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History and recent progress on chytridiomycosis in amphibians

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ARTICLE INFO

Article history:

Received 25 March 2015

Revision received 4 September 2015

Accepted 9 September 2015

Available online 6 October 2015

Corresponding editor:

Felix Bärlocher

Keywords:

Batrachochytrium dendrobatidis

B. salamandrorans

Wildlife

Extinction

Emerging infectious disease

Population decline

Conservation

Chytridiomycosis

ABSTRACT

Batrachochytrium dendrobatidis (Bd) emerged in the 1970s in Australia and the Americas, causing rapid and catastrophic declines and extinctions of naïve amphibian populations as it spread through remote rainforest and alpine regions. The description of chytridiomycosis in 1998 stimulated a large and diverse global research effort, including studies on phylogeny, distribution, ecology, and virulence – but mitigating its effect remains a major challenge. In 2010 a second *Batrachochytrium* species, *B. salamandrorans* (Bsal), emerged after spreading to Europe from Asia and has decimated fire salamanders in the Netherlands and Belgium. Bsal appears to be restricted to salamanders and newts whereas Bd can infect all amphibian orders. These cases show that despite the current advanced state of globalisation, severe pathogens are still spreading and some may currently be excluded by geographic barriers, hence biosecurity still has potential to mitigate spread of undiscovered and unpredictable pathogens of wildlife.

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Introduction

The emergence and spread of *Batrachochytrium* species in amphibians has overturned a traditional view that pathogens do not significantly affect wildlife populations (Skerratt et al., 2007; Martel et al., 2014). On the contrary, pathogens, even when acting alone, can cause catastrophic losses of wildlife

diversity when introduced into naïve host populations (Scott, 1988; Tompkins et al., 2015). Chytridiomycosis caused by *Batrachochytrium dendrobatidis* (Bd) has generated a huge research effort since it was first reported in 1998. Here we focus on Bd with a brief section on the recently discovered *B. salamandrorans* (Bsal), which also causes amphibian chytridiomycosis. Past reviews of Bd have covered immunology

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<http://dx.doi.org/10.1016/j.funeco.2015.09.007>

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(Rollins-Smith et al., 2011; Voyles et al., 2011), pathology, diagnosis (Berger et al., 2009), treatment (Berger et al., 2010; Baitchman and Pessier, 2013), probiotics (Bletz et al., 2013), genetics (Rosenblum et al., 2009) emergence and impacts (Skerratt et al., 2007; Fisher et al., 2009b; Kilpatrick et al., 2010), and management (Woodhams et al., 2011; Scheele et al., 2014b; Skerratt et al., accepted for publication). In this review, we describe the discovery of Bd and summarise recent research on phylogeny, distribution, ecology, and virulence in the global effort to mitigate this pandemic. Lastly, we discuss *Batrachochytrium* species in the context of emerging fungal diseases in wildlife. This review is not intended to be exhaustive, and we tend to cite Australian studies as examples.

Discovery and impacts of Bd

Some of the most dramatic amphibian population declines began in the late 1970s, particularly in remote and protected mountain regions of Australia and Central America. It took about a decade, however, for this global catastrophe to gain attention because amphibian populations can fluctuate dramatically and because mass mortality events were rarely observed. Determining the cause of amphibian “disappearances” became an urgent conservation task with researchers testing hypotheses on pollutants, increased UVB radiation, feral predators and climate change (Alford and Richards, 1999; Stuart et al., 2004). Habitat loss is a major cause of amphibian declines but was not linked to these “enigmatic” population crashes that were occurring in pristine and protected areas (Stuart et al., 2004).

In Australia, Keith McDonald (chief ranger of the Queensland Government) recruited Rick Speare (epidemiologist employed in public health at James Cook University) to examine the pattern of declines in his spare time. They proposed that an introduced fatal infectious disease of frogs had spread north across Queensland between 1979 and 1993, with a mean rate of spread of $\sim 100 \text{ km/yr}^{-1}$, wiping out populations of adults (but not tadpoles) within months of arrival (Laurance et al., 1996). McDonald and Speare conducted intense monitoring of abundant rainforest frog populations in the north where they predicted this disease would spread to next, including the last population of the, now extinct, sharp snouted dayfrog (*Taudactylus acutirostris*). The effort to monitor this population led to the detection of a die-off in late 1993 as it decimated the population (Laurance et al., 1996). A team of investigators with expertise in detecting emerging infectious diseases collected dead frogs and used pathology, microbiology, electron microscopy and DNA sequencing to diagnose a novel epidermal infection that they named chytridiomycosis (Berger et al., 1998).

While these diagnostic investigations were underway, an initial experiment was conducted to verify the pathogenicity of this superficial skin infection. This experiment involved exposing frogs to infected skin pieces and resulted in 100 % mortality within 3 weeks (Berger et al., 1998). Histopathology explained why tadpoles were not included in the mass mortalities; although tadpoles can carry infection in their keratinised mouthparts, the infections are not usually fatal until

after metamorphosis when the rest of the skin becomes keratinised and infection becomes widespread (Berger et al., 1998; Marantelli et al., 2004). In 1997, researchers had also found rainforest frogs dying during an outbreak of chytridiomycosis in Panama, confirming that this disease was the global culprit for widespread declines (Berger et al., 1998). Contemporaneously, Bd was discovered in metamorphs of South American dendrobatid frogs that died at the National Zoological Park, Washington, USA. Bd was isolated into pure culture from these frogs, studied and described as a new genus and species (Longcore et al., 1999; Pessier et al., 1999).

The spread of declines in areas of North and Central America enabled researchers to monitor Bd at remaining sites with abundant amphibians. The disease arrived in well studied sites in both Panama and California in 2004 and researchers documented a steep rise in Bd prevalence as amphibian populations crashed (Lips et al., 2006; Vredenburg et al., 2010). Transmission experiments with pure cultures involving even low numbers of zoospores resulted in fatal infections (Berger et al., 1999, 2004; Woodhams et al., 2003; Carey et al., 2006). It has since become accepted that the spread of chytridiomycosis has caused hundreds of species worldwide to decline with numerous extinctions, and chytridiomycosis is now regarded as the most devastating disease on record to impact vertebrate biodiversity (Skerratt et al., 2007). In Australia, extinctions include iconic species such as the southern and northern gastric brooding frogs (*Rheobatrachus silus*, *R. vitellinus*), last seen in 1981 and 1985, respectively.

Chytridiomycosis has become endemic through many regions where it can usually be found at more than 5 % prevalence and where disease outbreaks may occur seasonally (Berger et al., 2004; McDonald et al., 2005; Skerratt et al., 2010). Persisting amphibian species exhibit different responses in post-epidemic systems; some have lower abundance and smaller distributions and some are continuing to decline and suffer significant annual mortality from chytridiomycosis, even decades after introduction (McDonald and Alford, 1999; Murray et al., 2009; Pilliod et al., 2010; Phillott et al., 2013; Brannelly et al., 2015a). For example, annual mortality of the alpine tree frog (*Litoria verreauxi alpina*) results in almost complete population turnover after breeding (Scheele et al., 2015). Some critically endangered species now have very small populations and will need intervention to become secure. In Australia, six species have been placed in this category, including the corroboree frog (*Pseudophryne corroboree*), which relies on continual reintroductions to persist (Skerratt et al., accepted for publication). Populations of some susceptible species, however, are recovering in abundance and distribution albeit at levels lower than before chytridiomycosis was introduced (McDonald et al., 2005; Newell et al., 2013; Scheele et al., 2014a).

Taxonomy and phylogeny of Bd

Bd is a member of the Chytridiomycota, an early diverging lineage of true fungi whose members reproduce by forming uniflagellate zoospores. Although early studies (Berger et al., 1998; Longcore et al., 1999) placed the genus *Batrachochytrium*

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