across the globe from the late 1950s/early 1960s until the present. In Western Europe and North America, species declined throughout the 1960s, then stabilized in Western Europe, but continued declining in North America (Houlahan *et al*., 2000). Alford *et al*. (2001) agreed that there were declines whose magnitude varied regionally, but their reanalysis of the same data led them to conclude that the declines were supported only in North, Central and South America, and only since the early 1990s. Importantly, both groups agreed that populations are declining and the rate has increased in some regions at least in the last decade, perhaps since the 1950s. It is certain that land use change and alien species are partial answers to the question, 'Why are amphibian populations declining?' However, we still need better quantitative data linking these factors to the loss of populations and species. We know of no case where a non-native species caused complete extinction of a native amphibian species, but alien species diminish population numbers regularly, restrict native species to marginal habitats and increase the likelihood of extinction of natives from other factors (e.g. disease or land use change; see Kats & Ferrer, 2003). Improving

our understanding of how class I hypotheses interact with class II hypotheses is key to unravelling the complexity of amphibian declines.

We are reaching a point where we can envision each cause of amphibian declines and dissect systematically the relative contribution of each alone and together. It is important to understand the human contribution to global amphibian declines because, at least in principle, these would seem to be the easiest to reverse. Thus, explanations in class I have the advantage that their direct effects are relatively easy to see at work. If a wetland is converted to farmland, we would predict that amphibian species richness and population sizes will decrease (Lannoo *et al*., 1994). Protecting wetlands, controlling habitat fragmentation and restricting movement of alien species all conserve native amphibians (Semlitsch & Bodie, 1998). For class I hypotheses, biological mechanisms are at the root of why amphibians are declining, but the solutions are often in the policies that translate human values into environmental consequences. In this issue, Kats & Ferrer discuss management strategies to deal with non-native species.

Testing class II hypotheses is a more difficult task, as illustrated by efforts to understand the contribution of emerging infectious diseases to amphibian declines. Despite an important link with biodiversity, disease is a comparatively neglected topic in ecology, evolution and conservation biology, even as emerging diseases remind us that pathogens can have a major effect on biodiversity (Harvell *et al*., 1999).

A combination of forces can propel a benign parasite into a virulent pathogen (Lafferty & Gerber, 2002). Once a host becomes susceptible and is infected, parasite virulence and host–pathogen dynamics can combine to cause the death of one individual, or under the right conditions, extinction of a population or species. Global change, land use change or alien species acting alone or together are among many environmental sources of stress that could increase disease susceptibility or virulence (Carey *et al*., 2003; Blaustein *et al.*, 2003; Carey & Alexander, 2003). Then, as long as disease incidence is increasing in the population, theory predicts that parasites will be selected for greater virulence (Ebert, 1999). Any behaviour that enhances contact can also increase transmission between susceptible hosts, further increasing selection for high virulence. For example, envision a situation whereby increased temperatures due to global warming constrict a prolonged amphibian breeding season in the tropics. As a result, animals are forced to breed at higher densities, which can increase disease transmission (Pounds, 2001) and consequently pathogen virulence. While this is a hypothetical example of a complex interaction among class II hypotheses, it illustrates the importance of using a multi-factoral approach. A real example includes work by Kiesecker *et al*. (2001), who reported that boreal toad (*B. boreas*) embryonic mortality resulted from interactions of UV-B radiation and a fungus, *Saprolegnia ferax*.

In general, we need a better understanding of the forces that might tip the balance from host–parasite co-existence to host extinction. Amphibians and their pathogens offer ideal, if sometimes unfortunate, cases for studying these forces because interactions cover a continuum from host–parasite co-existence to declines and extinctions. Ultimately, the goal is anticipating the onset of new diseases and eliminating situations that facilitate their spread. Levins *et al*. (1994) argued that to achieve this goal, 'We must see disease as the outcome of multiple conditions arising from changes not only within cell nuclei, but also around the globe, including changes in climate, economic patterns, and communities of species.' Their argument makes it clear that solving the declining amphibian problem requires collaboration of researchers from diverse areas of expertise. It is a problem that lends itself to integrative, collaborative analysis that draws upon scientific expertise from molecular biology to ecosystems biology, from immunology to global climate change (Collins *et al*., 2003b).

Collaborative research must also be employed to increase our overall understanding of class II factors and interactions among class I and class II factors. The intrinsic complexity of global change, by which we mean to include global climate change, increases in environmental levels of toxic chemicals, and increases in levels of UV radiation reaching the earth's surface, lends itself to interdisciplinary, multifactorial studies. Studying interactions between class I and class II factors is critical for improving our understanding of the causes of amphibian declines.

The problem of declining amphibians, for these reasons, serves as a model for the general

decline in global biodiversity. An important lesson is that 'conservation as usual', for example, protecting a species or population by isolating it in a refuge, is not sufficient. Protected areas are affected by many factors, including introduced alien species (Knapp *et al.*, 2001; Kats & Ferrer, 2003), toxins that may blow into these areas (Davidson *et al.*, 2001; Blaustein *et al.*, 2003), climate change (Pounds *et al.*, 1997) and pathogens that can invade these systems. Thus, we have to redefine what we mean by a refuge. 'Science as usual' will also not solve complex questions such as what is causing amphibian declines? Studies by individual investigators help us to understand changes in amphibian population dynamics, but accelerating our progress is most probably undertaken with an integrated approach (Collins *et al.*, 2003b). Teamwork invites collective knowledge and experience, and presents the opportunity for the rapid resolution of complex challenges.

In the case of class I hypotheses the reasons for amphibian declines are obvious, but for class II hypotheses possible explanations remain elusive and complex. The goal is to find answers, set research priorities and make management recommendations that will help guide researchers, policy makers, and funding agencies toward the vision required to conserve amphibians and their habitats. In this issue of *Diversity and Distributions*, researchers explore elements of several leading hypotheses to help us understand why amphibian populations and species are declining.

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