A REVIEW OF THE CURRENT KNOWLEDGE ON AMPHIBIAN CHYTRIDIOMYCOSES AND THEIR EPIDEMIOLOGY IN EASTERN EUROPE

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Abstract:
Amphibian chytridiomycoses are emerging fungal diseases caused by Batrachochytrium dendrobatidis (Bd) and Batrachochytrium salamandrivorans (Bsal). They are a significant threat to amphibians worldwide, driving catastrophic species declines and extinctions with documented knock-on impacts on the wider ecosystem and human health. This review examines the historical discovery and expanding distribution of Bd and Bsal, with a focus on Eastern Europe. Advances in diagnostics — including histopathology, PCR, and environmental DNA detection —, including their strengths and limitations, are discussed. This review considers morphological characteristics, pathogen life cycles, mechanisms of pathogenesis, and clinical signs useful for guiding infection and disease detection. Innate and acquired host immune responses in response to Bd and Bsal infection are discussed within the context of host resistance and tolerance. Finally, potential transmission routes are explored, with a focus on the role the pet trade plays in pathogen spread, and current treatment and mitigation approaches for both wild and captive amphibians are summarised. Insights into the epidemiology of Bd and Bsal and environmental factors influencing pathogen spread and resistance can inform proactive conservation and disease management strategies essential for protecting at-risk amphibian populations.

Key words*: Chytridiomycoses; Batrachochytrium dendrobatidis; Batrachochytrium salamandrivorans; amphibians; epidemiology; Eastern Europe*

INTRODUCTION

Amphibians represent the most threatened vertebrate class on Earth (Luedtke et al., 2023). This situation is being driven by multiple anthropogenic threats, including habitat loss, climate change, pollution, overexploitation, invasive species, and emerging infectious diseases such as amphibian chytridiomycosis (Luedtke et al., 2023; Fisher et al., 2012). Global enigmatic amphibian declines documented since the 1970s spurred an intense interdisciplinary interest in amphibian conservation research (Laurance et al., 1996, Collins & Storfer, 2003, Stuart et al., 2004, Berger et al., 2016). This led to the establishment, in 1998, of a direct connection between chytridiomycosis, caused by the previously unknown fungus *Batrachochytrium dendrobatidis* (Bd), and amphibian declines in Central America and Australia (Berger et al., 1998, Longcore et al., 1999, Pessier et al., 1999). In 2010, a closely related fungal pathogen, *Batrachochytrium salamandrivorans* (Bsal) was discovered linked to acute mortality and population declines in fire salamanders (*Salamandra salamandra*) in Western Europe (Martel et al., 2013, Spitzen-van der Sluijs et al., 2013).

To this date, Bd has been detected on all continents where amphibians are present (Castro Monzon et al., 2020), while Bsal is apparently restricted to Asia and some parts of Europe (Laking et al., 2017). Bd is known to affect at least 500 species and has led to the

presumed extinction of at least 90 species (Scheele et al., 2019). Therefore, amphibian chytridiomycosis has been considered to be the worst infectious disease known to date in terms of the number of species impacted and its capacity to drive population declines and species extinctions (Van Rooij et al., 2015, Scheele et al., 2019). The Bd-driven collapse of amphibian populations has led to knock-on impacts on the wider ecosystem, including declines in snake populations (Zipkin et al., 2020) and an increase in malaria cases in humans (Springborn et al., 2022).

Considering the importance of amphibian chytrid fungi and their widespread, dramatic effects (Lips, 2016), this review aims to provide a brief overview about the current knowledge of Bd and Bsal with an emphasis on their presence in Eastern Europe and, specifically, Romania.

GENETIC DIVERSITY AND ORIGIN

The chytrid fungi Bd and Bsal belong to the phylum Chytridiomycota, an early-diverging non-hyphal fungal lineage characterized by motile, flagellated zoospores (Longcore et al., 1999). Unlike most chytrid fungi, which are saprobic or are parasitic on plants, algae, or invertebrates, *Bd* and *Bsal* are the only chytrid fungi known to infect vertebrates, with the possible exception of *Ichthyochytrium vulgare*, a poorly-described pathogen of freshwater fish (Martel et al., 2018).

While most cases of amphibian decline have been associated with a globally-distributed, hypervirulent lineage of Bd termed the global pandemic lineage, Bd-GPL, several other genetic groups of varying virulence and more patchy geographical distribution have been identified (Fisher & Garner, 2020; O'Hanlon et al., 2018). Similarly, Bsal strains present multiple differences at both phenotypic and genotypic levels, which can influence variability in amphibian individual and population response following infection (Kelly et al., 2021, Kelly et al., 2024). The earliest debate regarding the origin of Bd and the onset of declines due to chytridiomycosis was between the Endemic Pathogen Hypothesis (EPH) and the Novel Pathogen Hypothesis (NPH). The EPH proposed that Bd infection had long been widespread in amphibian populations and only recently became pathogenic due to environmental changes or shifts in host-pathogen dynamics. In contrast, the NPH posits that Bd was a recent introduction to naïve, susceptible populations (Fisher et al., 2009, Farrer et al., 2011, Rosenblum et al., 2013). The majority of studies favour the NPH. Using whole-genome analyses, O'Hanlon et al. (2018) identified East Asia as the likely source of Bd, with the BdASIA-1 lineage exhibiting ancestral genetic signatures. Their findings also indicate that Bd-GPL originated in this region in the early 20th century and has since colonized various parts of the world, likely facilitated by both intentional and unintentional human-driven movement of amphibians (O'Hanlon et al., 2018). Similarly, evidence suggests that Bsal likely has an Asian origin, and that the pathogen was introduced to Europe through the amphibian pet trade (Martel et al., 2013; Fitzpatrick et al., 2018, Castro Monzon et al., 2022, González et al., 2024).

MORPHOLOGY AND LIFE CYCLE

Batrachochytrium dendrobatidis (Bd) and *Batrachochytrium salamandrivorans* (Bsal) share a biphasic life cycle, consisting of a motile zoospore stage and a sessile, reproductive zoosporangium stage. Zoospores are unicellular and flagellated, allowing them to disperse in aquatic environments before invading the host epidermis (Robinson et al., 2022) and transitioning into sessile thalli (Van Rooij et al., 2015). Bsal has a second, non-flagellated, environmentally resistant zoospore, which may allow prolonged survival in dry soil (Stegen et al., 2017). The encysted zoospores absorb the flagellum and develop a cell wall and rhizoids, which anchor the organism while facilitating nutrient absorption (Berger et al., 2005a). Within the zoosporangium, cytoplasmatic cleavage

produces new flagellated zoospores, which are released through a discharge tube, completing the cycle within 4–5 days at optimal temperatures (Voyles et al., 2011).

While their life cycles are mostly similar, at least one strain of Bsal can have a saprotrophic life cycle, being able to feed on plant material, such as hay (Kelly et al., 2021). Furthermore, Bsal differs morphologically from Bd in forming tubular germ extensions from encysted zoospores, which can develop into new sporangia, and in producing a greater proportion of colonial thalli (Van Rooij et al., 2015).

Thermal preference in the laboratory differs between the two species: Bd grows optimally between 17–25°C, at 28°C growth ceases, and dies after a week at > 29°C (Spitzen-van der Sluijs, Zollinger, 2010). Bsal thrives at 10–15°C and can survive at 5°C, and temperatures ≥25°C are lethal for Bsal (Martel et al., 2013).

Both fungi can attach to non-living keratinous substrates, suggesting potential for environmental persistence (Van Rooij et al., 2015, Kelly et al., 2021).

TRANSMISSION

Understanding the transmission and introduction pathways of these fungi is crucial for mitigating their impact. Water acts as a major vector, as the infective life stage of these pathogens is a waterborne zoospore that persist in freshwater (Johnson & Speare, 2003). Additionally, Bd and Bsal can survive in wet environments, such as in biofilms and moist substrates, enabling indirect pathogen transmission (Stegen et al. 2017, Johnson & Speare, 2005, Kolby et al., 2015). Two studies also indicate that Bd zoospores might spread through rain (Kolby et al., 2015) and fog (Prado et al., 2023), although these results need repeating to rule out any contamination errors. In addition to the motile zoospore, Bsal has an environmentally resistant non-motile spore (Stegen et al. 2017), and a saprophytic lifecycle has been identified for one isolate (Kelly et al. 2021), which in combination suggest environmental transmission can be particularly relevant for this pathogen. In addition, transmission of both Bd and Bsal can occur through direct contact between infected and susceptible individuals (Stegen et al. 2017, Voyles et al., 2009).

Beyond amphibians, other organisms can theoretically act as passive vectors or as alternative hosts for Bd. Birds and mammals, such as waterfowl and amphibian-eating predators, may transport spores between habitats (Johnson & Speare, 2005). Non-amphibian hosts such as experimentally-modified zebrafish larvae can become infected with Bd and develop disease, and could potentially also act as Bd reservoirs in aquatic environments (McMahon et al., 2013, Liew et al., 2017).

The pet trade is a primary driver of Bd and Bsal introductions into naïve populations (Connelly et al., 2023). Many amphibians in the international trade are aclinical carriers, allowing these pathogens to spread undetected. Notably, *Lithobates catesbeianus* (American bullfrog), which is farmed for food and trade, frequently harbours Bd without showing clinical signs (Schloegel et al., 2009). The intentional or unintentional release of captive amphibians, has facilitated Bd and Bsal introduction into the wild (Fisher & Garner, 2007, Peel et al., 2012, Tamukai et al., 2014) . Beyond trade, human-mediated transport via eco-tourism, research activities, and conservation translocations has the potential of contributing to the spread of chytrid fungi, often through contaminated equipment or direct movement of infected animals (Walker et al., 2008, Phillott et al., 2010).

BD/BSAL IN EASTERN EUROPE AND ROMANIA

Compared to Western Europe and other global Bd research hotspots, such as Australia and Central and South America, Eastern Europe remains significantly underrepresented in *Bd* studies, with large geographical and taxonomic gaps (Baláž, 2013). Figure 1 and table 1 below

present an overview of Bd prevalences in Central, Eastern Europe and the Balkans. In Hungary, *Bd* has been detected in multiple species, with *Bombina variegata* and *Pelophylax esculentus* exhibiting the highest prevalences and infection intensities. Climatic factors appear to influence infection dynamics, as prevalence is negatively correlated with temperature and positively correlated with precipitation (Vörös et al., 2018). In a study by Baláž et al., (2014), positive qPCR samples were found in Hungary, the Czech Republic and Slovakia. The authors suggest the use of *Alytidae* and *Bombinatoride* as sentinel clades to be included in European national surveillance programmes due to their relative abundances, wide geographical European distributions, and their higher Bd infection prevalences. It might also be useful to include *Pelophylax* spp. to fill geographical gaps where *Alytidae* and *Bombinatoridae* are absent. In Serbia, *Bd* has been recorded in *Pelophylax* spp., including in two sites on the Danube River. As the role of large river systems in the spread of Bd is poorly understood, the authors raise the concern that the Danube should be investigated as a potential corridor for Bd transmission across Europe (Mali et al., 2017). One study in Montenegro, Albania, and North Macedonia reported Bd in *Pelophylax* spp., *B. variegata*, and *Triturus macedonicus*, with an overall infection prevalence of 14.3%. The authors suggested that the Carpathian Mountains could be an important area for future Bd research, particularly for *B. variegata* and *Ichthyosaura alpestris* (Vojar et al., 2017). In Russia, *Bd* has been found in *Bufo bufo*, often with ranavirus co-infection, complicating assessments of its impact (Reshetnikov et al., 2014). Further, Bd has been detected through qPCR screening surveys in Greece (Azmanis et al., 2016), Czech Republic (Civiš et al., 2012), Poland (Sura et al., 2010) and Austria (Sztatecsny & Glaser, 2011).

With 20 native amphibian species present, and considering that the Danube Delta Biosphere Reserve, one of Europe's largest biodiversity hubs, is located entirely on Romanian territory, Romania has one of the richest mosaics of ecosystems and amphibian diversity in Europe (Cogălniceanu et al., 2013, Cogălniceanu & Rozylowicz, 2014). Yet Romania represents a critical gap in European Bd epidemiology, with few studies available. Bd was first reported in Romania by Vörös et al. (2013), with PCR-positive detections in *B. variegata, Lissotriton vulgaris ampelensis,* and *Rana temporaria*. A more extensive study by Scheele et al. (2015) surveyed 60 ponds in Transylvania, and found Bd to be present in 26.6% of sites, with an overall prevalence of 4.5%. Notably, the prevalence of infection was significantly higher in juveniles (14.8%) than in adults (2.7%), suggesting differential susceptibility to infection or pathogen exposure at different life stages.

Bsal has not been yet detected in Eastern Europe, including in Romania. In Europe, in the wild this pathogen remains insofar restricted to the Netherlands, Germany, Belgium, and Spain (Spitzen-van der Sluijs et al., 2013, Martel et al., 2014; Schulz et al., 2020, Lastra González et al., 2019), but has also been detected in captive amphibians in the UK, Spain and Germany (Fitzpatrick et al. 2018).

PATHOGENESIS AND MECHANISMS OF HOST DEFENSE

The infection process of Bd involves host attraction, attachment to keratinised tissue, penetration into the skin cells with endobiotic zoospore germination, and invasive growth into the stratum corneum and stratum granulosum, leading to host cell destruction and cytoplasm loss.

Chemotaxis plays a crucial role, as zoospores are attracted to keratin and amphibian skin mucus, which contains carbohydrate components that facilitate movement toward the host, and promote encystation (Moss et al., 2008, Van Rooij et al., 2015, Robinson et al., 2022). Conversely, amphibian skin mucus

serves as a defence barrier, limiting zoospore survival (Meyer et al., 2007).

Adherence of Bd to host skin occurs within 2-4 hours from contact, involving fibrillar projections (Van Rooij et al., 2012). Various genes related to the production of cell adhesion proteins are upregulated in sporangia (Zamudio et al., 2020). The presence of a chitin-binding module (CBM18) in Bd suggests a role in survival and pathogen spread through various non-host chitinous structures, such as insect or crustacean exoskeletons (Abramyan & Stajich, 2012, McMahon et al., 2013).

Once adhered, Bd invades the epidermis, generally developing intracellularly within 24 hours and spreading through rhizoid-like structures which develop into zoospore-producing thalli. The pathogen colonizes keratinized layers (the entire skin surface of adult amphibians and the mouth parts of many amphibian larvae), transitioning to new areas as keratinization progresses and the layers advance to the surface (Berger et al., 2005, Voyles et al., 2009, Greenspan et al., 2012).

Bsal follows a similar infection pattern, although the specifics of its attraction and adhesion mechanisms remain largely unknown (Rollins-Smith & Le Sage, 2021).

Chytrid infection impairs amphibian skin function, which is vital for osmoregulation, respiration, and defence. Bd secretes proteases and virulence factors that degrade host skin integrity, disrupt intracellular junctions, and impair osmoregulatory function. The infection reduces plasma sodium, potassium, and chloride levels, leading to ion imbalances and potentially fatal cardiac arrest (Voyles et al., 2009, Campbell et al., 2012). Besides the more evident skin effects, organism-wide impacts of Bd infection have been reported. Such impacts include hematopoietic tissue depletion, which may be related to the species' susceptibility to infection (Grogan et al., 2018), and catastrophic failure of normal homeostatic mechanisms and pronounced dysregulation of cellular energy metabolism (Brannelly et al., 2016).

The availability of the Bd full genome has enhanced the understanding of host-pathogen interactions, revealing potential pathogenicity factors targeting amphibian skin (Joneson et al., 2011).

Research on Bsal is still in its early stages, with critical unknowns regarding its host specificity, infection processes, and host immune response (Rollins-Smith & Le Sage, 2021).

Bd is known to infect a wide variety of hosts, which inevitably will put forward an equally wide variety of defence mechanisms. Torres-Sánchez et al. (2022) have shown that Bd displays plastic infection strategies when challenged by hosts with different disease susceptibilities.

Amphibians exhibit varying susceptibility to both infection and disease caused by Bd and Bsal at individual, population, and species levels. Some species, such as *Lithobates catesbeianus* and *Xenopus laevis*, serve as aclinical reservoir hosts, while others experience high mortality and population declines (Berger et al., 2009, Kilpatrick et al., 2010, Savage & Zamudio, 2011). Susceptibility varies due to genetic factors, immune responses, and environmental conditions (Ribas et al., 2009, Ellison et al., 2014; Bataille et al., 2015, Zamudio et al., 2020).

The innate immune system plays a critical role in limiting Bd infections. Antimicrobial peptides (AMPs) secreted by dermal granular glands in some species inhibit Bd growth in vitro, although their effectiveness in vivo is uncertain due to degradation and fungal countermeasures, and it might not be a mechanism available to all species (Rollins-Smith, 2009, Van Rooij et al., 2015). Additionally, Bd can secrete proteases that degrade AMPs (Thekkiniath et al., 2013). Symbiotic skin bacteria can contribute to defence by producing antifungal metabolites

such as violacein, 2,4-diacetylphloroglucinol, and indol-3-carboxaldehyde, which inhibit Bd infection (Harris et al., 2009, Lam et al., 2011). Lysozyme present in amphibian skin mucus is also presumed to have an antifungal effect (Rollins-Smith et al., 2009). McMahon et al. (2014) found that individuals of at least three amphibian species can acquire behavioural or immunological resistance after exposure to live or dead Bd zoospores.

Despite detectable Bd-specific antibodies in some species, a robust acquired immune response is largely absent, with Bd infections generally persisting despite repeated exposures (Ellison et al., 2014, Van Rooij et al., 2015).Studies suggest Bd suppresses lymphocyte activation and complement pathways, impairing effective immune responses (Fites et al., 2013, Fites et al., 2014). Immunization trials with heat-killed Bd have largely failed, with some exceptions such as in *X. laevis*, where Bd-specific antibodies were detected (Stice & Briggs, 2010, Ramsey et al., 2010). Oral vaccination with killed Bd led to a vigorous immune response in hellbenders (*Cryptobranchus alleganiensis alleganiensis*), but this response was ineffective at controlling disease (Kaganer et al., 2023).

Host factors such as major histocompatibility complex (MHC) show varying influence on Bd resistance (Savage & Zamudio, 2011, Bataille et al., 2015). Corticosterone levels seem to be an unreliable indicator of susceptibility, with studies having conflicting results (Gabor et al., 2013, Searle et al., 2014). Warmer microhabitats and thermoregulatory behaviours reduce Bd infection rates (Bielby et al., 2008), and higher temperatures (>25°C) are known to inhibit Bsal growth (Blooi et al., 2015). Species with high aquatic dependency are disproportionately affected, as are individuals with increased social behaviours (Rowley & Alford, 2007). Conversely, behaviour can also function as a mechanism of host resistance, as some species exhibit learned avoidance of Bd after previous exposure to the pathogen (McMahon et al., 2014, 2021).

CLINICAL ASPECTS, BIOSECURITY AND TREATMENT

Bd infections manifest variably, ranging from subclinical infections to sudden death (Baláž, 2013). Infected metamorphosed individuals often display lethargy, anorexia, abnormal posture, and loss of righting reflex, with signs typically appearing only in the final stages of infection (Berger et al., 1998, Pessier, 2008). The most consistent external signs include excessive skin shedding, discolouration, and erythema (Van Rooij et al., 2015, Berger et al., 2009). Histopathology reveals epidermal hyperplasia, hyperkeratosis, and disordered epidermal structure, with Bd sporangia localized to the stratum corneum and stratum granulosum (Berger et al., 1999).

In tadpoles, infection is usually restricted to depigmentation and loss of the mouthparts with minimal direct mortality (Baláž, 2013).

Bsal infection primarily affects metamorphosed urodeles (but it can also infect and cause disease in anurans; Gray et al., 2023, causing widespread epidermal ulceration and necrosis (Martel et al., 2013, Van Rooij et al., 2015). When infected, susceptible urodeles exhibit excessive skin shedding, ataxia, anorexia, and rapid disease progression, often leading to death within days (Martel et al., 2018). Unlike Bd, Bsal does not induce hyperkeratosis but instead penetrates deeper skin layers, leading to severe epidermal destruction and ulceration (Martel et al., 2013).

Strict biosecurity protocols are essential to prevent human-mediated spread. As previously mentioned, Bd and Bsal can persist on soil, water, and fomites, therefore requiring effective chemical decontamination to prevent the inadvertent introduction or spread of these pathogens. Various disinfecting agents and protocols have been tested (Johnson et al., 2003, Webb et al., 2007, Rooij et al., 2017, Bletz et al., 2023). As a result, we are now aware that ethanol (70%) will kill both Bd and Bsal within 30s, Virkon S® 1% in 2 min,

Bleach 4% in 30s, while oxygen peroxide is ineffective.

Given the thermal sensitivities of Bd and Bsal, host temperature manipulation has been proposed for clearing infections in some species. Amphibians that can access heat refuges, such as sun-exposed areas or warm microhabitats, have a greater chance of clearing Bd infections (Waddle et al., 2024). Controlled studies have demonstrated that exposing Bd-infected amphibians at various high temperature protocols can effectively eliminate infections (Woodhams et al., 2003, Daskin et al., 2011, Blooi et al., 2015). However, the applicability of host temperature manipulation is likely restricted to relatively heat-tolerant amphibian species.

Azoles such as itraconazole and voriconazole are the most studied antifungal treatments for clearing Bd and Bsal infections in live animals. Itraconazole (0.01%) applied daily via 5–10 minute baths for 7–11 days effectively clears Bd (Brannelly et al., 2012, Jones et al., 2012, Brannelly, 2014, Hudson et al., 2016). Voriconazole shows good efficacy, with a relatively safe risk profile (Martel et al., 2011, Brannelly et al., 2024), whereas terbinafine proved to be ineffective against Bd (Roberts et al., 2019).

Certain skin bacteria, such as *Janthinobacterium lividum*, produce antifungal compounds that inhibit Bd growth (Bletz et al., 2013, Kueneman et al., 2016). Therefore, probiotic therapy through using beneficial microbes to combat Bd has been proposed and mostly tested under controlled conditions, but its effectiveness in the wild remains unclear, especially as environmental conditions and the ability of hosts to maintain microbial taxa and to recruit them from the environment play a key role in determining their skin microbiome.

DETECTION AND DIAGNOSTICS

Accurate detection of Bd and Bsal is critical for amphibian disease management and conservation efforts. In the absence of overt, pathognomonic or clinical signs for direct visual diagnosis of Bd and Bsal (other than histopathology), several detection methods have been developed, each with varying degrees of sensitivity, specificity and applicability in different research and field settings. The most commonly used method for Bd and Bsal detection is quantitative/real-time PCR, and culture and histopathology are considered gold standards in the diagnosis of chytrid infections. Table 2 below summarises the detection methods currently available.

MITIGATION

Our knowledge about the control and mitigation of Bd and Bsal impacts on amphibians in the wild remains very limited (Garner et al., 2016; Fisher & Garner, 2020). Additionally, given the complex nature of host-parasite interactions, no single intervention is likely to be sufficient to fully control these pathogens and mitigate their impacts. There are at least two stages at which mitigation can be targeted: 1) prevention of Bd or Bsal spread into a naive population, and 2) managing an already established infection (Fisher & Garner, 2020). In Table 3, we present a brief overview of potential mitigation measures and actions that have been reported in the literature. Eradicating the pathogen once it has established itself in a population can prove extremely challenging, if not impossible under most circumstances. As an example, intense Bd eradication efforts on the island of Mallorca have been only partially successful in tackling the pathogen (Bosch et al., 2015).

CONCLUSION

The chytrid fungi *Batrachochytrium dendrobatidis* (Bd) and *Batrachochytrium salamandrivorans* (Bsal) pose significant threats to amphibian biodiversity globally, driving severe population declines and even species extinctions. Over the past years we have been witnessing a considerable surge in advances in understanding their origins, genetic diversity, pathogenesis, and complex relationships between the pathogens and their

hosts. However, substantial knowledge gaps remain, particularly in under-researched regions such as Eastern Europe, including Romania. We hope this review will lead the way to a series of efforts to help close these gaps, particularly concerning the distributions and impacts of Bd and Bsal in Romania. Continued efforts should prioritize enhanced surveillance, ideally through standardized national monitoring programs. Also, rigorous biosecurity measures within the pet trade and field research activities, and the development of effective therapeutic strategies should be advanced. Addressing these pathogens effectively will require interdisciplinary collaboration, targeted diagnostics, improved mitigation strategies, and increased awareness, especially in biodiversity-rich yet underrepresented regions.

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TABLES AND FIGURES

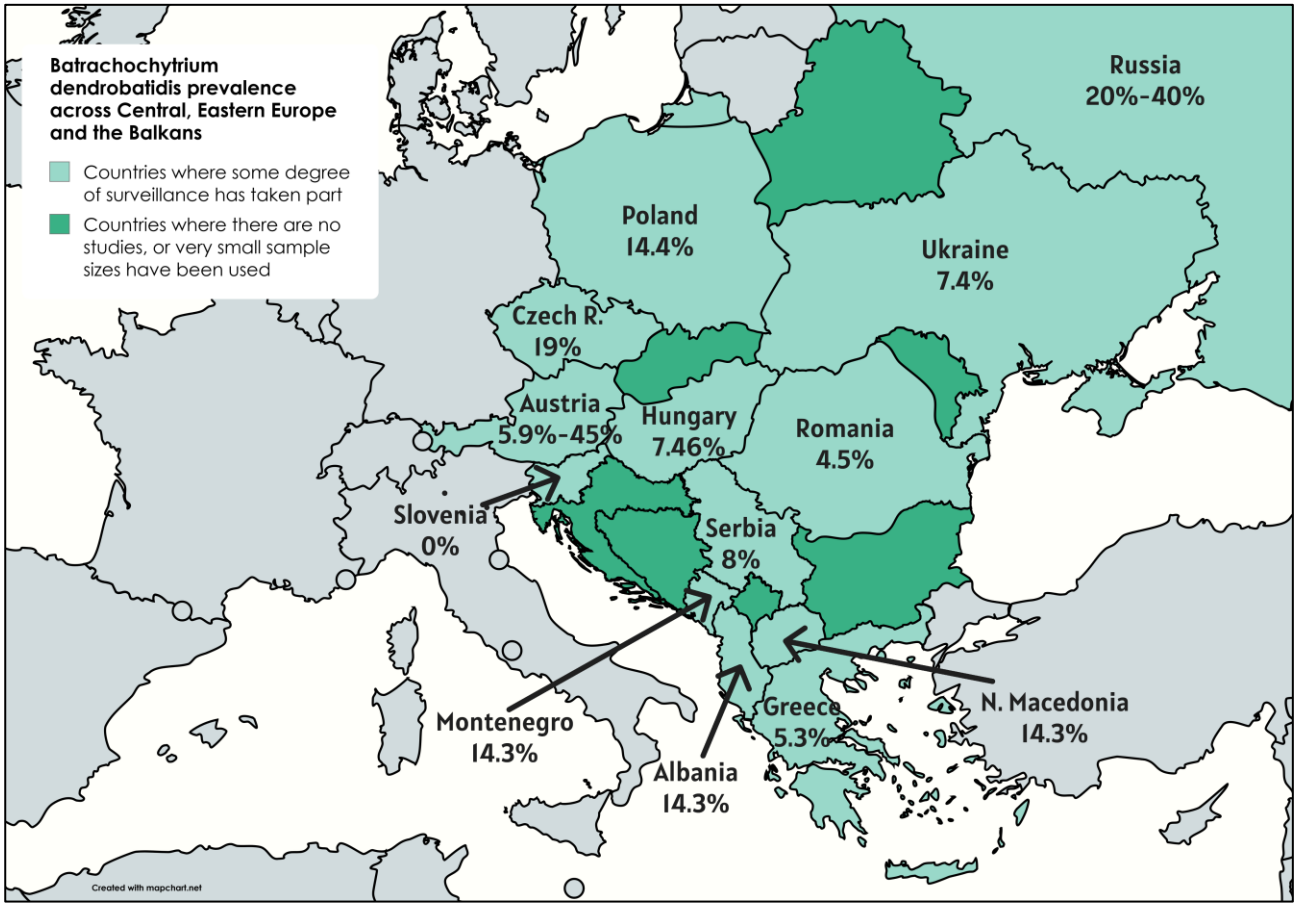

Figure 1. Overview of *Batrachochytrium dendrobatidis* prevalences across Central, Eastern Europe and the Balkans

Table 1. Prevalence values and references per country used for Figure 1.

Country	Bd Prevalence	Reference
Albania	14.3	Vojar et al., 2017
Austria	5.9 - 45%	Sztatecsny & Glaser, 2011
Belarus	N/A	N/A
Bosnia and Herzegovina	37%	Zimić et al., 2020
Bulgaria	N/A	N/A
Croatia	N/A	N/A
Czech Republic	19	Balá et al., 2014
Greece	5.3	Strachinis et al., 2022
Hungary	7.46	Vörös et al., 2018
Kosovo	N/A	N/A
Moldova	N/A	N/A
Montenegro	14.3	Vojar et al., 2017
North Macedonia	14.3	Vojar et al., 2017
Poland	14.4	Palomar et al., 2021
Romania	4.5	Scheele et al., 2015
Russia	20-40	Reshetnikov et al., 2014
Serbia	8	Mali et al., 2017
Slovakia	N/A	N/A
Slovenia	0	Kostanjsek et al., 2021
Ukraine	7.4	Jakóbik et al., 2024

Table 2. Summary of existing detection methods for *Batrachochytrium dendrobatidis* (Bd) and *Batrachochytrium salamandrivorans* (Bsal)

Methodology	Use	Strengths	Drawbacks	References
Histopathology	Examines keratinised tissue for fungal particles and associated tissular effects	Provides direct visualization of the pathogen and its effects on the host.	Requires biopsy or euthanizing the animal	Berger et al., 1999; Green & Kagarise Sherman, 2001; Knapp & Morgan, 2006; Kriger et al., 2006; Hyatt et al, 2007; Borteiro et al., 2019; Thomas et al., 2018; Ossiboff et al., 2019
Immunohistochemistry (IHC), RNAScope in-situ hybridisation (ISH)	Uses antibodies to detect chytrid fungi in tissues, and target-specific (Bsal) oligonucleotide probes	High specificity; useful for confirming presence in infected tissue samples	Labor-intensive; requires special antibodies and lab expertise	
Quantitative PCR (qPCR)	Gold standard. Detection of Bd from skin swabs.	Highly sensitive; detects low levels of infection; quantifiable results; rapid	Expensive; requires specialized equipment; vulnerable to laboratory errors, such as sample or lab contamination.	Boyle et al., 2004; Kriger et al., 2006; Retallick et al., 2006; Hyatt et al, 2007; Kriger & Hero, 2007; Smith, 2007; Blooi et al., 2013; Fisher et al., 2018**;** Thomas et al., 2018
Standard PCR	Amplifies DNA of chytrid fungi for detection	Useful for detecting known strains; relatively cheaper than qPCR	Lower sensitivity compared to qPCR; not quantitative; vulnerable to laboratory errors, such as sample or lab contamination.	
Environmental DNA (eDNA)	Detects *B. dendrobatidis* in water and soil samples	Non-invasive; good for large-scale monitoring	Detection does not indicate infection in specific animals; limited by environmental degradation of DNA; vulnerable to laboratory errors, such as sample or lab contamination.	Walker et al., 2007**;** Goldberg et al., 2015**;** Olson & Chestnut, 2016; Schumer & Pilliod, 2016
DNA sequencing	Used for characterisation rather than detection, in evolutionary studies, to assess pathogen diversity	Allows strain differentiation	Expensive and resource-intensive; sample quality and DNA degradation can affect sequencing accuracy	Farrer et al., 2017; Wacker et al., 2023
Culture Techniques	Grows the fungus in lab settings from infected tissues	Useful for isolating and studying different fungal strains; confirms viability	Time-consuming; requires specialized fungal culture conditions; not easily cultured	Fisher et al., 2018; Robinson et al., 2020
Lateral Flow Test (LFT)	Rapid immunoassay detecting Bd/Bsal antigens using antibody-coated strips.	Quick results (minutes), field-deployable, minimal equipment needed.	May have lower sensitivity/specificity than molecular methods, qualitative rather than quantitative.	Dillon et al., 2017
Loop-Mediated Isothermal Amplification (LAMP)	Amplifies DNA of *B. dendrobatidis* at a constant temperature	Portable; allows in-field detection without advanced equipment; faster than PCR	Less widely used and validated; can have issues with specificity in field samples	Boyle & al, 2013**;** Fischbach et al, 2018
Field-deployable, Isothermal, Nucleotide-based Detection Method (FINDeM)	CRISPR-based molecular DNA detection method	Can be used on-site, with immediate results and minimal costs	Developed for Bsal only; sensitivity is lower than qPCR	Hoenig et al., 2024)

Table 3. Overview of actions that have been used or have potential of being used towards *Batrachochytrium dendrobatidis* (Bd) and *Batrachochytrium salamandrivorans* (Bsal) mitigation.

Mitigation type	Details	References
Pre-emergence measures (targeted on preventing disease)		
Biosecurity-oriented practices	Use of quarantine; strict disinfection protocols	Fisher & Garner, 2020, Thomas et al., 2019
Amphibian trade restrictions	USA, Europe, Canada and Australia have taken heed of the danger Bsal poses and tightened trade regulations	Thomas et al., 2019 Gray et al., 2015
International and local institutional recognition	The World Organisation for Animal Health has declared Bd and Bsal as notifiable diseases, however local governments should ideally institute internal reporting protocols	Schloegel et al., 2010
Creation and management of geographic refuges	Areas free of Bd/Bsal: based on preventing Bd introduction, implementing of strict biosecurity protocols.	Woodhams et al., 2011
Post-emergence measures (targeted on managing disease)		
Ex situ programmes and translocations	Captive breeding for reintroductions and reinforcements, as well as the potential selective breeding and/or translocation of resistant or tolerant individuals, cryopreservation banks	Garner et al., 2016, Thomas et al., 2019, Knapp et al., 2024, Scheele et al., 2019
Mitigating other threats	Control of comorbidities, habitat degradation, invasive species, etc. The aim is to decrease mortality or sub-lethal negative impacts arising from other causes different to Bd or Bsal. This can also allow demographic compensatory mechanisms to operate efficiently.	Scheele et al., 2019, Fisher & Garner, 2020, Valenzuela-Sánchez et al., 2022
Creation and management of environmental refuges	Based on manipulating environmental conditions to decrease suitability for Bd, decreasing disease-associated mortality rates	Scheele et al., 2019, Garner et al., 2016
Manipulation of Bd virulence	Although laboratory settings show attenuation in Bd virulence with frequent Bd passages, this has not been found to be true in the wild. The method remains yet untested and may not prove efficient.	Scheele et al., 2019
Vaccination	Even when an immune response can be obtained, susceptibility to infection or disease might not be reduced. There is evidence of behavioural and acquired resistance in three species after exposure to live and dead Bd zoospores.	Woodhams et al., 2011 Garner et al., 2016, Thomas et al., 2019, Kaganer et al. 2023, McMahon et al. 2014
Biocontrol with predators of Bd	Zooplankton, microcrustaceans	Woodhams et al., 2011
Bioaugmentation using probiotic therapy	Aimed at encouraging the maintenance of topical protective microbiota, its effectiveness in the wild remains unclear	Woodhams et al., 2011, Garner et al., 2016, Thomas et al., 2019
Use of pathogens of Bd/Bsal	Use of mycoviruses: recently the first Bd mycovirus BdDV 1 was discovered and characterised, no in vivo studies yet	Woodhams et al., 2011, Clemons et al., 2024
Reducing contact between susceptible and tolerant hosts	An experiment to test the effectiveness of exclusionary fences to limit the contact of individuals of a highly susceptible species with potential Bd reservoirs is being conducted in Southern Chile	A. Valenzuela-Sánchez, pers. Comm.