PHILOSOPHICAL
TRANSACTIONS B

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Review

Cite this article: Lips KR. 2016 Overview of chytrid emergence and impacts on amphibians. *Phil. Trans. R. Soc. B* **371**: 20150465.
http://dx.doi.org/10.1098/rstb.2015.0465

Accepted: 26 May 2016

One contribution of 18 to a discussion meeting issue 'Tackling emerging fungal threats to animal health, food security and ecosystem resilience'.

Subject Areas:
ecology

Keywords:
amphibians, biodiversity, chytrid fungi, disease, populations

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Overview of chytrid emergence and impacts on amphibians

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Chytridiomycosis is an emerging infectious disease of amphibians that affects over 700 species on all continents where amphibians occur. The amphibian–chytridiomycosis system is complex, and the response of any amphibian species to chytrid depends on many aspects of the ecology and evolutionary history of the amphibian, the genotype and phenotype of the fungus, and how the biological and physical environment can mediate that interaction. Impacts of chytridiomycosis on amphibians are varied; some species have been driven extinct, populations of others have declined severely, whereas still others have not obviously declined. Understanding patterns and mechanisms of amphibian responses to chytrids is critical for conservation and management. Robust estimates of population numbers are needed to identify species at risk, prioritize taxa for conservation actions, design management strategies for managing populations and species, and to develop effective measures to reduce impacts of chytrids on amphibians.

This article is part of the themed issue 'Tackling emerging fungal threats to animal health, food security and ecosystem resilience'.

1. Introduction

Declining amphibian populations have been a concern of scientists ever since the first World Congress of Herpetology in 1988. There scientists realized many amphibians that had previously been common, abundant or reliably encountered had disappeared for no obvious reason, often from remote or protected areas [1]. The publication of the IUCN Global Amphibian Assessment (GAA) eventually revealed the extent of the problem. The GAA [2] showed that 43% of amphibian species were in decline and 32% of species threatened; not only was the problem widespread, it was recent, with 100 of the 168 presumably extinct species having disappeared since 1980. Threats varied regionally, with declines associated with habitat loss and alteration concentrated in the developed areas of Europe and North America, but a disproportionate number of severe 'enigmatic' declines, had occurred in species-rich tropical areas. Collins & Storfer [3] explored the various threats to amphibians and developed a framework that included traditional threats (e.g. land-use change, overexploitation and chemical contaminants) as well as novel threats (e.g. invasive species, emerging infectious diseases and climate change). These novel threats are more intractable than traditional threats because they are regional or global problems not contained within socio-political boundaries and whose solutions require global collaborations. The chytrid pathogen *Batrachochytrium dendrobatidis* (*Bd*; [4]) is a good example of these new threats, as it is both an emerging infectious disease and an invasive species. In a short period of time, *Bd* has contributed to the threatened status of almost 400 amphibian species—a greater impact than predation by established and well-known invasive species that affect all classes of vertebrates [5].

Bd infects over 700 species across three orders of vertebrates [6], causes species extinctions, mass mortality events and precipitous and persistent population declines where it has invaded [7–9]. Yet not all species respond equally to infection, with some species going extinct, others declining and persisting at low numbers, and some species declining very little or rebounding post-decline [10–12]. Today, we know that the amphibian–chytridiomycosis system is complex, and that the response of any amphibian species to chytrid depends on

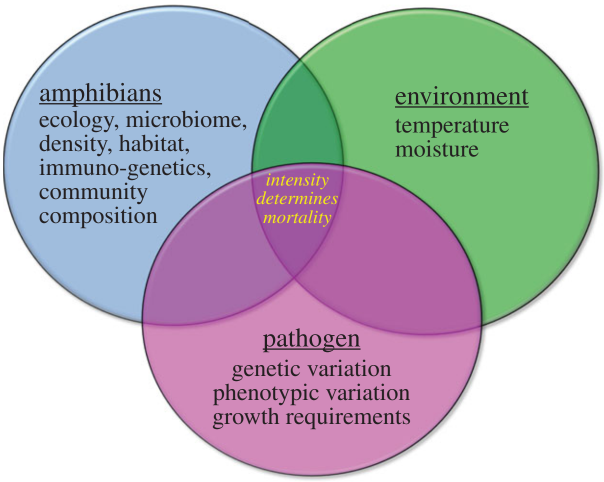

Figure 1. The interaction of host ecology and evolution, fungal genotype and phenotype, and environmental conditions are thought to be key drivers of disease intensity, which ultimately determines individual mortality and host response to infection. (Online version in colour.)

many aspects of the ecology and evolutionary history of the amphibians [10], the genotype and phenotype of the fungus [12,13], and how the biological and physical environment can mediate the interaction [14]). The interaction of host, pathogen and environment are thought to be key drivers of disease intensity, which ultimately determines mortality (figure 1) of host and the degree of response seen in host individuals, the population and the species.

Our understanding of this new disease has changed greatly since it was first described in 1997 [4,15]. Then, it was thought that *Bd* was a clonal organism that had spread globally, and that we could expect to see many more epizootics as it invaded naive populations. Since then, we have observed only a few die-offs [7–9] although *Bd* has been found on every continent, often without any obvious impact on populations of amphibians, suggesting a long history or variation in virulence. Recent studies have shown that *Bd* is actually comprised of several genetically distinct lineages that vary in virulence and phenotype [16]. Of these lineages, the global pandemic lineage (GPL) is clearly an invasive species that has spread across the globe and caused mass mortality, population declines and extinctions.

Scientists have identified some traits that make some species more likely to decline by comparing responses among species from the same region and relating extirpation to species-specific traits. Lips *et al.* [10] described species-specific patterns of population decline among the amphibian communities at four sites where invasion by *Bd*-GPL was identified as the cause. They found that declining populations shared aquatic habitats, restricted elevational ranges and large body sizes. Most of these traits are similar to those associated with general conservation concern, meaning that traditional conservation prioritization efforts are likely to identify species at risk of chytridiomycosis, even when definitive data are lacking.

Few other comparisons of species response to chytrid invasion have been possible, because few other epidemics have been reported, or because where invasion has occurred, species richness is very low [9]. Comparing responses of species where *Bd* is endemic has been more difficult because of the lack of historic data on population response or on species composition. Still, some biotic (e.g. variation in pathogen virulence [12,16]; host ecology [10]; immunogenetic variation [17–19]; antimicrobial peptides [20]; skin bacteria [21,22]) and abiotic (e.g. temperature and moisture [23]; habitat [10]) factors have consistently been associated with higher probabilities of population persistence or decline across many locations.

Not only can *Bd* change community composition through unequal impacts on species, but the presence of species that amplify or dilute infection could also alter the response of a community to disease. Community composition is especially important in disease dynamics because of the broad host range of *Bd*. *Bd* infects over 700 species [6], which means that potentially all species of amphibians can serve as host, vector or reservoir. Laboratory studies have shown that the species composition of tadpole communities affects disease transmission [24,25] as do studies of artificial adult communities [25]. In these cases, some species reduced infection in co-occurring species. The lack of information on the ecology of many amphibians and insufficient information on the global distribution and history of chytrid lineages make predicting amphibian response difficult.

I describe the range of responses of amphibians to chytrid pathogens and where additional research is needed. I divide this review into a description of case studies from (i) areas where chytrids are an invasive species, (ii) areas where impacts on amphibians are varied or unknown, and (iii) areas where chytrid is not present.

2. Impacts of chytrid on amphibian populations

(a) Chytrids as invasive pathogens

(i) Australia

Some of the earliest amphibian die-offs and unexplained declines were detected across many protected sites in tropical rainforest streams during the 1980s [7]. At least six species of frogs have not been seen for one to three decades and are presumed extinct, whereas six other species have declined so greatly that the probability of extinction is high [26]. Berger *et al.* [15] identified a skin infection associated with dead frogs and population declines from three regions that they would attribute to *Bd*, which had just been described [4]. In the decades to follow, extensive research on many of the surviving species has confirmed the role of *Bd* in contributing to population declines across Australia [27], and has shown how species-specific differences in ecology and behaviour contribute to variation in disease dynamics [14,28]. Despite continued declines in many species [25], others have developed ways to persist with infection. Retallick *et al.* [29] described a population of *Taudactylus eungellensis* persisting with stable infections that had experienced an epidemic die-off 10 years earlier. A 7-year capture–mark–recapture study of the endangered *Mixophyes fleayi* showed increased abundance after an initial population decline that was attributed to *Bd* [30]. Others have shown how warmer and drier microclimates might provide a refuge from *Bd* for some species [31]. Recent evidence suggests that some Australian amphibians may be adapting to *Bd*; in both laboratory [19] and field studies [32], populations of *Litoria verreauxii alpina* that had been previously exposed to *Bd* survived longer than those that had not.

(ii) Central America

Central America has played a key role in the *Bd* story for many reasons. First, it provided one of the early examples of enigmatic declines in the form of Monteverde's golden toad (*Incilius periglenes*) [33]. Second, this was one of the first sites where *Bd* was found infecting wild animals at sites of population decline and mass mortality, and served as definitive proof that a pathogen could cause mortality and declines in multiple species [30,34,35]. Third, the spatio-temporal spread of *Bd* through Central America provided definitive proof of an invasive pathogen moving in an epidemic wave [8,36]. Subsequent genetic studies have revealed that these die-offs were attributable to a single lineage, identified as the invasive *Bd*-GPL [37].

The Neotropics have been especially hard hit by these declines [38], with hundreds of species threatened with extinction. The high rates of loss are associated with the exceptionally high diversity and endemism in this region, with over 50% of all described amphibian species found in the Neotropics [38]. In the Neotropics amphibian endemism is concentrated in the montane areas, where the cool moist climate supports chytrid growth. For some tropical amphibians, an entire species could be eliminated by chytridiomycosis because of the small population size, small range and rapid spread of disease. The impact of *Bd* on Central American amphibians has been devastating [34,35,39]. In species-rich cloud forests of Lower Central America [8], mass die-offs were observed, followed by numerous population declines of many species, including extirpations of dozens of species in a matter of months [8]. To the north in Mexico, Guatemala and Honduras, die-offs were not seen, but unexplained disappearances of dozens of species were noted throughout the region in the 1990s and 2000s [39,40]. Decades later, scientists were able to revisit historic collecting sites and search for *Bd* [39,40] or to test museum specimens collected from these sites [40]. They found that the first appearance of *Bd* in the museum record was followed by the rapid loss of wild populations of both anurans [39] and salamanders [41], further extending the epidemic wave from Mexico through Panama.

In Central America, chytridiomycosis has reshaped the patterns of amphibian biodiversity, obscuring historical biogeographic patterns such that distance between sites is no longer correlated with community similarity. Community composition in the region was severely disrupted by epidemics at multiple sites and many of the unique species of these communities were eliminated, with disproportionate effects on endemic species. This resulted in a homogenization of the regional fauna and ecological homogenization of reproductive mode and habitat [42]. As a result, the impacts of chytridiomycosis have altered community structure and our ability to detect biogeographic patterns.

Among Neotropical amphibians, the harlequin frogs (genus *Atelopus*) are an iconic species in both research and conservation. As a group, the harlequin frogs (genus *Atelopus*) are one of the most threatened groups of amphibians in the world, having experienced severe population declines and extinctions from *Bd* throughout their range from Costa Rica and Panama to Colombia, Ecuador, Venezuela and Peru [43]. The similarity of response among such a large number of closely related species is the best example of taxonomy predicting response to disease. At least 40 of 97 described species have disappeared in the past 20 years, with three species listed as extinct and 82 species listed as endangered or critically endangered [38]; only 10 species are not threatened [36,43]. Declines have been so widespread and so obvious that Lips *et al.* [36] used the reports of losses to map the spatio-temporal pattern of population declines in *Atelopus* to represent the hypothesized spread of *Bd* through South American Andes. *Atelopus* species are also important because they may play a disproportionate role in disease dynamics. DiRenzo *et al.* [44] demonstrated that *Atelopus zeteki* is an acute supershedder, producing exceptionally high numbers of zoospores over several weeks prior to death. This led to the hypothesis that *Atelopus* species might contribute to increasing the pool of zoospores in the environment and the prediction that the presence of *Atelopus* species in a community might amplify disease and cause populations of other species to decline. This will be a key concern as conservation programmes consider reintroduction of *Atelopus* and other susceptible species into communities where they have been extirpated and where surviving species have achieved coexistence with *Bd*. While some species that had been missing for many years have been 'rediscovered', the low numbers, continued mortality and lack of large-scale recovery indicate that disease must still be causing unobserved mortality or lack of recruitment in amphibian populations at these sites. To effectively manage *Atelopus* or other species where *Bd* is present, we need to know how disease has altered demographic rates of species such as survivorship, recruitment and transitions between life stages. Quantitative data from four species of *Atelopus* [45–47] can provide the baseline data for reintroductions and help understand stages limiting to natural population recovery. As in Australia, there is some evidence that warmer regions where environmental conditions could mitigate the impacts of disease [48] might be the best option for reintroductions.

(iii) California

California has been important because it is the site of some of the earliest enigmatic declines and die-offs of amphibians from remote protected areas. One of the earliest, enigmatic population declines in the USA was noted in the Wyoming toad (*Anaxyrus hemiophrys baxteri* [49]) in the mid-1970s; it became extinct in the wild within 10 years [50], but no definitive cause has been attributed. The Yosemite toad (*A. canorus*) experienced population declines in 1976–1979 [51]. Some of those carcasses were later found to be infected with *Bd* [52], and it is presumed that *Bd* caused those declines. A mass die-off of mountain yellow-legged frogs (*Lithobates muscosa*) in the Sierra Nevada of California was seen in 1979, followed by population declines and extirpation by 1983 [53].

Understanding the mechanisms that drive a chytridiomycosis epidemic came from long-term studies of mountain yellow-legged frogs in alpine lakes across the California Sierra Nevada [9,54]. These researchers documented the invasion of *Bd*-GPL into naive populations of amphibians where it caused die-offs, population declines and extirpations. They identified intensity of infection as the key predictor of mortality, with higher intensities associated with individual mortality and the average intensity of the population determining whether a population persists or is extirpated [9]. For mountain yellow-legged frogs in the Sierra Nevada, individuals die at 10 000 zoospores, and populations are extirpated when average infection is 10 000 zoospores [9]. However, these values cannot be applied to all systems, as the mortality threshold varies among species [44,55]. Higher frog density was identified as the mechanism causing more infections, greater numbers of zoospores and a larger environmental pool of zoospores that caused higher intensities and mortality

[54]. Similar data do not exist for any other species or system, although other studies have shown that higher intensity of disease is generally associated with greater mortality or morbidity. The large number of ponds spread out across a large area has allowed repeated observations of epidemics, to document the epidemic spread of *Bd* across the landscape. These results are consistent with the epidemic wave hypothesis, and provide an example independent of those from Central America, Andean South America and Australia.

The single-species system of the California Sierra Nevada also offers a contrast to the multiple-species, highly complex tropical cloud forest amphibian fauna of Central America. For two systems that are so different in terms of climate, habitat and biological composition, it is remarkable that the patterns of disease spread and epizootics are so similar. The next step is to determine whether disease dynamics of the epidemics described in Panama [8] match those reported for the Sierra Nevada system, and whether frog density and disease load are the key predictors of tropical epizootics and species response to infection.

(iv) Puerto Rico

In Puerto Rico, three endemic species of amphibians became extinct in the 1970s [56]. No die-offs were ever observed, but museum specimens showed that *Bd* has been present since 1976. Like species that disappeared from Panama and Costa Rica, these species were habitat specialists, and at least one was associated with streams. Using capture–mark–recapture and disease surveillance, researchers were able to document ongoing population declines associated with disease despite the lack of detectable mortality. Today, surviving species are at lower abundance than historically, and populations fluctuate with climate patterns [56]. Burrowes *et al.* [56] proposed a synergism between disease and climatic conditions to explain fluctuations. They proposed that during the dry season when these frogs aggregate in retreat sites, the localized high density promotes the spread of *Bd*, and highly infected individuals die in the retreat site. It is not known how this *Bd*-GPL lineage got to the island; however, severe outbreaks of chytridiomycosis on other Caribbean islands such as the extirpation of mountain chicken frogs (*Leptodactylus fallax*) on Dominica and Montserrat [57] have been caused by *Bd*-GPL, showing that this lineage is actively island-hopping across this region.

(v) Salamander chytrid

Batrachochytrium salamandrivorans (*Bsal*) is a recently discovered species of salamander-specific chytrid [58] that has been introduced into Europe, where it is causing mass die-offs and population declines in several species [58,59]. Field and museum sampling has shown that *Bsal* has been present in Asia for over 150 years and is present in the wild in at least three countries [58–60], although the impact on Asian populations is not known. *Bsal* has not been found in North America [46,61], although several species are highly susceptible in the laboratory. Because North America is a global hotspot for salamanders, with 10 families and 675 species [48], the US Fish and Wildlife Service has taken preventative measures and imposed a moratorium on imports of 201 species belonging to genera known to be carriers of *Bsal*. Because the USA lacks a formal policy requiring inspection or testing of live imports of most wildlife species for diseases or pathogens, native species remain at risk of invasion by these and other pathogens. Switzerland has taken similar steps and passed a law banning the import of all salamanders into that country.

(b) Chytrid present, but impacts on amphibians varied or unknown

(i) Africa

At least two lineages of *Bd* are present in Africa, *Bd*-Cape, an endemic lineage from South Africa, and the invasive *Bd*-GPL [16]. Neither the geographical nor taxonomic distribution of either lineage has been described for Africa, and no demographic studies have assessed impacts of either lineage on wild populations. *Bd* has been present in South Africa since at least 1938 and is commonly found in Ghana, Kenya, South Africa and Western Africa [62]. *Bd* is widespread in many of the highland regions [63], whereas tropical West African areas regions are reported to be clear of *Bd* [64]. Recent reports from Cameroon [65] found *Bd* present in several species, several of which had shown recent declines and they suggested *Bd* as a likely cause. One epidemic of chytridiomycosis has been reported from Africa, that of the Kihansi Gorge in Tanzania. In 2003, a mass mortality event was followed by population declines of many species that was attributed to *Bd* [66]. It is not known which lineage of *Bd* caused this mortality event, although patterns suggest the invasive *Bd*-GPL. It was hypothesized that infected frogs arrived at the site in construction material, although how the site remained *Bd*-free after a century of *Bd* presence in surrounding areas is curious. Luckily, a captive population of the endemic Kihansi spray toad (*Nectophrynoides asperginis*) had been established in captivity, and more than 2000 animals were reintroduced to the site in 2013, despite the fact that chytrid has never been eliminated from any site where it occurs. Many kinds of laboratory and field studies are needed to explain amphibian–chytrid history at Kihansi Gorge, and across Africa.

(ii) Asia

Studies in Asia are likely to be very enlightening in understanding the history of the amphibian–chytrid system. *Bd* is widely distributed throughout Asia [67] and has been present in the region since at least 1911 [68], but no reports exist of disease-driven mortality or population declines [67]. Many distinct genotypes are being described from the regions, including Japan [69], Korea [70] and India [71] as well as *Bsal* [58]. The growing diversity of chytrid pathogens of amphibians from Asia suggests a likely site of origin for these pathogens. Unfortunately, Asia has one of the poorest records of amphibian demographic research both in general and in relation to chytrid infection, and this greatly limits conclusions on the evolutionary history of the system and hampers effective conservation and management.

(iii) Europe

In their meta-analysis of published studies, Houlahan *et al.* [72] identified rapid and widespread population declines in many amphibians in the UK and western Europe starting in the late 1950s and lasting into the late 1960s. Further research is needed to assess causes and patterns of these historic declines, but disease is one of several possible causes. Europe is home to at least three species of chytrid: an endemic Swiss lineage, the invasive *Bd*-GPL lineage and invasive *Bsal*. Despite extensive research across the region, evidence for epidemics is limited to several recent die-offs and population declines in montane regions of Spain and the French Pyrenees. The earliest confirmed case of mass mortality and subsequent population declines from *Bd* was during 1997–1999 [73] from Central Spain. By 2007, populations of *Salamandra salamandra* also began to decline in this park and mass mortalities of *Bufo bufo* were observed [74,75]. Garner *et al.* [76] surveyed field and museum samples collected across Europe between 1994 and 2004, and found evidence for infections in Spain, Portugal, Italy, Switzerland and Great Britain from as early as 1998. They concluded that chytrid is widespread, even though epidemics and mass mortalities have rarely been reported. Walker *et al.* [77] modelled the geographical distribution of *Bd* in Iberia and looked for evidence of both spread and environmental forcing of disease emergence. They found multiple distinct genotypes consistent with either a history of multiple introductions or of a single ancient introduction of *Bd* into Iberia. The impact of chytrids on amphibians in other parts of Europe is less clear. Switzerland has its own unique, ancient lineage of *Bd* (*Bd*-CH [16]) that may be hypovirulent as there are no confirmed chytrid-related die-offs or population declines from that region [78]. Many Swiss populations of amphibians are missing from many historical localities, although causes are complex and none have definitively been attributed to disease. The situation is similar to that in Italy, where *Bd* has been present for several decades and populations of some species are declining, but no causative link has been established [79,80]. Spitzen-Van Der Sluijs *et al.* [81] showed that in the Netherlands *Bd* was present in many species but at low prevalence and low intensity. They concluded that in Europe host responses are geographically and taxonomically inconsistent and are influenced by environmental factors or strain-dependent variation in virulence. For example, they found that *Alytes obstetricans* in the Netherlands is infected but not declining, whereas populations of that species in upland areas of Spain are highly susceptible. As *Bsal* continues to spread in the region [59], researchers will have opportunity to establish capture–mark–recapture studies to quantify the response of native amphibians to co-infection by multiple chytrid lineages.

(iv) Brazil

Brazil presents one of the most complex amphibian–chytrid stories and has contributed to our understanding of the amphibian–chytrid system in several unique ways. Brazil was among the first sites to show evidence of mass die-offs of a diverse community of amphibians. Heyer *et al.* [82] observed a mass die-off of an entire community of amphibians in a protected site in the Atlantic Coastal Forest of Brazil in 1979. They attributed the loss to a particularly bad winter, but *Bd* has since been found throughout the Atlantic coastal forest [83], although no definitive link has been made between losses at this site and chytridiomycosis. This is the general situation for most of the country, where reports of mass mortality are lacking [84] and definitive impacts of chytrids on amphibian populations are inconsistent or lacking. Like Europe, Brazil hosts multiple lineages of chytrid but is the first to show evidence of hybridization between lineages [83,85,86]. Brazil is unique in having amphibians infected by both the endemic lineage (*Bd*-Brazil) and the invasive *Bd*-GPL for over 100 years. Importantly, the long history of *Bd*-GPL in Brazil suggests additional vectors of pathogen introduction beyond the trade in amphibians. The lack of clear evidence of population declines, the long occurrence of *Bd* in Brazil and the low but steady prevalence of infection in Brazil suggests that these amphibians have evolved ways of coexisting with chytrid [83] and may produce insights for long-term planning in other regions of the world.

(v) Eastern United States

Bd is widespread in North America [6] and generally occurs at low prevalence and low intensity in the eastern US [37]. *Bd* has been present in the USA for at least 140 years, with the oldest records from southern leopard frogs (*Lithobates sphenocephala*) collected in Illinois in 1888 [87]. In this region, no die-offs have been reported, no species have been lost, and no recent dramatic population declines have been identified. Disease prevalence in Illinois today is some of the highest reported, and infection intensity is sufficient to cause death in California ranids. It is not known which lineage of *Bd* is present in Illinois, and whether it is native or introduced. Such a long coexistence between host and pathogen in Illinois suggests that amphibians and chytrids may have a long coevolutionary history there or that the USA is home to an endemic lineage [61].

That is not to say populations have not experienced declines or are at risk of future declines. An older, slower, silent wave of population declines occurred in the USA with little note, and is continuing today. Houlahan *et al.* [72] described widespread declines in amphibians in North America and Europe in the 1950–1960s. Most of these populations did not recover, but experienced a second round of declines in the 1970s and 1980s. To date, no cause of those declines has been put forward. A pattern of slow, unnoted declines has been shown for amphibians across the USA [88]. These authors synthesized amphibian monitoring data and detected a 3.7% annual decline in occupancy, with southern species of amphibians (especially salamanders) showing the greatest declines. They concluded that declines may be more widespread and severe here than previously recognized, but did not assign any specific cause to any of these declines. Grant *et al.* [89] compared the spatial patterns and intensities of four threats—including chytridiomycosis—to declines in species occupancy for those US Geological Survey data and concluded that no single threat was consistent in explaining observed trends and that amphibian response to the threats varied spatially.

One of the largest and most widespread reports of salamander declines comes from the Appalachian Mountains. Declines in populations in terrestrial forest salamanders (Family Plethodontidae: Plethodon) occurred throughout the eastern US in the late 1970s to early 1980s [90], although die-offs were not noted and no definitive cause has been identified. Caruso & Lips [91] resurveyed many of Highton's historic collecting sites and found that occupancy and detection were lower for many species of *Plethodon* in the Great Smoky Mountain National Park. They resurveyed more species at Highton's historic sites and found that many populations of multiple genera have declined in both occupancy and detection (Caruso *et al.* 2012, unpublished data). Extensive testing for disease in living animals and in preserved museum specimens from these sites produced very few animals infected with *Bd*. The lack of mortality, species extinction or disease epidemics all suggest either that the eastern US lineage of *Bd* has been present for a long time, and native species have evolved to avoid infection, that it is hypovirulent like *Bd*-CH, or that undiscovered lineages of chytrid fungi are present but not detected with current molecular assays.

(c) Chytrid-free areas

Places where *Bd* has not yet arrived are rare, but generally are oceanic islands such as Papua New Guinea, Fiji, the Solomon Islands [67,92] and the Seychelles [93]. The Seychelles support an amphibian fauna that is 92% endemic [93], which makes it impossible to predict responses based on phylogeny. However, in the case of Papua New Guinea, the fauna has strong connections to that of Australia, which was severely affected by *Bd* in the 1980s [7], suggesting that impacts of introduced chytrids there are likely to be devastating. Understanding how are these areas have not become infected can inform efforts to prevent its establishment. Human movements and commercial trade have been linked to international movement of chytrid fungi across large scales [16,94]. The recent detection of *Bd* on Madagascar [95]—which is 1800 km from the Seychelles—is especially worrisome. Conservationists were prepared for a devastating effect when *Bd* was first detected on Madagascar, but so far, these have not materialized [95]. Unfortunately, the Madagascar chytrid has not been sequenced, so we do not know which lineage it is, or how it got there. Also lacking are experimental data on the response of Madagascar amphibians to infections. It will be important to institute disease surveillance and amphibian monitoring in these uninfected places to provide information on the arrival and spread of disease. Testing species in the laboratory for susceptibility will be critical to predict the response in the field and design conservation measures.

3. Conclusion

This paper along with other recent reviews [37,81] of global patterns of amphibian responses to chytridiomycosis all show that host responses are context-dependent. In particular, four key factors seem to be the primary drivers of host responses to disease: (i) the genetic lineage of the fungal pathogen, (ii) the length of time the host and pathogen have been interacting (i.e. is chytrid epizootic or enzootic), (iii) host population and species ecology and evolutionary biology, and (iv) environmental conditions.

In particular, two recent advances have greatly altered our understanding of amphibian–chytridiomycosis dynamics: the recognition that *Bd* is not one species, but is instead many genotypically and phenotypically distinct lineages that vary in distribution and virulence, and the recognition that these chytrid fungi have been infecting amphibians for much longer than we thought. Thus, host–pathogen interactions are much more complicated than we originally thought (figure 2), and we now must include the possibility that long co-occurrence might have allowed amphibians to develop resistance or tolerance to the pathogens, or that the pathogens have lost virulence. This is borne out by laboratory and field studies showing that prior exposure can increase survival [18,32,96] and that inherent immunogenetic variation in species [17] and populations [97] is correlated with response to disease.

Just as individual species respond variously to different pathogens, so too will communities comprised of different host species. Moving forward, we need to understand how multiple infections by multiple pathogens will affect species and communities, especially as these pathogens will represent mixtures of endemic, established and invasive lineages and effects may vary depending on the order in which they arrive and their previous history with amphibian hosts.

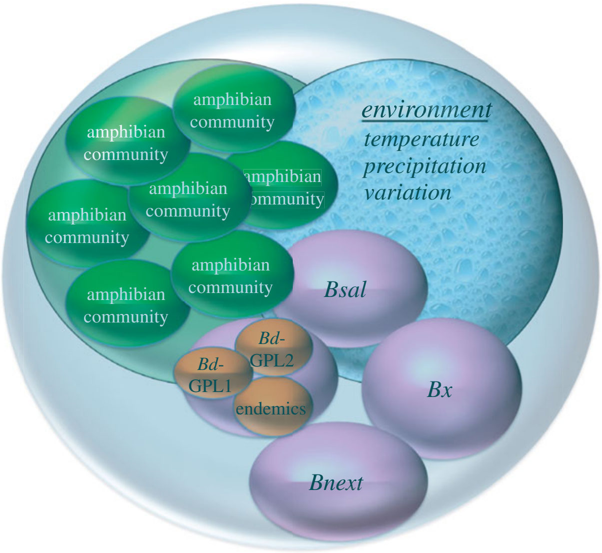

Figure 2. The evolving view of amphibian–chytrid interactions that includes responses of the entire amphibian community, multiple pathogens infecting a host community, and the effects of both abiotic environment and microbiome on host response. (Online version in colour.)

In this review, I have highlighted what we know about the impacts of chytrids on amphibian populations. Yet even in the best-studied cases, we are still lacking basic information on numbers of amphibian species, population sizes, trends in occupancy and abundance, and how chytrids are impacting any of these estimates. Ultimately, governments and conservation organizations base decisions on species endangerment, funding and conservation priority on the numbers of individuals and populations and how quickly those numbers are going up or down. We need robust data on all these if we wish to accurately identify species at risk, prioritize taxa for conservation actions, design management strategies for or develop measures to reduce impacts of chytrids on amphibians.

We have learned a lot since *Bd* was first described in 1997, but the story is changing rapidly with new molecular techniques, access to new geographical areas and sharing of information among research groups. Novel statistical approaches and modelling techniques provide new tools to better estimate amphibian abundance, and it is time we made a concerted effort to obtain quantitative field data on the numbers and trends of amphibian populations from around the world if we wish to do more than document the problem.

Competing interests. I declare I have no competing interests.

Funding. I received no funding for this study.

Acknowledgements. Thanks to conference organizers Mat Fisher, Sarah Gurr and Neil Gow for the invitation to participate. Thanks to G. Direnzo, A. Longo, J. Mendelson, M. Fisher and two anonymous reviewers for comments on previous drafts. This work was supported by the National Science Foundation (DEB 1120161). The author declares no competing financial interests.

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