FUNGAL BIOLOGY REVIEWS 21 (2007) 2–9

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journal homepage: www.elsevier.com/locate/fbr

Fungal Biology Reviews

Opinion Article

The relationship between the emergence of *Batrachochytrium dendrobatidis*, the international trade in amphibians and introduced amphibian species

Matthew C. FISHER[a,*], *Trenton W. J. GARNER*[b]

[a]*The Department of Infectious Disease Epidemiology, Imperial College London, Norfolk Place, London W2 1PG UK*
[b]*The Institute of Zoology, Zoological Society of London, Regent's Park London NW1 4RY UK*

Keywords:
Amphibian
Batrachochytrium dendrobatidis
Chytrid
Chytridiomycosis
Emerging infectious disease
Introduced species

ABSTRACT

Chytridiomycosis is an emerging infectious disease of amphibians caused by the chytrid *Batrachochytrium dendrobatidis*. The disease has been associated with global amphibian declines and species extinctions, however the principle drivers that underly the emergence of chytridiomycosis remain unclear. Current evidence suggests that the world trade in amphibians is implicated in the emergence of chytridiomycosis. Here, we review the evidence that the amphibian trade is driving the emergence of chytridiomycosis by (1) spreading infected animals worldwide, (2) introducing non-native infected animals into naïve populations and (3) amplifying infection of amphibians by co-housing, followed by untreated discharge of infectious zoospores into water supplies. We conclude that the evidence that the amphibian trade is contributing to the spread of *Batrachochytrium dendrobatidis* is strong, and that specific actions are necessary to prevent the introduction of the pathogen into thus-far uninfected areas. Specifically, we recommend the development of national risk-abatement plans, focused on firstly preventing introduction of *Bd* into disease free areas, and secondly, decreasing the impact of the disease on populations that are currently infected.

Amphibian species across the globe are declining at an alarming rate and a fungal disease, cutaneous chytridiomycosis, is now known to be a major driver of these declines (Stuart *et al.* 2004; Lips *et al.* 2006). The causative agent, the nonhyphal zoosporic euchytrid *Batrachochytrium dendrobatidis* [*Bd*; phylum Chytridiomycota, class Chytridiomycetes, order Chytridiales; (Longcore *et al.* 1999; James *et al.* 2006)], is a generalist pathogen and is known to infect over 90 amphibian species on five continents (Daszak *et al.* 2003; Rachowicz *et al.* 2005). Of these species, a continuum exists in the host response to *Bd*; several species are known to carry infection without any recognised pathogenic effects, while other species suffer up to 100 % mortality, rapid species declines and in some cases, extinction (Berger *et al.* 1998; Daszak *et al.* 2003; La Marca *et al.* 2005). The scale of these declines has been such that amphibian chytridiomycosis has been described as "*the worst infectious disease ever recorded among vertebrates in terms of the number of species impacted, and its propensity to drive them to extinction*" (ACAP 2005).

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[*] Corresponding author.
E-mail address: matthew.fisher@imperial.ac.uk (M.C. Fisher).

1749-4613/$ – see front matter
doi:10.1016/j.fbr.2007.02.002

Due to its recent, and largely simultaneous, recognition as a globally widespread pathogen, chytridiomycosis has been designated an emerging infectious disease (Daszak *et al.* 2003). Two hypotheses have been advanced to account for the emerging nature of disease caused by *Bd*; on one hand, the 'novel pathogen hypothesis' (NPH) states that *Bd* has recently spread into new geographic areas, and host species, as a result of the anthropogenically-mediated spread of *Bd*. On the other hand, the 'endemic pathogen hypothesis' (EPH) states that the emergence of chytridiomycosis has been caused by amphibian hosts becoming more susceptible to pre-existing infections as a consequence of changes in the environment.

The purpose of this review is not to weigh up the evidence for the NPH versus the EPH; this was ably undertaken by Rachowicz *et al.* (2005). Ours, and other, research show that both hypotheses contribute to explaining the current pandemic. The NPH receives support from the fact that epidemic fronts of introduction have been identified (Lips *et al.* 2006), that globally-recovered isolates of *Bd* show little genetic diversity suggestive of a recent expansion from a point-origin (Morehouse *et al.* 2003) and that infected amphibians are detected in the amphibian trade (Mazzoni *et al.* 2003; Weldon *et al.* 2004; Garner *et al.* 2006). The EPH receives support from data showing that *Bd* was present in global amphibian populations decades ago [USA 1974; Canada 1961; Australia 1978; South Africa 1938 (Rachowicz *et al.* 2005)] and that there are measurable associations between amphibian condition (Reading 2006), global warming and the onset of chytridiomycosis (Bosch *et al.* 2006; Pounds *et al.* 2006). It is likely that the contemporary emergence of *Bd* is driven by a combination of NPH and EPH-like mechanisms; here we will focus on a subset of the NPH and will review the evidence that the international trade in amphibians has contributed to the emergence of chytridiomycosis by a process of continually introducing *Bd*, primarily through species introductions, into naïve amphibian populations and species.

1. Amphibian trade, introduced amphibians and the prevalence of *Bd* in commercial amphibian species

The global trade in amphibians is substantial, involves hundreds of species and occurs on every continent where amphibians and *Bd* occur (Nace *et al.* 1971; Gorzula 1996; Schlaepfer *et al.* 2005). National imports of live animals may annually run into the millions (Schlaepfer *et al.* 2005) and efforts to procure wild amphibians for trade may be so intense as to cause local population declines (Jennings & Hayes 1985; Wang *et al.* 2004). More importantly, commercial practices bring traded animals into contact with wild populations. Introductions are common and in many cases intentional, leading to the establishment of numerous feral populations (Conant & Collins 1991; Reimchen 1991; Kraus & Campbell 2002; Lever 2003; Vorburger & Reyer 2003; Weldon *et al.* 2004; Denoël 2005; Govindarajulu *et al.* 2005; Jancovich *et al.* 2005; Li *et al.* 2006; Pagano *et al.* 2003). Amphibians have been intentionally released for farming, to ornament garden ponds, as biocontrol agents and even as part of amphibian conservation efforts (Easteal 1981; Buley & Garcia 1997; Helfrich *et al.* 2001).

The data regarding amphibians known to carry *Bd* infections show that numerous species that are involved in both transient and established introductions have the capability to act as vectors of *Bd* (Table 1). We have searched the Global Amphibian Assessment (http://www.globalamphibians.org/), the Global Invasive Species Database (http://www.issg.org/database/) and the primary literature for information regarding introduced amphibian species that have successfully established a breeding population for at least one generation, or have been introduced but failed to establish a breeding population. In nearly all cases we report findings that involve well-established populations. We have cross-referenced the results of this search with the available primary literature and unpublished reports made available on the Amphibian Diseases Homepage (http://www.jcu.edu.au/school/phtm/PHTM/frogs/ampdis.htm) for evidence of infection with *Bd*. We have also taken advantage of the database we have compiled while screening tissue samples and DNA extracts from amphibians primarily sampled in Europe and Canada. Here, we have screened samples using the quantitative polymerase chain reaction (qPCR) method of Boyle *et al.* (2004), including positive and negative controls and a minimum of two-fold replication per sample (as per Garner *et al.* 2005, 2006). We have determined that a minimum of 28 species of introduced amphibians are also known carriers of *Bd* (Table 1). At least one of these species is known to be experiencing die-offs due to chytridiomycosis (*Alytes obstetricans*, Bosch *et al.* 2001), but the majority are species that are asymptomatically infected, and in some cases have been introduced on an enormous scale.

The three most widely introduced species, the African clawed frog *Xenopus laevis*, the North American Bullfrog *Rana catesbeiana* (Fig. 1) and the Cane toad *Bufo marinus*, have established feral populations in the Americas, Europe, Australia, Asia and many oceanic and coastal islands. Weldon *et al.* (2004) reported the first case of *Bd* infections in *Xenopus laevis* collected and preserved in the late 1930s. It was at this time *Xenopus* spp. were first being exported to the USA, Australasia and Europe as pregnancy assays. Subsequently, *Xenopus* has become the model amphibian genus for primary research and continues to be widely traded (Weldon *et al.* 2004). Captive colonies of *Xenopus* spp. are known to harbour *Bd*-infected animals (Parker *et al.* 2002; Fisher unpubl. data) and *Xenopus* escapes and establishments are still being reported (Cunningham *et al.* 2005). This pool of evidence has led to the popularization of the 'Out of Africa' hypothesis (Weldon *et al.* 2004). Weldon *et al.* (2004) postulated that once the trade in *Xenopus* had been established, the potential for horizontal transfer among amphibian species involved in commercial trading should speed the spread of *Bd*. This scenario seems likely, as standards at the time did not take into account the possibility of disease transmission among individual amphibians or through nonsterile handling practices, and commercial suppliers commonly traded in two or all three of these species (Nace *et al.* 1971). The first evidence of *Bd* infections in archived North American amphibians comes from frogs collected and preserved in 1961 (Ouellet *et al.* 2005). Intentional introductions of bullfrogs across western North America began in the 1930s and continued for decades afterwards