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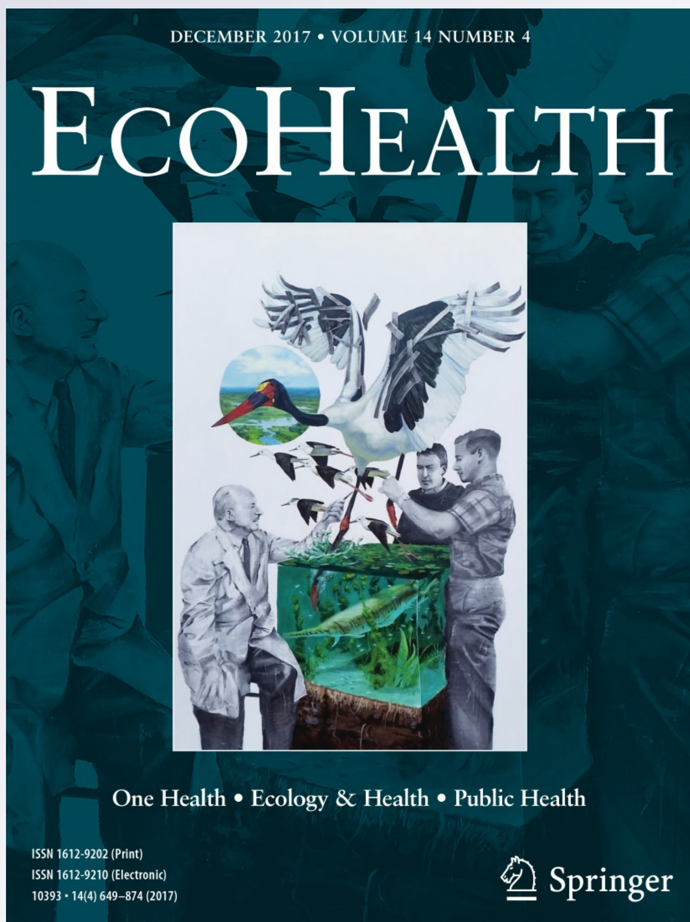

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Review

Batrachochytrium salamandrivorans and the Risk of a Second Amphibian Pandemic

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Abstract: Amphibians are experiencing devastating population declines globally. A major driver is chytridiomycosis, an emerging infectious disease caused by the fungal pathogens *Batrachochytrium dendrobatidis* (*Bd*) and *Batrachochytrium salamandrivorans* (*Bsal*). *Bd* was described in 1999 and has been linked with declines since the 1970s, while *Bsal* is a more recently discovered pathogen that was described in 2013. It is hypothesized that *Bsal* originated in Asia and spread via international trade to Europe, where it has been linked to salamander die-offs. Trade in live amphibians thus represents a significant threat to global biodiversity in amphibians. We review the current state of knowledge regarding *Bsal* and describe the risk of *Bsal* spread. We discuss regional responses to *Bsal* and barriers that impede a rapid, coordinated global effort. The discovery of a second deadly emerging chytrid fungal pathogen in amphibians poses an opportunity for scientists, conservationists, and governments to improve global biosecurity and further protect humans and wildlife from a growing number of emerging infectious diseases.

Keywords: *Batrachochytrium salamandrivorans* (*Bsal*), *Bsal* Task Force, Chytridiomycosis, Amphibian pandemic, Emerging infectious diseases in wildlife, Wildlife disease, Global biosecurity

Introduction

In the midst of a sixth mass extinction (Wake and Vredenburg 2008; Barnosky et al. 2011; Ceballos et al. 2015), amphibians are the most threatened vertebrate group with > 40% of species threatened (IUCN 2016) and approximately 200 species collapsing to or near extinction since the 1970s (Stuart et al. 2004; Alroy 2015). Amphibians are important in many ecosystems because they play key roles in trophic dynamics (Arribas et al. 2015; Rowland et al. 2017) and the carbon cycle (Best and Welsh 2014; Semlitsch et al. 2014). They are often considered ecosystem health indicators due to their permeable skin and sensitivity to environmental disturbances (Hecnar and M'Closkey 1996; Lambert 1997; Welsh and Ollivier 1998). However, amphibians are also survivors, as evidenced by their survival through the last four mass extinction events on earth. Yet today they have suffered dramatic declines indicative of a new mass extinction event (Wake and Vredenburg 2008). Assessment of potential

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threats can help guide conservation management plans to protect this significant and ancient group of terrestrial vertebrates as well as the overall health of ecosystems.

Emerging infectious diseases (EIDs) in wildlife are causing drastic declines across multiple taxa worldwide (Daszak et al. 2000, 2001; Gibbon et al. 2000; Smith et al. 2006; Fisher et al. 2012), particularly in amphibians (Daszak et al. 1999; Lips et al. 2006; Rachowicz et al. 2006). Chytridiomycosis, an EID caused by the fungal pathogens *Batrachochytrium dendrobatidis* (*Bd*) and *Batrachochytrium salamandrivorans* (*Bsal*), has severely impacted amphibian biodiversity globally (Berger et al. 1998; Daszak et al. 1999; Carey et al. 2004; Weldon et al. 2004; Rachowicz et al. 2006; Crawford et al. 2010; Cheng et al. 2011; Martel et al. 2013). *Bd*, discovered in 1998 (Lips 1998) and described in 1999 (Longcore et al. 1999), has been found on every continent where amphibians occur and has been recorded infecting over 500 species from all three orders of Amphibia (Anura, Caudata, Gymnophiona) (Olson et al. 2013). *Bd* is implicated in the declines and extinctions in at least 200 species, most of which occurred in anurans (Skerratt et al. 2007; Fisher and Garner 2007), though there have been documented *Bd*-related declines in some salamanders (Caudata) as well (Cheng et al. 2011; Sette et al. 2015). *Bsal* was discovered in 2010 and described in 2013 (Martel et al. 2013). It has thus far been found to cause mortality only in salamanders (Martel et al. 2014); however, a recent study has shown that anurans can become infected and act as *Bsal* reservoirs (Stegen et al. 2017), which suggests that *Bsal* may be a threat to anurans as well. Global trade likely facilitated the international movement of *Bd* (Hanselmann et al. 2004; Garner et al. 2006; Fisher and Garner 2007; Schloegel et al. 2012; Liu et al. 2013) and may now play a role in the spread of *Bsal* (Martel et al. 2014; Cunningham et al. 2015; Sabino-Pinto et al. 2015). Here, we review the current state of knowledge of *Bsal* and the predicted risk of *Bsal* spread. We discuss global efforts intended to avoid another wave of amphibian extinctions and the current limitations of global wildlife disease policy and management.

Batrachochytrium salamandrivorans—What We Know

Biology

Bsal is a chytrid fungus closely related to *Bd* in the order Rhizophydiales (Martel et al. 2013). Phylogenetic analyses suggest that *Bsal* and *Bd* diverged in the late Cretaceous or early Paleogene (115–30 million years ago) (Martel et al. 2014). Salamander species endemic to Asia were identified as putative *Bsal* reservoir hosts based on their ability to survive infection in laboratory studies and their low infection loads found in the wild, which led to the hypothesis that *Bsal* originated in Asia (Martel et al. 2014). This is supported by a more recent study that found *Bsal* to be relatively widespread geographically at low prevalence (2.9%) in salamanders in Vietnam, which suggests that *Bsal* may be in an enzootic (endemic in wildlife) state in Vietnam and those species may serve as reservoir hosts (Laking et al. 2017).

A previous study suggested that only salamanders were susceptible to *Bsal* infection; however, initial host challenge experiments conducted with *Bsal* were at low zoospore exposures ($\leq$ 10,000), and only 10 out of over 6500 known anuran species were tested (Martel et al. 2014; Amphibiaweb 2016). A more recent study has shown that the midwife toad (*Alytes obstetricans*) is susceptible to *Bsal* infection when exposed to higher doses (100,000 zoospores) (Stegen et al. 2017). While *A. obstetricans* does not show clinical signs of disease, it is able to transmit *Bsal* to susceptible salamander species (Stegen et al. 2017). The authors also identify the alpine newt (*Ichthyosaura alpestris*) as another potential *Bsal* reservoir, as individuals were able to clear infection on their own after being exposed to low doses of *Bsal* (Stegen et al. 2017). This is similar to the varying mortality outcomes of different species from *Bd* infection, as an infection intensity $>$ 10,000 *Bd* zoospores has been found to correlate with anuran deaths and declines (Vredenburg et al. 2010; Kinney et al. 2011), though there are exceptions in which species can survive higher infection intensities (Reeder et al. 2012). More studies are needed to determine whether *Bsal* infection can occur with other anuran species that could be potential reservoirs or susceptible to disease.

Like *Bd*, *Bsal* has two distinct life stages. There is an infectious aquatic zoospore stage, in which free-living zoospores use their flagella to move between hosts or within a host. *Bsal* zoospores have similar ultrastructural features as *Bd* zoospores, with the nucleus located away from the ribosomal mass, numerous mitochondria and lipid globules, and the centriole positioned at an angle or parallel to the kinetosome (Martel et al. 2013). The initial infection begins when zoospores encyst on the skin and enter keratinized skin cells (Longcore et al. 1999; Martel et al. 2013). Once inside the cell, the second life stage begins; the zoospore develops into a thallus and produces zoosporangia, wherein zoospores develop (Longcore et al. 1999; Martel et al. 2013). Mature zoospores are released into the surrounding water, free to re-infect the same animal or find another host. The thallus can be monocentric, in which only one zoosporangium forms, or colonial, in which multiple zoosporangia form along internal septa (Longcore et al. 1999; Martel et al. 2013). *Bsal* thalli are predominantly monocentric; however, colonial thalli are more abundant with *Bsal* compared to *Bd* (Martel et al. 2013). In culture, *Bsal* sporangia were found to form germ tubes, which has not been found with *Bd* sporangia (Longcore et al. 1999; Martel et al. 2013).

Bsal also produces a second type of spore that is non-motile and floats at the water's surface (Stegen et al. 2017). These spores can survive and continue to be infective for over 30 days in filtered pond water (Stegen et al. 2017). As they float, they are able to attach to salamander skin and the feet of waterfowl, though it is unclear whether *Bsal* remains alive and infective on non-amphibian hosts (Stegen et al. 2017). In addition, *Bsal* spores were found to be able to survive and remain infective in soil for up to 48 h (Stegen et al. 2017). If *Bsal* is capable of surviving outside of amphibian hosts in the wild, its movement in the environment or translocation by other species could lead to broad dispersal and indirect transmission to other amphibians (Johnson and Speare 2003, 2005; Rowley et al. 2006; Kilburn et al. 2011; Garmyn et al. 2012; McMahon et al. 2013; Hagman and Alford 2015; Kolby et al. 2015a, b; Courtois et al. 2016; Burrowes and De la Riva 2017; Stegen et al. 2017).

Similar to *Bd*, growth of *Bsal* is temperature dependent. In culture, *Bsal* is capable of growth at 5–25°C, with optimal growth at 10–15°C (Martel et al. 2013). This is substantially lower than the temperature preference of *Bd*, which can grow at 10–25°C, but demonstrates optimal growth at 17–25°C (Piotrowski et al. 2004; Woodhams et al. 2008; Voyles et al. 2012). However, in a recent field survey in Vietnam *Bsal* was detected on salamanders in ponds where water temperatures were over 26°C, indicating that *Bsal* on salamanders may have a more expansive temperature range (Laking et al. 2017).

Disease Pathology

Bsal infects keratinized epidermal cells and invades the deeper layers of the epidermis, which leads to multifocal superficial erosions, deep ulcerations with significant degradation of the epidermis, excessive shedding, and thickening of the skin (Martel et al. 2013; Blooi et al. 2015b; Gray et al. 2015). Upon histological examination, necrotic keratinocytes with marginated nuclei and intracellular colonial thalli of *Bsal* are found at the periphery of, and directly underneath, the eroded keratin layer (Martel et al. 2013).

Clinical signs of infection often include lethargy, anorexia, ataxia, and abnormal posturing prior to death (Martel et al. 2014). *Bsal* infection can cause rapid mortality in experimentally infected fire salamanders (*Salamandra salamandra*), and death typically occurs within 7–54 days after *Bsal* infection (Martel et al. 2013, 2014). Like with *Bd*, the prevalence and severity of *Bsal* infection is likely dependent on the host's developmental stage, host susceptibility, and environmental temperature (Berger et al. 2004; Skerratt et al. 2007; Murray et al. 2009, 2010, 2011, 2013; Phillott et al. 2013; Blooi et al. 2015a, b; Van Rooij et al. 2015; Berger et al. 2016; Stegen et al. 2017).

Known Distribution and Susceptible Species

It is hypothesized that *Bsal* spread via international trade from Asia to the Netherlands, where it was discovered causing mass mortalities in native wild salamander populations (Martel et al. 2013, 2014). Since then, *Bsal* has been found in other wild salamander populations in Belgium and Germany (Martel et al. 2013; Spitzen-van der Sluijs et al. 2016). In Europe, *Bsal* has now been identified in wild populations of *S. salamandra, I. alpestris,* and *Lissotriton vulgaris* (Table 1) (Martel et al. 2014; Spitzen-van der Sluijs et al. 2016). It has also been documented in captive species in the UK (Cunningham et al. 2015) and Germany (Sabino-Pinto et al. 2015), including *S. algira*, *S. corsica*, *S. infraimmaculata*, and *S. salamandra* (Table 1).

The presence of *Bsal* has been recorded in wild species in Japan, Thailand, and Vietnam (Martel et al. 2014; Laking et al. 2017). Species from which *Bsal* has been detected in the wild include *Cynops ensicauda, C. pyrrhogaster, Hynobius nebulosus, Onychodactylus japonicus, Paramesotriton deloustali, Salamandrella keyserlingii*, *Tylototriton asperrimus*, *T. uyenoi, T. vietnamensis*, and *T. ziegleri* (Table 1) (Martel et al. 2014; Laking et al. 2017). In Vietnam, *Bsal* appears to be the predominant chytrid pathogen found on salamanders, with a prevalence of 2.9% compared to 0.7% for *Bd* ($n = 583$ salamanders sampled) (Laking et al. 2017). While only species from the families Salamandridae and Hynobiidae have been recorded to harbor *Bsal* in the wild, species from Sirenidae and Plethodontidae have been

Table 1. Species Detected with *Batrachochytrium salamandrivorans.*

Order	Family	Species name	Sample type	Location of specimen	Infection outcome	References
Species native to Europe						
Anura	Alytidae	*Alytes obstetricans*[a]	Laboratory	Not applicable	∼ 60% infection, 0% mortality in experimental infection trials	Stegen et al. (2017)
Caudata	Plethodontidae	*Hydromantes strinatii*	Laboratory	Not applicable	100% mortality in experimental infection trials	Martel et al. (2014)
Caudata	Salamandridae	*Ichthyosaura alpestris*[a]	Wild	Netherlands Belgium	Detected in wild populations Some evidence of disease in the wild Dose-dependent response in experimental infection trials; high doses lead to mortality, low doses lead to eventual pathogen clearance	Spitzen-van der Sluijs et al. (2016), Martel et al. (2014), and Stegen et al. (2017)
Caudata	Salamandridae	*Lissotriton vulgaris*[a]	Wild	Netherlands Belgium Germany	Detected in wild populations Some evidence of disease in the wild	Spitzen-van der Sluijs et al. (2016)
Caudata	Salamandridae	*Pleurodeles waltl*	Laboratory	Not applicable	100% mortality in experimental infection trials	Martel et al. (2014)
Caudata	Salamandridae	*Salamandra algira* (native to Northern Africa)	Captive	Germany	Lethal in captive specimens (sample size not given)	Sabino-Pinto et al. (2015)
Caudata	Salamandridae	*Salamandra corsica*	Captive	Germany	Lethal in captive specimens (sample size not given)	Sabino-Pinto et al. (2015)
Caudata	Salamandridae	*Salamandra infraimmaculata* (native to the Middle East)	Captive	Germany	Lethal in captive specimens (sample size not given)	Sabino-Pinto et al. (2015)
Caudata	Salamandridae	*Salamandra salamandra*	Wild Captive Laboratory	Netherlands Belgium Germany	Mass mortalities in wild populations in the Netherlands and Belgium Detected in wild populations in Germany Lethal in captive populations 100% mortality in experimental infection trials	Martel et al. (2013), Martel et al. (2014), and Spitzen-van der Sluijs et al. (2016)

Table 1. continued

Order	Family	Species name	Sample type	Location of specimen	Infection outcome	References
Caudata	Salamandridae	*Triturus cristatus*	Laboratory	Not applicable	100% mortality in experimental infection trials	Martel et al. (2014)
Species native to Asia						
Caudata	Hynobiidae	*Hynobius nebulosus*[a]	Wild	Japan	Detected in wild populations Disease disposition in the wild unknown	Martel et al. (2014)
Caudata	Hynobiidae	*Onychodactylus japonicus*[a]	Wild	Japan	Detected in wild populations Disease disposition in the wild unknown	Martel et al. (2014)
Caudata	Hynobiidae	*Salamandrella keyserlingii*[a]	Wild Laboratory	Japan	Detected in wild populations Disease disposition in the wild unknown 100% infection, 0% mortality in experimental infection trials	Martel et al. (2014)
Caudata	Salamandridae	*Cynops cyanurus*[a]	Wild Laboratory	China	100% infection, 60% mortality in experimental infection trials	Martel et al. (2014)
Caudata	Salamandridae	*Cynops ensicauda*[a]	Wild	Japan	Detected in wild populations Disease disposition in the wild unknown	Martel et al. (2014)
Caudata	Salamandridae	*Cynops pyrrhogaster*[a]	Wild Laboratory	Japan	Detected in wild populations 100% infection, 50% mortality in experimental infection trials	Martel et al. (2014)
Caudata	Salamandridae	*Paramesotriton deloustali*[a]	Wild Laboratory	Vietnam	Detected in wild populations No sign of disease in the wild 100% infection, 75% mortality in experimental infection trials	Martel et al. (2014) and Laking et al. (2017)
Caudata	Salamandridae	*Paramesotriton sp.*[a]	Wild	Vietnam	Detected in wild populations No sign of disease in the wild	Laking et al. (2017)
Caudata	Salamandridae	*Tylototrion asperrimus*[a]	Wild	Vietnam	Detected in wild populations No sign of disease in the wild	Laking et al. (2017)
Caudata	Salamandridae	*Tylototriton uyenoi*[a]	Wild	Thailand	Detected in wild populations Disease disposition in the wild unknown	Martel et al. (2014)

Table 1. continued

Order	Family	Species name	Sample type	Location of specimen	Infection outcome	References
Caudata	Salamandridae	*Tylototriton vietnamensis*[a]	Wild	Vietnam	Detected in wild populations No sign of disease in the wild	Laking et al. (2017)
Caudata	Salamandridae	*Tylototriton wenxianensis*	Laboratory	Not Applicable	100% mortality in experimental infection trials	Martel et al. (2014)
Caudata	Salamandridae	*Tylototriton ziegleri*[a]	Wild	Vietnam	Detected in wild populations No sign of disease in the wild	Martel et al. (2014) and Laking et al. (2017)
Species native to North America						
Caudata	Salamandridae	*Notophthalmus viridescens*	Laboratory	Not applicable	100% mortality in experimental infection trials	Martel et al. (2014)
Caudata	Salamandridae	*Taricha granulosa*	Laboratory	Not applicable	100% mortality in experimental infection trials	Martel et al. (2014)
Caudata	Sirenidae	*Siren intermedia*[a]	Laboratory	Not applicable	100% infection, 0% mortality in experimental infection trials	Martel et al. (2014)

[a]Potential *Bsal* reservoirs, defined as species observed with *Bsal* infection in wild populations and/or species that were successfully infected with *Bsal* and had survival in experimental infection trials.

shown to be susceptible to infection under experimental conditions (Table 1) (Martel et al. 2014).

Diagnostic Methods

Methods that have been developed to detect *Bsal* on amphibian hosts include histopathology, culture, and polymerase chain reaction (PCR) (Martel et al. 2013; Blooi et al. 2013; White et al. 2016; Iwanowicz et al. 2017). While histological and culture methods require invasive sampling of hosts, PCR methods allow for noninvasive testing from swab samples (Blooi et al. 2013; Martel et al. 2013), which makes PCR the most useful method for screening for *Bsal* in wild populations. A duplex real-time quantitative PCR (qPCR) method was developed to rapidly detect the presence and infection intensities of *Bd* and *Bsal* simultaneously (Blooi et al. 2013). While PCR is an accepted screening technique, it is important to differentiate between the presence of *Bsal* and the manifestation of *Bsal*-caused chytridiomycosis. One study defines diagnostic criteria for *Bsal*-caused chytridiomycosis to include a combination of positive results from PCR (or culture) and histopathology (White et al. 2016).

Potential Treatments

Although *Bsal* is a newly emerging infectious disease and treatment studies are limited, there is evidence of relatively inexpensive procedures to eliminate *Bsal* infections in captive animals. Exposure to high temperatures or a combination of fungicides and heat may effectively remove *Bsal* infections (Blooi et al. 2015a, b). When infected *S. salamandra* were exposed to 25°C for 10 days, *Bsal* infection was eliminated (Blooi et al. 2015a). However, extended exposure to high temperatures may not be viable for many salamander species, since many species cannot tolerate the temperature required to eliminate *Bsal*. In addition, there may be other strains of *Bsal* that have differing temperature preferences, which could react differently to temperature treatments. Another potential treatment is the application of the fungicides polymyxin E and voriconazole for 10 days at an ambient temperature of 20°C, which was found to clear *Bsal* infections from *S. salamandra* in laboratory studies (Blooi et al. 2015b). This suggests that infected species with lower heat tolerance could benefit from a combination treatment of less extreme heat and fungicides. While these findings are promising, more studies are needed to determine species-specific disease dynamics, as these studies were only conducted on one host species using one strain of *Bsal*; the effectiveness of these treatments and any side effects may vary among host taxa and *Bsal* strains.

Assessing Risk of *Bsal* Spread

Understanding the global distribution of *Bsal* and its potential introduction to naïve populations is crucial for disease prevention and management. In Europe, *Bsal* has spread in wild salamander populations from the Netherlands to Belgium and Germany in less than 6 years (Martel et al. 2013; Spitzen-van der Sluijs et al. 2016), and it may already be more widely distributed than currently recognized. Observed declines have occurred with wild *S. salamandra* populations (Martel et al. 2014), and Stegen et al. (2017) suggest that *A. obstetricans* and *I. alpestris* are potential *Bsal* reservoirs. In addition, *Bsal* was detected in wild *L. vulgaris* (Spitzen-van der Sluijs et al. 2016), which makes it another potential reservoir in Europe. This is concerning because these species have expansive ranges that overlap with each other, and infected individuals could facilitate disease spread to other co-occurring species (Fig. 1a). Additionally, Schmidt et al. (2017) predicted that *Bsal* may spread at a rate of ~ 11 km per year even in areas with a host density as low as one host per hectare, putting nearly all wild populations at risk once it is introduced (Schmidt et al. 2017). With *Bsal* already in the environment, the risk of disease spread to salamander populations in Europe is high, and by the year 2110, *Bsal* could be present throughout most of Europe (Fig. 1a).

While *Bsal* and associated declines have been documented in wild salamander populations in Europe (Martel et al. 2014; Spitzen-vander Sluijs et al. 2016), *Bsal* has not yet been detected in North America (McDonald et al. 2005; Muletz et al. 2014; Bales et al. 2015; Parrott et al. 2016; Iwanovicz et al. 2017), where ~ 50% of the world's salamander species occur (AmphibiaWeb 2016). With the potential spread of *Bsal* through wildlife trade and the availability of suitable habitat and hosts, the threat that *Bsal* poses in North America is high (Yap et al. 2015; Richgels et al. 2016). Risk models have identified that the West Coast of the United States, the Southeastern United States, and the highlands of Mexico have the greatest risk of *Bsal* introduction and spread (Yap et al. 2015; Richgels et al. 2016). In addition, salamander species that are in the same genera as potential reservoir species, *Cynops* and *Paramesotriton* (Martel et al. 2014), were the most actively traded

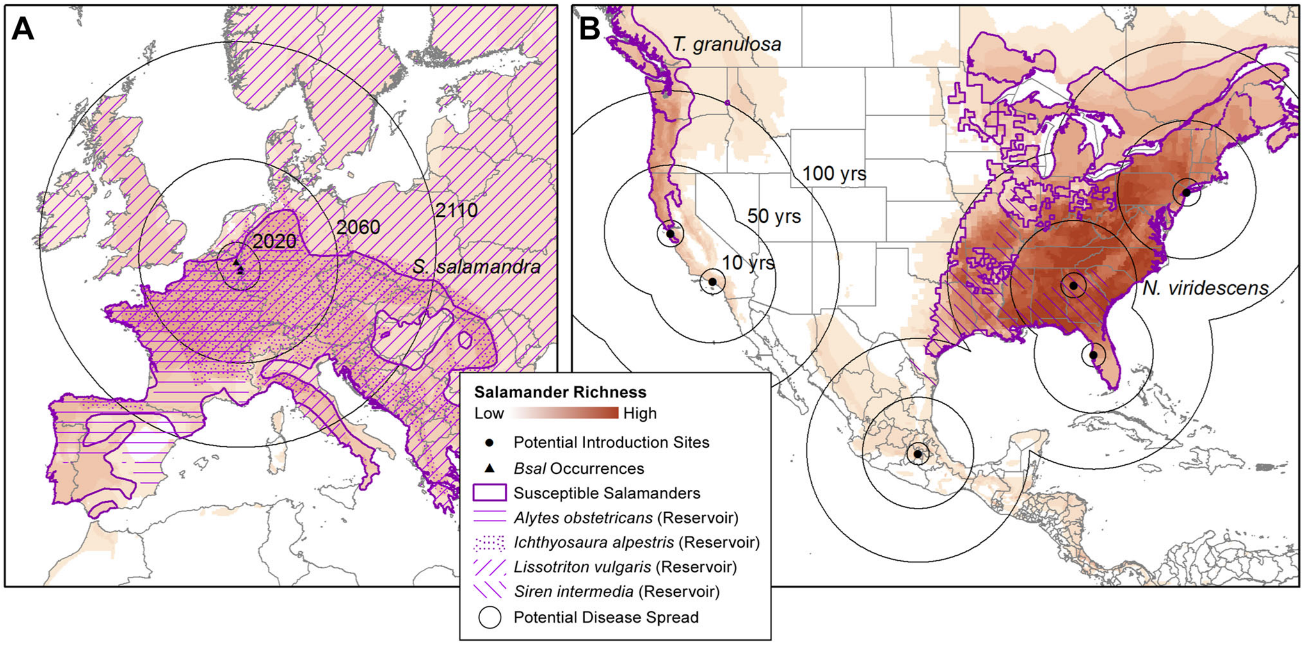

Fig. 1. Potential spread of *Batrachochytrium salamandrivorans* (*Bsal*) over time in Europe (**a**) and North America (**b**). Deeper red indicates higher salamander richness, and purple outlines indicate the geographic ranges of known, susceptible species *Salamandra salamandra*, *Notophthalmus viridescens*, and *Taricha granulosa* (Martel et al. 2014). Purple horizontal hash, dots, right hash, and left hash represent the geographic ranges of potential *Bsal* reservoirs, *Alytes obstetricans*, *Ichthyosaura alpestris*, *Lissotriton vulgaris*, and *Siren intermedia*, respectively. Black outlines indicate the area of spread, given the predicted rate of ~ 11 km/year (Schmidt et al. 2017), at 10, 50, and 100 years after introduction. Black triangles indicate areas of known *Bsal* outbreak sites in 2010 and 2013 (Martel et al. 2013; Spitzen-van der Sluijs et al. 2016). Black dots indicate potential points of introduction based on US salamander trade data (Yap et al. 2015). Species range and richness data are from the IUCN and AmphibiaWeb (IUCN 2016; AmphibiaWeb 2016).

salamanders in the USA from 2010 to 2014 (Gray et al. 2015; Yap et al. 2015; Richgels et al. 2016). The potential for *Bsal* to be introduced is alarming because two widespread North American species, the rough-skinned newt (*Taricha granulosa*) and the eastern newt (*Notophthalmus viridescens*), have been shown to be highly susceptible to *Bsal* in laboratory studies (Martel et al. 2014). The ranges of these two species encompass high disease risk zones (Yap et al. 2015; Richgels et al. 2016) and overlap with many species in the families Salamandridae and Plethodontidae (Fig. 1b). Thus, these species may succumb to disease and could facilitate the spread of *Bsal* to a wide range of other co-occurring species, including the lesser siren (*Siren intermedia*), which may be another potential *Bsal* reservoir (Martel et al. 2014). Within a century of its introduction, *Bsal* could potentially spread across an area that would encompass the distributions of nearly all known salamander species in North America (Fig. 1b).

Discussion

The rise of global trade has led to increases in EIDs in wildlife (Daszak et al. 2000; Karesh et al. 2005; Fèvre et al. 2006; Fisher and Garner 2007; Jones et al. 2008; Tompkins et al. 2015). In particular, unregulated wildlife trade enhances disease spread by transporting infected animals worldwide, introducing non-native pathogens into previously unexposed populations, and increasing the contact rate among different species (Daszak et al. 2001; Karesh et al. 2005; Fisher and Garner 2007; Liu et al. 2013). Disease outbreaks that result from wildlife trade can subsequently have severe impacts on native wildlife populations, ecosystems, livestock, and human health, and they are estimated to have caused hundreds of billions of dollars in economic loss (Daszak et al. 2000; Karesh et al. 2005; Fèvre et al. 2006; Jones et al. 2008). Although the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES) regulates the trade of endangered species, implementation of the regulations and commitments held by CITES is not consistent among participating countries (Wyler and Sheikh 2013). In addition, there is substantial trade in non-listed or less protected wildlife species, but regulation of these species in trade is fragmented with many challenges, including gaps in policy and legal frameworks, a lack of international consensus of specific regulations often eroded by competing priorities, and limited resources to implement regulations (Wyler and Sheikh 2013; Langwig et al. 2015). The complexities of uneven socioeconomic and political conditions in different countries interfere with enforcing wildlife trade regulations even when they exist (Jones et al. 2008; Wyler and Sheikh 2013). These deficiencies limit the ability to effectively address EIDs in wildlife. For human health, the World Health Organisation (WHO) was created to be the international body that assumes responsibility for setting standards and organizing responses when human populations are threatened by disease, but no such organization exists for wildlife.

Without a governing agency establishing and enforcing standardized guidelines globally, responses to new EIDs in different countries or regions can be varied, as evidenced by the current international response to *Bsal* emergence. In Europe, Switzerland was the first country to take preventive policy action by establishing a ban on all salamander imports since early 2015 (Schmidt 2016). The Netherlands, where the first *Bsal* outbreaks were documented (Martel et al. 2013), is focused on surveillance and monitoring in the wild, passive screening of imported animals, and funding *Bsal* research (Natuurpunt 2016). In Flanders, the Flemish Region of Belgium where *Bsal* outbreaks have also occurred (Martel et al. 2014), biosafety protocols and surveillance programs have been developed (Natuurpunt 2016). In December 2015, the European Council recommended immediate salamander trade restrictions, pre-import screening for infectious diseases in live animal trade, the establishment of monitoring and surveillance programs, the application of biosafety rules in the field and in captive collections, and the development of emergency action plans (Standing Committee to the Convention on the Conservation of European Wildlife and Natural Habitats 2015). In March 2017, the European Food and Safety Authority (EFSA) published a scientific report suggesting feasible mitigation measures in the EU, including restricting salamander movements, requiring animals to be free of *Bsal* before movement can take place, quarantining salamanders, tracking all traded species, and increasing public awareness (Balàž et al. 2017).

In North America, the Partners in Amphibian and Reptile Conservation formed the National Disease Task Team in January 2015 to facilitate the development of a Bsal strategic plan for the USA (Gray et al. 2015). In March 2015, the Canadian Wildlife Health Cooperative recommended import controls and initiating surveillance programs (Stephen et al. 2015). Then, in June 2015, the *Bsal* Task Force was formed (Gray et al. 2015; Grant et al. 2016). This *ad hoc* group is comprised of individuals from federal and state agencies, universities, and non-governmental organizations that are pooling their resources and knowledge to prevent and/or mitigate the spread of *Bsal* into naïve populations in North America. The Task Force is leading regional efforts to implement a targeted surveillance strategy, standardize diagnostic techniques, establish laboratory methods for containment and disposal of *Bsal*, conduct prioritized research to better understand species susceptibility, develop intervention strategies to aid in species survival, develop response plans for *Bsal* containment and management, and identify pathways of introduction and transmission to inform management actions. They have created an amphibian disease web portal (https://amphibiandisease.org) to aggregate and share information quickly, with the goal of helping scientists optimize research and monitoring efforts and to facilitate a rapid response to *Bsal* crises. The system maintains data confidentiality, allowing investigators to retain intellectual property while expediting the release of emerging critical information and encouraging collaborations.

The first implementation of import controls that could prevent the spread of *Bsal* in North America occurred in the USA in January 2016, approximately 2 years after the threat from trade was identified (Martel et al. 2014). In total, 201 salamander species were listed as "injurious" to wildlife under the Lacey Act, restricting the importation and interstate movement of species identified as potential *Bsal* vectors (USFWS 2016). This is an unconventional use of the Lacey Act, a law enacted in 1900 and written to protect non-agricultural ecosystems from the introduction and spread of invasive wildlife species. It was not written for wildlife disease prevention, and this is only the second time the Lacey Act has been implemented to help prevent the spread of a wildlife pathogen (18 U.S.C. 42: 50 CFR §16.13; Kolby and Daszak 2016). Previous efforts to apply the Lacey Act to protect amphibians from *Bd* in the USA (e.g., Defenders of Wildlife 2009) failed. In May 2017, Canada amended their Wild Animal and Plant Trade Regulations to restrict all salamander imports (SOR/2017-86). These policy actions are important for amphibian conservation; however, several years passed before they were implemented, during which time *Bsal* could have been introduced through ongoing trade. The current lack of legislation in many countries to address wildlife EID threats can limit the rapid response needed to mitigate wildlife disease spread.

Wildlife trade has been implicated in the spread of *Bd* (Hanselmann et al. 2004; Garner et al. 2006; Fisher and Garner 2007; Schloegel et al. 2009), yet little preventive action has been taken to mitigate its spread, which has resulted in a global pandemic (Stuart et al. 2004; Voyles et al. 2014; Catenazzi 2015). Now, with the threat of *Bsal*, there has been a quicker global response with proactive management in hopes of preventing a second wave of amphibian declines and extinctions (Grant et al. 2017). However, the lack of wildlife trade regulations and appropriate policies that explicitly address wildlife diseases can limit local and regional efforts to prevent *Bsal* invasion or effectively respond if *Bsal* becomes established. The threat of *Bsal*, along with other EIDs that have severely impacted wildlife, such as white-nose syndrome in bats (Blehert et al. 2009) or colony collapse disorder in bees (Cox-Foster et al. 2007; vanEngelsdorp et al. 2009), provides the impetus for the establishment of an international wildlife disease prevention and response network. For human diseases, the WHO coordinates international collaboration and the sharing of resources and information to prevent, detect, report, and respond to crises. The WHO also supports targeted research and development for human disease diagnostics and treatments. The formation and actions of the *Bsal* Task Force reflect these same objectives. They coordinate a regional effort to mitigate *Bsal* spread by engaging with the broader community, facilitating rapid information sharing, encouraging collaborations, and developing and implementing strategies for efficient monitoring, surveillance, research, and disease management. The *Bsal* Task Force could serve as an exemplary model for an international wildlife disease prevention and response network that enhances global biosecurity and safeguards human and wildlife health against the spread of wildlife emerging infectious diseases.

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