The occurrence and effects of chytridiomycosis in amphibians

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A comparison between temperate regions of Europe and tropical regions of Central America

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Preface

This review was conducted as a finishing part of my study in Applied Biology at Aeres University of Applied Sciences. It is meant for policy makers and conservationists alike, as well as anyone else interested in (disease in) amphibians. I would like to thank my coach, Laura van Zonneveld, for continued assistance and providing valuable feedback.

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Abstract

English

Over the past fifty years, the disease chytridiomycosis has impacted at least 500 species of amphibians around the world. It is caused by the chytrid fungi *Batrachochytrium dendrobatidis* and *B. salamandrivorans*, and while it causes sporadic mortality in some amphibian species, it completely wipes out others. Because of that, it has been called “the worst pathogen in the history of the world, in terms of its impact on biodiversity”. However, the disease has had differing effects across different geographical regions. An extensive literature review was conducted in order to gain a better understanding of differences in occurrence and mortality rates of chytridiomycosis in temperate climates of Western Europe compared to tropical climates of Central America. This was done using a systematic review, where multiple online search engines were utilised to find both scientific and non-scientific sources. Based on a number of in- and exclusion criteria, sources were either used or discarded. From the results of this review, it could be concluded that the spread of the causative fungi is largely dependent on the number of amphibian species which can either develop clinical disease or act as vectors. Mortality rates depend less on taxonomical differences than on infection dose, which is in turn influenced by environmental temperature. These factors make that amphibian populations in Central America have been hit harder than those in Western Europe. However, since the fungi are already widespread in Western Europe and temperatures there are rising, action is needed to prevent further damage to amphibian populations. The spread of these fungi needs to be continually researched in both reviewed geographical areas. Furthermore, it is recommended that areas are identified where refugial habitat can be created on the short term, which offers suitable conditions to susceptible amphibians, while being less suitable for the chytrid fungi. This way, conservationists and policy makers alike can make a positive difference in guarding amphibian species from extinction.

Dutch

De afgelopen vijftig jaar heeft de ziekte chytridiomycose ten minste 500 soorten amfibieën negatief beïnvloed. Het wordt veroorzaakt door de chytride schimmels *Batrachochytrium dendrobatidis* en *B. salamandrivorans* en terwijl het in sommige soorten amfibieën sporadisch overlijden veroorzaakt, vaagt het andere soorten compleet uit. Daarom is het "in termen van invloed op de biodiversiteit de schadelijkste pathogeen in de geschiedenis van de wereld" genoemd. Echter, de ziekte heeft in verschillende geografische regio's verschillende effecten teweeg gebracht. Om een beter begrip te ontwikkelen over de verschillen in voorkomen en sterftecijfers door chytridiomycose in gematigd klimaat in West-Europa vergeleken met tropisch klimaat in Centraal Amerika, is een uitgebreide literatuurstudie uitgevoerd. Dit is gedaan door een systematische herziening te doen, waarbij meerdere online zoekmachines zijn gebruikt om zowel wetenschappelijke als niet wetenschappelijke bronnen te vinden. Bronnen werden ofwel gebruikt ofwel verwijderd op basis van een aantal criteria voor in- of uitsluiting. Uit de resultaten van deze herziening kon worden geconcludeerd dat de verspreiding van de causatieve schimmels grotendeels afhankelijk is van het aantal soorten amfibieën dat na infectie klinische ziekte kan ontwikkelen of als vector kan optreden. Sterftecijfers hangen minder samen met taxonomische verschillen dan met infectiedosis, dat weer beïnvloedt wordt door omgevingstemperatuur. Deze factoren maken dat amfibieënpopulaties in Centraal Amerika zwaarder getroffen zijn dan die in West-Europa. Omdat de schimmels al wijdverspreid zijn in West-Europa en de temperatuur daar stijgt, is optreden nodig om verdere schade aan amfibieënpopulaties te voorkomen. Er moet continue onderzoek gedaan worden naar de verspreiding van deze schimmels in beide onderzochte geografische gebieden. Daarbovenop wordt aangeraden om gebieden te identificeren waar op de korte termijn uitwijkmogelijkheden gerealiseerd kunnen worden, waarin de omstandigheden geschikt zijn voor vatbare amfibieën, maar minder geschikt voor de chytride schimmels. Op deze manier kunnen natuurbeschermers en beleidsmakers beiden een positie invloed uitoefenen in het tegen uitsterven beschermen van amfibieën.

Contents

1. Introduction

The European Environment Agency foresees a human population growth in some Western European countries of up to 50% by the end of this century (European Environment Agency, 2016). Not only will the world's population grow, the average wealth is projected to increase too (United Nations, 2019). Population growth and increased affluence result in global warming, having already caused an estimated 1,0°C increase since pre-industrial times (IPCC, 2018; Mitchell, 2012). The temperature even rose with 1,7°C in the Netherlands during the same period (KNMI, n.d.). Climate change has been (and likely will be) negatively affecting biodiversity (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Pereira et al., 2010; Thomas et al., 2004). The resilience of ecosystems is dependent on biodiversity, making biodiversity important to human populations relying on those ecosystems in both developing and developed countries (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011).

Being both a widely distributed taxonomic group and highly sensitive to environmental conditions, amphibians are good indicators of biodiversity and the health of an ecosystem (Xie, Towsey, Zhu, Zhang, & Roe, 2017; Tompkins, Carver, Jones, Krkošek, & Skerratt, 2015; IUCN Red List, n.d.). Unfortunately, 41% of amphibian species is at risk of extinction (IUCN Red List, n.d.). Habitat loss and climate change are widely known to endanger their existence (Ochoa-Ochoa, Rodríguez, Mora, Flores-Villela, & Whittaker, 2012; Griffiths, Sewell, & McCrea, 2010; Crist, 2007; Donnelly & Crump, 1998). On top of that, the past decades disease has also become a large threat to the survival of many amphibian species (NewScientist.com, 2019; Fisher et al., 2012a; Crist, 2007; IUCN Red List, n.d.).

One of those diseases is chytridiomycosis, caused by infection with the chytrid fungi *Batrachochytrium dendrobatidis [Bd]* or *Batrachochytrium salamandrivorans [Bsal]* (Fisher et al., 2012a; Crawford, Lips, & Bermingham, 2010; Voyles et al., 2009; Longcore, Pessier, & Nichols, 1999; Berger et al., 1998). Fisher, in an interview with National Geographic, called it "the worst pathogen in the history of the world, in terms of its impact on biodiversity" (Greshko, 2018). In total, the disease has impacted at least 500 amphibian species in the last fifty years (Scheele et al., 2019b). The illness causes sporadic mortality in some amphibian populations, while completely wiping out others (Australian Government, 2013). Recently, the likely origin of the disease has been traced back to the Korean peninsula (O'hanlon et al., 2018). It has since spread to Australia, the Caribbean, North America, Europe and Central America (Carvalho, Becker, & Toledo, 2017; Hudson et al., 2016; Creemers & Spitzen, 2013; Cheng, Rovito, Wake, & Vredenburg,, 2011; Skerratt et al., 2007; Rachowicz et al., 2006; Bosch, Martínez-Solano, & García-París, 2001).

Central America showed some of the largest declines in terms of numbers of frogs and toads (Scheele et al., 2019b). Besides fragmentation, degradation and loss of habitat, chytridiomycosis was a direct cause of this decline (Scheele et al., 2019b; Alford, Bradfield, & Richards, 2007; Skerratt et al., 2007). The first report of this disease in the neotropics came little over twenty years ago (Berger et al., 1998). Since then, some 200 amphibian species in Central America alone have been affected (Scheele et al., 2019b). In all but one amphibian species (*Salamandra salamandra*) in this geographic region, chytridiomycosis was caused by *Bd* (Scheele et al., 2019b).

While being present, the impact of *Bd* has remained low in temperate regions of Western Europe (Spitzen-van der Sluijs et al., 2014). However, a Dutch amphibian research foundation [RAVON] has expressed concern regarding the disease it causes (Spitzen, n.d.). Since 2008, Dutch *S. salamandra* populations have been decimated by *Bsal*: a chytrid fungus closely related to *Bd* (Greshko, 2018; Bossema, 2017; Creemers & Spitzen, 2013; Spitzen-van der Sluijs et al., 2013).

As of yet, there is no way to protect unafflicted areas from new outbreaks (Kolby & Daszak, 2016). Protection of habitats and the species that inhabit them can only be effective if the relations between those habitats and species are understood (Martin, Camaclang, Possingham, Maguire, & Chadès, 2017). Despite the growing threat of global warming and the presence of extensive research on chytridiomycosis, there is no comprehensive review of differences between tropical and temperate regions where it occurs and the effects it has in terms of mortality rates among different species. This lead to the main research question: *What are the differences in occurrence and mortality rates of chytridiomycosis in temperate climates of Western Europe compared to tropical climates of Central America?* Answers were sought by asking the following sub questions:

1. *What biological differences are there between fungi that cause chytridiomycosis?*
2. *Where did chytridiomycosis affect populations of amphibians in the reviewed geographical areas?*
3. *What are environmental parameters of affected areas?*
4. *What amphibian families do impacted species belong to in the reviewed geographical areas?*
5. *What factors influence mortality rate among different amphibian families in the reviewed geographical areas?*

The first expected difference is that there might be morphological differences between *Bd* and *Bsal* which render one more virulent than the other in certain climates (Longcore et al., 1999). Second, given that many fungi prefer humid, warm environments, it is also expected that affected areas are more widespread in Central America (Farson, 2017). Since chytridiomycosis has had an impact on over 200 species in Central America alone, it is expected that they stem from a wide array of amphibian families (Scheele et al., 2019b). When there are species that are immune to the disease, they can still act as vectors for the fungi (Hanselmann et al., 2004). Since there is such a high number of impacted species in Central America, it is expected that there are more immune species as well. Therefore, it is also expected that mortality rates overall are lower there. Answering the questions of this review might give insight in the relation between amphibian species, chytridiomycosis and the habitat they occur in, giving policy makers and conservationists comprehensible handholds to prepare methods of containment or even eradication of the disease. Furthermore, this review can serve as a baseline of knowledge regarding this topic, illustrating knowledge gaps that can be addressed in future research (Fierro et al., 2019).

2. Method

The research questions were answered by conducting a literary review. This chapter not only clarifies which geographical areas were considered and where literature was sought, but also gives a detailed account of used search terms. Furthermore, this chapter contains criteria used to determine whether or not a source was to be included in this review. This chapter also explains how used sources were analysed.

2.1 Reviewed Geographical areas

To avoid ambiguity as to what countries were meant by “Western Europe” and “Central America”, this review follows a definition given by the United Nations Statistics Department (United Nations, n.d.). Austria, Belgium, France, Germany, Liechtenstein, Luxembourg, Monaco, The Netherlands and Switzerland are considered Western Europe. The countries that form Central America are Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua and Panama.

2.2 Method

Studies by Müller et al. (2019) and Uman (2011) were used as guidelines for the methods. This systematic procedure provides a useful overview of the current state of knowledge (Snyder, 2019). After formulating the research questions, keywords were selected. Following that, multiple online search engines were used to find a wide array of both scientific and non-scientific sources. Searches for news articles and other non-scientific sources were done with Google.com. After that, scientific searches were done using Scholar.google.com, Sciencedirect.com, Wiley.com, Link.springer.com and Greeni.nl. Searches were conducted both in English and in Dutch. After inclusion of a source, its references were checked for other relevant articles. This was also done for sources resulting from that check, and repeated until no more new sources were found.

The sources that were used in this review were catalogued using a matrix (Appendix I). It states the number of the source, the title of the source, where it can be found online, the APA-citation, whether it is scientific or not and what useful information can be found in it. Lastly, each entry has a notation on which research question it helps answering.

2.3 Search terms

Several keywords were used separate and/or in combination with other keywords. Google Search Operators were used to form combined keywords (e.g. “Amphibian AND disease”, “Frog* AND (fungi OR Bd”). Keywords were only combined if it would lead to results relevant to the research questions, as some combinations (e.g. “Amphibian AND frog”) would widen the search results too much. Following Müller et al. (2019) and Uman (2011), keyword combinations include research content as well as actors involved.

Some keyword combinations applied to only one of the sub questions. For instance, “Batrachochytrium AND characteristics” only provided useful information for the question: “*What biological differences are there between fungi that cause chytridiomycosis?”* However, many keywords yielded information for more than one of the sub questions. Information for the question regarding mortality rates was found using search terms such as: “Amphibian AND (extinct OR decline)” and “Batrachochytrium AND “mortality rate””. At the same time, those combinations also revealed where and which amphibian species were affected. A complete list of used search terms and their combinations can be found in Appendix II.

2.4 Criteria for in- or exclusion

For this review it did not matter what year a source was published. It was taken in to account, as it might reveal something about how fast new outbreaks spread, but was neither an in- nor exclusion criterium. The sources had to be in Dutch or English, as the author was only sufficiently capable of interpreting those two languages. Most exclusion criteria inferred an opposite inclusion criterium (Table 2.1). However, if a source met one of the inclusion criteria, that did not automatically result in inclusion in the review. Every source had to be either a peer reviewed scientific report or a verifiable non-scientific source. In order to be considered a verifiable non-scientific source, it had to come from a recognised (non)governmental organisation (e.g. United Nations, IPCC, nationwide newspapers). Besides that, it needed to meet every inclusion criterium.

Table 2.1. *Inclusion and exclusion criteria.*

Inclusion criteria	Exclusion criteria
Sources in Dutch or English	Sources in languages other than Dutch or English
Verifiable non-scientific sources	Non verifiable sources
Sources that do contribute to answering one or more research questions	Sources that do not contribute to answering one or more research questions
Sources in the field of biology or epidemiology	Sources outside the field of biology or epidemiology
Peer reviewed scientific reports	

2.5 Analysis

The title of every search result was screened first (Fig. 1). If There were no relevant titles on a whole page of search results, the remaining results were excluded as well. Duplicates, resulting from similar search terms, were eliminated. After that, the abstract of every remaining title was assessed using the in- and exclusion criteria. This was also done for non-scientific sources, but then using comparable sections of those articles/news items. Reading of the introductions and conclusions (of scientific sources) was only done with the included sources. The chapters 'materials & methods' and 'results' were only read when specific information from those chapters was needed.

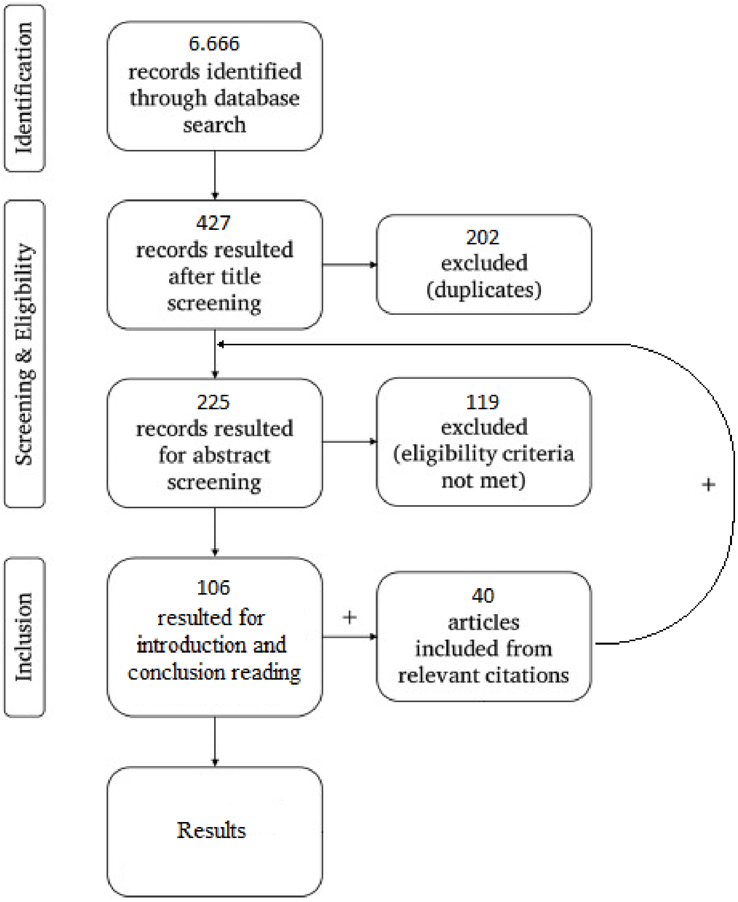

Figure 1. Flowchart of the number of sources and when they were in- or excluded. Adapted from Müller et al. (2019).

3. Results

The used search methods primarily yielded 106 (12 non-scientific, 94 scientific) sources useable for this review. 40 additional sources were found by screening the references of included sources. Appendix III contains a full list of which sources were used to answer which sub question(s). When citing every source behind a statement proved too detrimental to readability, just a few of them were named. In order to enhance readability of this chapter, the results of each sub question are treated separately below.

3.1 What biological differences are there between fungi that cause chytridiomycosis?

Morphology

Phylogenetic analyses show that *Bsal* has a significant genetic difference from *Bd* (3,47% - 4,47%), which is why they are named as separate species (Martel et al., 2013). Besides this genetic difference, there are some morphological characteristics that set them apart from each other. *Bsal* forms many colonial thalli (Martel et al., 2013), whereas (colonial) thalli are not always observed with *Bd* induced chytridiomycosis (Pessier, 2014). Also, *Bd* does not produce germ tubes, while *Bsal* does (Martel et al., 2013).

Although *Bsal* and *Bd* have some genetic and morphological differences, their way of reproduction is largely the same (Martel et al., 2013). When they infect a host, they encyst in dermal cells and develop rhizoids (Martel et al., 2013; Berger et al., 2005; Longcore et al., 1999). When the fungi mature, they form zoosporangia and produce zoospores (Farrer, 2019; Martel et al., 2013; Berger et al., 2005; Longcore et al., 1999). These zoospores are mobile, propelling themselves forward with a posterior flagellum (Berger et al., 2005; Longcore et al., 1999). During this stage, zoospores spread and infect other (naïve) hosts (Voyles, Rosenblum, & Berger, 2011; Berger et al., 2005; Longcore et al., 1999). In addition to motile spores, only *Bsal* produces non motile spores that can endure in the environment (Stegen et al., 2017).

Vectors

Both *Bd* and *Bsal* are waterborne fungi, largely associated with permanent bodies of water and streams (Skerratt et al., 2007). Their zoospores can survive for up to seven weeks in a sterile pool of water and several weeks in a moist environment such as river sand (Johnson & Speare, 2005). In such environments they can form biofilm on the water level and riverbed, facilitating dispersal (Silva, Matz, Elmassry, & San Francisco, 2019). Besides possibly being transported by (flowing) water (Kolby et al., 2015), another vector is (non-susceptible) animals. *Bd* can be transported on bird feathers to naïve environments, surviving up to three hours of drying time (Johnson & Speare, 2005). Next to waterfowl, other nonamphibian hosts may be fish and crayfish (Woodhams et al., 2001). While it is possible that the above vectors introduce the fungi to new areas, human activity seems to be the biggest vector (More et al., 2018).

Anurans do not seem susceptible to *Bsal*, but they can act as vectors for this *Batrachochytrium* species (More et al., 2018; Martel et al., 2013). Midwife toads (*Alytes obstetricans,* family: alytidae) that were experimentally exposed to *Bsal* did not develop chytridiomycosis (Martel et al., 2013), even though they are very vulnerable to *Bd* (Walker et al., 2010; Bosch et al., 2001). On top of that, some anurans do not develop clinical disease from infection with *Bd* either, thus possibly acting as active vectors for not only *Bsal*, but also *Bd* (Miaud et al., 2016; Hanselmann et al., 2004).

Temperature

Although there seems to be variation in thermal tolerance among different strains of *Bd* (Voyles, Rosenblum, & Berger, 2011), there are some widely accepted temperature tolerance spectrums of *Bd* and *Bsal* (Mutschmann, 2015; Martel et al., 2013; Carey et al., 2006; Berger, Hyatt, Speare, & Longcore, 2005; Longcore et al., 1999) The optimal temperature range of *Bd* is believed to be between 12°C - 23°C (Berger et al., 2005; Longcore et al., 1999). Although this fungus still grows at 28°C (Longcore et al., 1999), it remains pathogenic and virulent between 12°C - 27°C (Carey et al., 2006; Berger et al., 2005). Being exposed to 30°C for longer periods of time (>8 days) seems lethal for most *Bd* cultures (Mutschmann, 2015). *Bsal* grows between 5°C - 25°C and dies when the temperature exceeds this maximum (Martel et al., 2013). Optimal growth occurs between 10°C and 15°C (Martel et al., 2013). It is unknown what the lower temperature threshold is for virulence of *Bd* or *Bsal* (Skerratt et al., 2007).

Pathology

While *Bsal* and *Bd* both cause chytridiomycosis, the clinical manifestations of the disease depend on which of the two fungi was the causative agent (Farrer, 2019). In caudatans (salamanders and newts), *Bsal* causes multiple superficial erosions and deep ulcers in the skin (Farrer, 2019; Martel et al., 2013). *Bd* causes an opposite effect: thickening and hyperkeratosis of skin tissue (Farrer, 2019; Berger et al., 2005). In both clinical pictures, the amphibian's ability to osmoregulate decreases (Voyles et al., 2011; Vredenburg, Knapp, Tunstall, & Briggs, 2010). The *Bd* variant can infect every species of amphibian, while *Bsal* apparently only infects salamanders and newts (Berger et al., 2016; Martel et al., 2013; Woodhams et al., 2001).

3.2 Where did chytridiomycosis affect populations of amphibians in the reviewed geographical areas?

Central America

Chytridiomycosis has caused amphibian population declines in Panama (e.g. McCaffery, Richards-Zawacki, & Lips, 2015; Berger et al., 1998), Costa Rica (e.g. Zumbado-Ulate, García-Rodríguez, Vredenburg, & Searle, 2019; Bolaños & Ehmcke, 1996), Honduras (e.g. Kolby, Padgett-Flohr, & Field 2010; Puschendorf, Castaneda, & McCranie, 2006b), Guatemala (e.g. Rovito, Parra-Olea, Vásquez-Almazán, Papenfuss, & Wake 2009) and Mexico (e.g. Bolom-Huet, Pineda, Díaz-Fleischer, Muñoz-Alonso, & Galindo-González, 2019; Nava-González, Suazo-Ortuño, Parra-Olea, López-Toledo, & Alvarado-Díaz, 2019). It is also likely that *Bd* caused declines in El Salvador (Lawson, Jones, Komar, & Welch, 2011; Felger, Enssle, Mendez, & Speare, 2007). Although *Bd* is ubiquitous in Belize (Kaiser & Pollinger, 2012) and present in Nicaragua (García-Roa, Sunyer, Fernández-Loras, & Bosch, 2014), there are no reports detailing amphibian population declines in these countries.

Western Europe

The only place where *Bd* caused mass mortality events in Western Europe was the French Pyrenees (Fisher et al., 2012b; Garner et al., 2009). Spitzen-van der Sluijs et al. (2010) found *Bd* to be present in every province of the Netherlands and Belgium, except for Groningen, Zuid-Holland and Zeeland. In total, they found four percent of tested amphibians to carry *Bd.* However, not a single individual showed clinical signs of chytridiomycosis. Up until 2010, there has been one case of chytridiomycosis caused by *Bd* in the Netherlands and Belgium (Pasmans et al., 2010). Since then, a seven year study showed *Bd* to be endemic in the Netherlands and having an impact on *Bombina variegata* (family: bombinatoridae) (Spitzen-van der Sluijs, Canessa, Martel, & Pasmans, 2017).

Switzerland seems to have a high presence of *Bd* (Parrott et al., 2017; Garner et al., 2005). In fact, Fisher et al. (2012b) report *Bd* prevalence of over 80 percent at many sites in the northern half of Switzerland, which means over 80 percent of encountered amphibians was infected. Nonetheless, no mass mortality events have been reported there. There are no records of *Bd* caused declines in Austria either, despite prevalence of up to 40 percent (Sztatecsny & Glaser, 2011). One large scale study examined amphibian populations across Germany and found *Bd* to be widespread, but they did not find a link between population declines and chytridiomycosis there (Ohst, Gräser, Mutschmann, & Plötner, 2011). *Bsal* is only known to have had an impact in an area where the borders of Germany, Belgium and the Netherlands meet (Spitzen-van der Sluijs et al., 2016). There is no data on how widespread *Bsal* is in Western Europe.

3.3 What are environmental parameters of affected areas?

Number of (resistant) amphibian species

Because not every amphibian species is equally susceptible to *Bd*, some survive (longer) while infected, increasing prevalence of the fungus among more susceptible species (Brannelly et al., 2018). For instance, El Copé in Panama had high amphibian species richness prior to an enormous outbreak of chytridiomycosis (Velo-Antón et al., 2012; Lips et al., 2006), providing many potential hosts to spread the disease (Brannelly et al., 2018; De Castro & Bolker, 2005; McCallum & Dobson, 1995). Compared to Central America, Western Europe has a low amphibian species richness (Rödder et al., 2009; Temple & Cox, 2009).

Altitude

Bd is endemic at almost all altitudes in Costa Rica (Pounds et al., 2006; Puschendorf, Bolaños, & Chaves, 2006a). The fungus was also found across a wide variety of elevations in Panama (Kilburn et al., 2010), Honduras (Puschendorf et al., 2006b), Belize (Kaiser & Pollinger, 2012) and Mexico (Murrieta-Galindo, Parra-Olea, González-Romero, López-Barrera, & Vredenburg, 2014). Findings by Frías-Alvarez et al. (2008) suggest that *Bd* is widely distributed in high altitude (= more than 500 m.a.s.l.) forests of Mexico. Despite *Bd* presence at nearly all elevations; many declines (caused by chytridiomycosis) in Central America happened in areas higher than 500 meters above sea level (e.g. McCaffery et al., 2015; García-Roa, Sunyer, Fernández-Loras, & Bosch, 2014; Velo-Antón et al., 2012; Whitfield, Kerby, Gentry, & Donnelly, 2012; Brem & Lips, 2008; Lips et al., 2006; Pounds et al., 2006; Puschendorf et al., 2006a; Lips, Reeve, & Witters, 2003; Crump, Hensley, & Clark, 1992).

One example is given by Puschendorf et al. (2009), when they describe a case where *Craugastor ranoides* disappeared from the Costa Rican Guanacaste Volcanic range (high elevation), while persisting in low elevations of the Santa Elena Peninsula. Species of the genus *Atelopus* (family: bufonidae) show a similar trend (McCaffery et al., 2015). Although 38 percent of these species disappeared from neotropical lowlands, 75 percent of *Atelopus* species vanished in elevations above 1000 meters (La Marca et al., 2005). At a highland site in Guatemala, two species of plethodontidae were tested positive for *Bd,* but their populations did not show signs of decline (yet). However, three other species of plethodontidae have completely disappeared, despite being very abundant in the past. The cause of this disappearance has not been identified, although chytridiomycosis may have played a role. (Rovito et al., 2009)

As stated before, chytridiomycosis only caused amphibian population declines on a local scale in Western Europe, despite chytrid fungi being omnipresent at low altitudes (Parrott et al., 2017; Spitzen-van der Sluijs et al., 2017) and highly prevalent at higher altitudes (Fisher et al., 2012b; Sztatecsny & Glaser, 2011). *A. obstetricans* experienced mass mortality events in the French Pyrenean mountain range (Fisher et al., 2012b; Garner et al., 2009). The core of this outbreak region is at approximately 1900 meters above sea level (Clare et al., 2016). Even though this species also occurs in lower areas across Western Europe, where *Bd* is endemic, chytridiomycosis did not cause large declines there (Ohst, Gräser, Mutschmann, & Plötner, 2011; Pasmans et al., 2010).

Similar to *Bd*, *Bsal* only caused local declines in Western Europe (Stegen et al., 2017; Spitzen-van der Sluijs et al., 2016; Martel et al., 2014). These declines happened at low altitudes in the Netherlands, but *Bsal* is also present at altitudes around 500 meters above sea level (Spitzen-van der Sluijs et al., 2016). Severe outbreaks of *Bsal* in Belgium happened at roughly that altitude (Martel et al., 2014). According to Spitzen-van der Sluijs et al. (2016) the range of *Bsal* is currently around 10.000 km^2 and expanding to higher and lower altitudes.

Temperature

Data on *Bd* infection in Central American tropical lowlands shows that prevalence among amphibians varies between less than 5 percent in warm months to almost 35 percent in cool months (Whitfield et al., 2012). These cool months are closest to the optimal temperature range of *Bd* (Longcore et al., 1999). At a high altitude site (>3000 meters) in Mexico, there was a prevalence of up to 84 percent among aquatic salamanders and semi-aquatic frogs (Nava-González et al., 2019). However, even during the summer, temperatures there do not often reach the optimal temperature range of *Bd.* According to Nava-González et al. (2019), that temperature limited *Bd* virulence despite such a high prevalence. As previously mentioned, many amphibian species in El Copé in Panama were decimated by chytridiomycosis (Velo-Antón et al., 2012). This area has a mean annual temperature of 19°C - 26°C (Lips et al., 2006).

In the French Pyrenees, annual outbreaks of chytridiomycosis strongly correlate to the coming of spring (Clare et al., 2016). This study found a higher prevalence of *Bd* infection in some species during years when ice melted sooner, since temperatures were within the optimal temperature range of *Bd* for a longer period. Many sites in the northern half of Switzerland have a prevalence of over 80 percent (Fisher et al., 2012b). This high prevalence mainly occurs on the Swiss Plateau (Fisher et al., 2012b), where the mean annual temperature is 9°C - 10°C, the average temperature during the coldest month is between -1°C and 1°C and during the warmest month, the average temperature is between 16°C - 20°C (MeteoSwiss, 2020). Climatological information on Les Haute Fagnes, in the epicentre of *Bsal* outbreaks in Belgium (Martel et al., 2014), shows a mean winter temperature around a maximum of 2,2°C and a mean summer temperature around a maximum of 18°C (Mormal & Tricot, 2008).

3.4 What amphibian families do impacted species belong to?

There are many species/site specific studies that report on chytridiomycosis. Of these studies, many describe species of the bufonidae, craugastoridae, dendrobatidae and hylidae families being heavily impacted by *Bd* (e.g. Jacinto-Maldonado et al., 2020; Zumbado-Ulate et al., 2019; Velo-Antón et al., 2012; Whitfield et al., 2012; Puschendorf et al., 2009; Ryan, Lips, & Eichholz, 2008; Savage, 2002; Pounds, Fogden, Savage, & Gorman, 1997; Bolaños & Ehmcke, 1996).

Species from both craugastoridae and hylidae are infected with *Bd* more often than would be expected if infection occurred at random (Olson et al., 2013). While the bufonidae family as a whole are impacted less often than would be expected (Olson et al., 2013), the second largest genus of the family, *Atelopus*, has experienced extraordinarily large declines across Central America (Velo-Antón et al., 2012; La Marca et al., 2005; Savage, 2002). Sauer et al. (2020) found that bufonidae and hylidae are especially vulnerable to *Bd.*

The above pertains to Central American anurans, but there have been reports of caudatan populations being affected by *Bd* in Central America as well. These reports most often detail effects on plethodontidae (e.g. Bolom-Huet, Pineda, Díaz-Fleischer, Muñoz-Alonso, & Galindo-González, 2019; Mendoza-Almeralla, López-Velázquez, Longo, & Parra-Olea, 2016; Velo-Antón et al., 2012). Only one Central American salamandrid species (*S. salamandra*) has been proven to be impacted by *Bsal* (Scheele et al., 2019b)

Bsal had a devastating effect on some *S. salamandra* populations in Western Europe as well (Stegen et al., 2017; Spitzen-van der Sluijs et al., 2016; Martel et al., 2013). Dutch (Spitzen-van der Sluijs et al., 2013) and Belgian (Stegen et al., 2017) populations of this species have been (nearly) wiped out by *Bsal* induced chytridiomycosis. Stegen et al. (2017) showed that Alpine newts (*Ichthyosaura alpestris*), a salamandrid species that occurs alongside *S. salamandra* in Western Europe, is susceptible to *Bsal* infection as well. *Bsal* is possibly lethal to all species of salamandridae, except *Lissotriton helveticus,* which does not get infected, nor does it develop the disease (Martel et al., 2014). When *A. obstetricans* (family: alytidae) were experimentally infected with *Bsal*, they did not develop chytridiomycosis (Walker et al., 2010). They are, though, very susceptible to infection with *Bd* (e.g. Clare et al., 2016; Fisher et al., 2012; Pasmans et al., 2010; Tobler & Schmidt, 2010; Walker et al., 2010; Garner et al., 2009). *B. variegata* have been impacted in Western Europe too, but this species populations remain stable (Spitzen-van der Sluijs et al., 2017).

So far, it seems the only amphibian families to have been heavily affected by chytridiomycosis in Western Europe are the salamandridae and alytidae (e.g. Stegen et al., 2017; Spitzen-van der Sluijs et al., 2016; Martel et al., 2013; Fisher et al., 2012b; Garnet et al., 2009).

3.5 What factors influence mortality rate among different amphibian families in the reviewed geographical areas?

Some amphibian families appear to be more vulnerable to chytridiomycosis than others (Scheele et al., 2019b; Martel et al., 2013). Experiments have shown that *Bsal* is lethal to most of the caudatans that occur in Western Europe, while other species might not develop clinical disease at all (Spitzen-van der Sluijs et al., 2016; Martel et al., 2014). In addition to taxonomical differences which render some families more susceptible to *Bd* or *Bsal* than others, there are other factors that seem to have a big influence on mortality rate, regardless of geographical area (Sauer et al., 2020). Data by Clare et al. (2016) even shows that species thought to be highly resistant can still develop fatal chytridiomycosis when the circumstances are right for the disease. On the other hand, there are susceptible species that may recover from clinical disease (e.g. Martel et al., 2014; Puschendorf et al., 2009). Described below are factors that have been known to influence mortality rate.

Temperature

This factor influences mortality rate in several ways. First off, an increased temperature variability impairs amphibian immunity (Greenspan et al., 2017a). A thermal mismatch can occur when the environmental temperature varies a lot. This means *Bd*- or *Bsal*-infected amphibians from cool environments have a higher mortality rate in relatively warm temperatures and vice versa (Sauer et al., 2020). This was also the case in the French Pyrenees, where *Bd* prevalence was significantly higher among *A. obstetricans* (family: alytidae) during relatively warm years (Clare et al., 2016). Whether the Central American plethodontid *Pseudoeurycea leprosa* developed lethal chytridiomycosis was largely influenced by temperature as well (Mendoza-Almeralla et al., 2016).

Another way temperature influences mortality rate is when infected amphibians (deliberately) raise their body temperature to combat the fungus (Rowley & Alford, 2013). Amphibian immune systems often work better at higher temperatures (Sonn, Berman, & Richards-Zawacki, 2017). The temperature is notably warmer in Central American lowlands than in highlands, providing a greater chance of curing the disease (Woodhams, Alford, & Marantelli, 2003). The Central American *Atelopus zeteki* (family: bufonidae), to which *Bd* is highly lethal, survived infection significantly longer in higher temperatures than in lower temperatures (Greenspan et al., 2017b; Bustamante, Livo, & Carey, 2010). Similar results were shown by Sonn et al. (2017) in laboratory experiments. Temperature has little effect, however, on chances of getting infected (Wilber, Knapp, Toothman, & Briggs, 2017).

Dose

Whether an amphibian species goes extinct due to chytridiomycosis is influenced less by the probability of infection than by host tolerance and resistance (Wilber et al., 2017). Despite high *Bd* presence in Switzerland, no chytridiomycosis related disappearances have been reported. In fact, Garner et al. (2005) report that all amphibians captured in Switzerland were reproducing successfully, despite infection with *Bd.*

The gravity of *Bd* infection positively predicts chytridiomycosis induced death (Sauer et al., 2020). Clinical signs and mortality occur in individuals that carry the most zoospores (Briggs, Knapp, & Vredenburg, 2010; Vredenburg et al., 2010; Voyles et al., 2009). So, whether an infected individual survives is largely dose-dependent (Sauer et al., 2020; Wilber et al., 2017; Voyles et al., 2011; Vredenburg et al., 2010; Garnet et al., 2009; Voyles et al., 2009).

Heightened tolerance of a disease decreases likelihood of that disease causing mortality and eventually extinction (Wilber et al., 2017). One example is the Panamanian bufonid *A. varius,* which was previously presumed extinct as a result of chytridiomycosis (Perez et al., 2014). They have been found again on a few places where they disappeared from, in spite of *Bd* still being present (McCaffery et al., 2015; Perez et al., 2014; González-Maya et al., 2013).

Martel et al. (2014) showed the Western European salamandrid *Ichthyosaura alpestris* to be highly vulnerable to *Bsal.* However, the outcome of the disease is dose-dependent for this species as well (Stegen et al., 2017). When Stegen et al. (2017) experimentally infected *I. alpestris* with a low dose of *Bsal*, these newts eventually cleared themselves of the fungus, while a high dose of the same fungus proved to be pathogenic and lethal. Recovering from a low dose infection did not render *I. alpestris* immune to re-infection in an environment where the fungus is still present (Stegen et al., 2017).

In a natural environment, infection dose correlates with microfauna at the site (Schmeller et al., 2014). Aquatic microfauna can forage on fungal zoospores (Schmeller et al., 2014; Hamilton, Richardson, & Anholt, 2012; Buck, Truong, & Blaustein, 2011), lowering not only the chance of infection (Hamilton et al., 2012), but also the infectious burden (Schmeller et al., 2014). The dose of the infection can be further lowered by amphibian skin bacteria (Bates et al., 2018).

life stage

In addition to taxonomy, temperature and dose, another influencing factor is the life stage of an individual (Sauer et al., 2020). Laboratory results show that amphibian larvae are less likely than adults to succumb to either *Bsal* (Stegen et al., 2017) or *Bd* (Sauer et al., 2020). While adult amphibians experience a higher mortality rate due to *Bd* than larvae, metamorphs are the most susceptible to this fungus (Sauer et al., 2020; Garnet et al., 2009). Mortality of *Bd* infected metamorphs varies and can even be up to 90 percent (Tobler & Schmidt, 2010). In the case of *Bsal*, however, sexually mature amphibians are infected and killed significantly more often than other life stages (Stegen et al., 2017).

4. Discussion

Chytridiomycosis has had a tremendous effect on amphibian populations in Central America (Scheele et al., 2019b). On the contrary, the effect of the disease was fairly limited in Western Europe (e.g. Spitzen-van der Sluijs et al., 2017; Fisher et al., 2012b; Garner et al., 2009). This report aimed to illustrate differences in occurrence and mortality rates of chytridiomycosis in temperate climates of Western Europe and tropical climates of Central America. The available data was sufficient to do so and the results of this comparison are interpreted and discussed below. After that, there are some critical notes regarding the used methods.

Literature shows that altitude is a factor that correlates to the outbreaks of lethal chytridiomycosis in Central America (e.g. McCaffery et al., 2015; Velo-Antón et al., 2012; Puschendorf et al., 2009). That does not mean there is a causality between altitude and chytridiomycosis. Since temperature is a limiting factor of mortality rates (Sauer et al., 2020; Greenspan et al., 2017a; Mendoza-Almeralla et al., 2016; Rowley & Alford, 2013), it is more likely that temperatures above 500 m.a.s.l. in Central America are better suited to *Bd.* This is supported by reports on chytridiomycosis in Western Europe, which show areas with high prevalence, while no mass mortality occurred at roughly the same altitude as Central America but where temperatures are lower (Fisher et al., 2012b). There is a limit to higher altitudes providing better temperatures for *Bd,* since temperatures at the highest altitudes (>3000 m.a.s.l.) do not reach *Bd* optimal in either Central America or Western Europe (Mosher, Bailey, Muths, & Huyvaert, 2018).

Looking at climate requirements of *Bd,* nearly the entire Western European region is theoretically suitable for *Bd* (Rödder et al., 2009). The fact that Western European temperatures are predicted to rise during this century (IPCC, 2018) is cause for concern, since *Bd* is already widespread in many of this region's countries (Parrott et al., 2017; Spitzen-van der Sluijs et al., 2017; Ohst et al., 2011; Sztatecsny & Glaser, 2011; Spitzen-van der Sluijs et al., 2010). Increasing temperatures could cause more thermal mismatches in amphibians (Sauer et al., 2020), lowering their ability to combat the fungus while they were successful in doing so before (Greenspan et al., 2017a). Not only that, increasing temperatures in Western Europe means they approach temperatures in which *Bd* has shown to be highly pathogenic in Central America and laboratory experiments, potentially causing similar die-offs in Western Europe.

Bd is much more tolerant to and virulent under higher temperatures than *Bsal* (Martel et al., 2013; Longcore et al., 1999). This could explain why *Bd* has caused so many more amphibian population declines in Central America than *Bsal* (Scheele et al., 2019b). However, most declines in Central America happened in the highlands (e.g. García-Roa et al., 2014; Whitfield et al., 2012; Brem & Lips, 2008). These highlands, especially higher up, offer a suitable climate to *Bsal* as well, as shown by its presence there. Having many reports on population declines caused by *Bd* and few caused by *Bsal* may indicate an information bias, as reports on *Bd* date back to 1998, while *Bsal* was first described in 2013. There has simply been more time to report on *Bd* than on *Bsal.*

Even though there have not yet been many reports on population declines due to *Bsal* in Central America, does not mean there have not been any or will not be any in the future. Especially since Central America is home to a large number of amphibian species (Scheele et al., 2019b), heightening the chance of *Bsal* finding suitable hosts to infect or act as vectors (Brannelly et al., 2018). This is more so given the high virulence of *Bsal* among caudatans (Martel et al., 2014). While Western Europe does not have as many amphibian species as Central America, three fourths of salamander species there belong to Salamandridae family (AmphibiaWeb, 2020), many of which have been shown to be susceptible to *Bsal* infection (Martel et al. 2014). Amphibians in both Central America and Western Europe will benefit greatly from rapid identification of *Bsal*-infected areas.

However, management based on knowledge of presence alone will not be sufficient in containing chytridiomycosis, since virulence of the disease is impacted more by dose than by chance of infection (Wilber et al., 2017). There may be environmental refuges where the fungi occur but mortality is low (Zumbado-Ulate, Bolanos, Gutiérrez-Espeleta, & Puschendorf, 2014). In such refuges, amphibians with small advantages in tolerance or immunity can be naturally selected (Scheele et al., 2019a). Even when a species has no intrinsic advantage in shedding *Bd* or *Bsal,* their chance of survival increases significantly when they manage to limit the dose of infection (Stegen et al., 2017; Wilber et al., 2017). This dose is limited by temperature (Martel et al., 2013; Longcore et al., 1999), so the availability of microhabitat where an (infected) individual can increase its body temperature may be helpful in combatting the disease (Woodhams et al., 2003). Infection dose is further limited by microfauna which consume *Bd* and *Bsal* spores at the site (Schmeller et al., 2014).

All the above indicates an intricate relationship between the amphibian hosts, the pathogenic fungi and the environment they occur in both in Western Europe and Central America. Mitigation strategies based on this relationship could be applicable in both reviewed geographical regions (Scheele et al., 2019a). Findings by Heard et al. (2018) reveal that climates where hosts are already less susceptible to the disease offer the highest chance of success for habitat management. While Western European amphibian families are not per definition less susceptible than Central American species (Martel et al., 2014; Scheele et al., 2019a), temperatures in Western Europe render *Bd* and *Bsal*, as of yet, still less virulent there (Martel et al., 2013; Longcore et al., 1999). So in that regard, habitat management may be successful in Western Europe. The second finding by Heard et al. (2018) is that it may be more effective to create refugial habitat that is less favourable to the disease than to manipulate existing habitat. Such habitat may increase recruitment in vulnerable species which develop better tolerance or even immunity (Scheele et al., 2019a).

Should this review be used as a guideline to conduct other literary reviews, a critical note regarding the used methods is in place. First off, the criteria for in- or exclusion of a source were not specific enough. Some sources seemed promising after reading the title and abstract and were therefore included, but later proved to be irrelevant. This meant the number of included sources was slightly higher on paper than in practice. Secondly, the used search terms yielded a lot of useable sources, but were not exhaustive enough. After all, screening the references of used sources turned up 40 additional useable sources, which were not found using the initial search terms. Despite such a large number of useable sources, there is a third noteworthy limitation of this method, namely that only found sources could be reviewed. It is unknown how many sources were missed.

5. Conclusions and recommendations

In order to give conservationists and policy makers handholds to prepare methods of containment of chytridiomycosis, the following research question was answered: "*What are the differences in occurrence and mortality rates of chytridiomycosis in temperate climates of Western Europe compared to tropical climates of Central America".* Answering sub questions led to a number of conclusions:

1. The most important biological difference between *Bd* and *Bsal* is that the former is more virulent under higher temperatures than the latter. In addition, *Bd* causes hyperkeratosis, while *Bsal* causes lesions and ulcers. The effect is the same, however: an amphibian's reduced capability to osmoregulate.
2. *Bd*-induced Chytridiomycosis has critically affected amphibian populations in nearly every part of Central America, while having severe effects on only local populations in Western Europe. Climate change might cause more frequent chytridiomycosis outbreaks in Western Europe, however. *Bsal* has caused population declines on a much smaller scale, but it is unknown how widespread that fungus is in the reviewed geographical areas.
3. Central America contains many more amphibian species susceptible to the disease than Western Europe. The climate in both geographical areas is suitable to both pathogenic fungi, but the higher average temperatures in Central America make *Bd* more virulent there. Temperatures in Western Europe rise during spring, approaching the suitable range for both chytridiomycosis causing fungi. Outbreaks of *Bd* in the French Pyrenees correlate to the rising temperatures of spring. However, temperatures there do not reach the optimal for amphibian immune systems, causing mass die-offs. Outbreaks of chytridiomycosis are limited in the rest of Western Europe, partly because amphibian immune systems function better there due to slightly higher temperatures.
4. Amphibians of the bufonidae, craugastoridae, dendrobatidae and hylidae families in Central America are impacted more often than other families. Despite only affecting one species of salamandrid in Central America, *Bsal* might cause many more declines in the future, due to already suitable conditions and many present amphibian species. In Western Europe, only salamandridae and alytidae are heavily impacted by the chytrid fungi. However, nearly all caudatan species in Western Europe are susceptible to *Bd* and *Bsal.* Due to climate change and the already substantial presence of *Bd,* other Western European amphibian species might experience population declines in the future.
5. There are some taxonomical differences that render some species more or less susceptible to the disease, but infection dose and life stage play a larger role in predicting mortality rate. Both in Central America and Western Europe, metamorphs and adults experience higher mortality rates than tadpoles. Mortality rate is further predicted by infection dose. On top of that, mortality is higher when thermal mismatches occur.

Following these conclusions, it is recommended that areas are identified where refugial habitat can be created on the short term, which offers suitable conditions to susceptible amphibians, while being less suitable to the chytrid fungi. Furthermore, On the long term, such created habitat may boost recruitment in vulnerable species. In the creation of refugial habitat, a few things must be taken in to account. Since amphibians can deliberately raise their body temperature to boost their immune response, refugial habitat must contain sites where they can do so. This can be in the form of unshaded rocky or concrete slopes, facing the sun. Not only does that provide amphibians with a place where they can directly bask in the sunlight, the material absorbs sunlight, staying warm for longer periods of time. The pathogenic fungi do not survive drying for longer periods of time. Since rock or concrete dries faster than soil, for instance, these refugial areas are not likely to become a reservoir for the disease. Given the projected rising temperatures, it is expected that the effectivity of this measure increases over time, both in Central America and in Western Europe. In addition to providing sites where amphibians can raise their body temperature, it is important that refugial habitat is highly suitable to microfauna which forage on zoospores. Abundant microfauna directly lowers chance of infection and the infectious burden. While these factors do not contain or eradicate the disease, it helps in sustaining amphibian species which may otherwise go extinct. Finally, since it remains unknown how widespread *Bsal* is in either Western Europe or Central America, it is recommended to continually research (the spread of) *Bsal* in both reviewed geographical areas.

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Appendices

Appendix I. Source matrix example

Source No: 1 **Title**: **Origin:** **Apa:** **Scientific? yes / no**	**Useful info or remarks:** Which question does it answer?

Source No: 2 **Title**: **Origin:** **Apa:** **Scientific? yes / no**	**Useful info or remarks:** Which question does it answer?

Etc.

Appendix II. All used keywords and their combinations

General Keyword	Google Operator	Combined with
Batrachochytrium	AND	(Characteristics OR Dendrobatidis OR Salamandrivorans OR “mortality rate”)
Chytridiomycosis	AND	(Europe OR “temperate climate” OR “Central America” OR tropic OR temperate OR “mortality rate”)
Chytridiomycose	AND	(Nederland OR België OR Duitsland OR Europa OR klimaat)
Chytridiomycota	AND	(Europe OR “temperate climate” OR “Central America” OR tropic OR temperate)
Chytridiales	AND	(Europe OR “temperate climate” OR “Central America” OR tropic OR temperate)
Amphibian*	AND	(Extinct OR disease OR fungi OR fungus OR decline OR chytridiomycosis OR chytridiales OR Chytridiomycota OR Batrachochytrium OR Bd OR Bsal)
Frog*	AND	(Extinct OR disease OR fungi OR fungus OR decline OR chytridiomycosis OR chytridiales OR Chytridiomycota OR Batrachochytrium OR Bd OR Bsal)
Toad*	AND	(Extinct OR disease OR fungi OR fungus OR decline OR chytridiomycosis OR chytridiales OR Chytridiomycota OR Batrachochytrium OR Bd OR Bsal)
Salamander*	AND	(Extinct OR disease OR fungi OR fungus OR decline OR chytridiomycosis OR chytridiales OR Chytridiomycota OR Batrachochytrium OR Bd OR Bsal OR ziekte OR schimmel OR schimmelziekte OR uitgestorven)
Caecilian*	AND	(Extinct OR disease OR fungi OR fungus OR decline OR chytridiomycosis OR chytridiales OR Chytridiomycota OR Batrachochytrium OR Bd OR Bsal)
Kikker*	AND	(Bd OR Bsal OR Chytridiomycose OR Batrachochytrium OR chytridiales OR Chytridiomycota OR ziekte OR schimmel OR schimmelziekte OR uitgestorven)
Pad*	AND	(Bd OR Bsal OR Chytridiomycose OR Batrachochytrium OR chytridiales OR Chytridiomycota OR ziekte OR schimmel OR schimmelziekte OR uitgestorven)
Amfibie*	AND	(Bd OR Bsal OR Chytridiomycose OR Batrachochytrium OR chytridiales OR Chytridiomycota OR ziekte OR schimmel OR schimmelziekte OR uitgestorven)

Appendix III. List of sources used to answer research questions

Author(s)	Year	Reviewed for sub question				
		1	2	3	4	5
Ackleh, A. S., Carter, J., Chellamuthu, V. K., & Ma, B.	2016	x				
Alexander, M. A., & Eischeid, J. K. (2001). Climate variability in regions of amphibian declines. *Conservation Biology*, *15*(4), 930-942.	2001	x		x		
BalÁŽ, V., Voeroes, J., CiviŠ, P., Vojar, J., Hettyey, A., Sos, E., ... & Fisher, M. C.	2014		x			
Becker, M. H., Harris, R. N., Minbiole, K. P., Schwantes, C. R., Rollins-Smith, L. A., Reinert, L. K., ... & Gratwicke, B.	2011		x			
Berger, L., Hyatt, A. D., Speare, R., & Longcore, J. E.	2005	x				
Beukema, W., Martel, A., Nguyen, T. T., Goka, K., Schmeller, D. S., Yuan, Z., ... & Loyau, A.	2018	x	x	x		
Blaustein, A. R., Romansic, J. M., Scheessele, E. A., Han, B. A., Pessier, A. P., & Longcore, J. E.	2005				x	
Bolom-Huet, R., Pineda, E., Díaz-Fleischer, F., Muñoz-Alonso, A. L., & Galindo-González, J.	2019		x	x	x	
Bosch, J., Martínez-Solano, I., & García-París, M.	2001	x				
Bozzuto, C., & Canessa, S.	2019	x	x			
Bradley, P. W., Gervasi, S. S., Hua, J., Cothran, R. D., Relyea, R. A., Olson, D. H., & Blaustein, A. R.	2015					x
Brannelly, L. A., Webb, R. J., Hunter, D. A., Clemann, N., Howard, K., Skerratt, L. F., ... & Scheele, B. C.	2018					x
Brem, F. M., & Lips, K. R.	2008					
Briggs, C. J., Knapp, R. A., & Vredenburg, V. T.	2010	x				x
Brutyn, M., D'Herde, K., Dhaenens, M., Van Rooij, P., Verbrugghe, E., Hyatt, A. D., ... & Martel, A.	2012	x				
Bustamante, H. M., Livo, L. J., & Carey, C.	2010		x			x
Clare, F. C., Halder, J. B., Daniel, O., Bielby, J., Semenov, M. A., Jombart, T., ... & Garner, T. W.	2016		x	x		
Coghlan, A.	2013		x			x
Cohen, J. M., Venesky, M. D., Sauer, E. L., Civitello, D. J., McMahon, T. A., Roznik, E. A., & Rohr, J. R.	2017			x		
Creemers, R., & Spitzen, A.	2013	x	x			
Daum, J. M., Davis, L. R., Bigler, L., & Woodhams, D. C.	2012				x	x
DiRenzo, G. V., & Grant, E. H. C.	2019	x				
EFSA Panel on Animal Health and Welfare (AHAW), More, S., Angel Miranda, M., Bicout, D., Bøtner, A., Butterworth, A., ... & Good, M.	2018	x	x			
EFSA Panel on Animal Health and Welfare (AHAW), More, S., Bøtner, A., Butterworth, A., Calistri, P., Depner, K., ... & Bicout, D.	2017		x			x
European Food Safety Authority (EFSA), Balàž, V., Gortázar Schmidt, C., Murray, K., Carnesecchi, E., Garcia, A., ... & Zancanaro, G.	2017	x	x			

Farrer, R. A.	2019	x	x			
Fisher, M. C., Bosch, J., Yin, Z., Stead, D. A., Walker, J., Selway, L., ... & Garner, T. W.	2009	x				
Fisher, M. C., Schmidt, B. R., Henle, K., Schmeller, D. S., Bosch, J., Aanensen, D. M., ... & Garner, T. W. J.	2012		x			
Frías-Alvarez, P., Vredenburg, V. T., Familiar-López, M., Longcore, J. E., González-Bernal, E., Santos-Barrera, G., ... & Parra-Olea, G.	2008		x		x	
Fu, M., & Waldman, B.	2017					x
Garcia, M. J., Rodríguez-Brenes, S., Kobisk, A., Adler, L., Ryan, M. J., Taylor, R. C., & Hunter, K. L.	2019		x		x	x
Garner, T. W., Rowcliffe, J. M., & Fisher, M. C.	2011	x			x	x
Garner, T. W., Walker, S., Bosch, J., Hyatt, A. D., Cunningham, A. A., & Fisher, M. C.	2005		x		x	
Garner, T. W., Walker, S., Bosch, J., Leech, S., Marcus Rowcliffe, J., Cunningham, A. A., & Fisher, M. C.	2009					x
González-Maya, J. F., Belant, J. L., Wyatt, S. A., Schipper, J., Cardenal, J., Corrales, D., ... & Fischer, A.	2013					x
Greenberg, D. A., Palen, W. J., & Mooers, A. Ø.	2017			x		
Greenspan, S. E., Bower, D. S., Webb, R. J., Berger, L., Rudd, D., Schwarzkopf, L., & Alford, R. A.	2017a	x				x
Han, B. A., Kerby, J. L., Searle, C. L., Storfer, A., & Blaustein, A. R.	2015				x	x
Holmes, I., McLaren, K., & Wilson, B.	2014			x		
Hossack, B. R., Russell, R. E., & McCaffery, R.	2020					x
Jacinto-Maldonado, M., García-Peña, G. E., Paredes-León, R., Saucedo, B., Sarmiento-Silva, R. E., García, A., ... & Suzán, G.	2020		x		x	
James, T. Y., Toledo, L. F., Rödder, D., da Silva Leite, D., Belasen, A. M., Betancourt-Román, C. M., ... & Ruggeri, J.	2015	x				
Johnson, M. L., & Speare, R.	2003, 2005	x				
Kilburn, V. L., Ibáñez, R., Sanjur, O., Bermingham, E., Suraci, J. P., & Green, D. M.	2010	x	x	x		
Kilpatrick, A. M., Briggs, C. J., & Daszak, P.	2010	x				
Knapp, R. A., Briggs, C. J., Smith, T. C., & Maurer, J. R.	2011	x		x		x
Kolby, J. E., Ramirez, S. D., Berger, L., Griffin, D. W., Jocque, M., & Skerratt, L. F.	2015	x				
Lam, B. A., Walke, J. B., Vredenburg, V. T., & Harris, R. N.	2010				x	x
La Marca, E., Lips, K. R., Lötters, S., Puschendorf, R., Ibáñez, R., Rueda-Almonacid, J. V., ... & García-Pérez, J. E.	2005			x	x	
Lambertini, C., Becker, C. G., Jenkinson, T. S., Rodriguez, D., da Silva Leite, D., James, T. Y., ... & Toledo, L. F.	2016			x		

Lindauer, A., May, T., Rios-Sotelo, G., Sheets, C., & Voyles, J.	2019	x				
Lips, K. R., Brem, F., Brenes, R., Reeve, J. D., Alford, R. A., Voyles, J., ... & Collins, J. P.	2006		x		x	x
Longo, A. V., & Burrowes, P. A.	2010					x
Marquis, O., Miaud, C., Gibault, C., & Chai, N.	2019					
Martel, A., Spitzen-van der Sluijs, A., Blooi, M., Bert, W., Ducatelle, R., Fisher, M. C., ... & Pasmans, F.	2013		x		x	
McCaffery, R., Richards-Zawacki, C. L., & Lips, K. R.	2015		x			x
Medina, D., Hughey, M. C., Walke, J. B., Becker, M. H., Pontarelli, K., Sun, S., ... & Belden, L. K.	2019					x
Mendoza-Almeralla, C., López-Velázquez, A., Longo, A. V., & Parra-Olea, G.	2016	x	x			
Miaud, C., Dejean, T., Savard, K., Millery-Vigues, A., Valentini, A., Gaudin, N. C. G., & Garner, T. W.	2016	x				
Milius, S.	2014		x			x
Muletz-Wolz, C. R., Barnett, S. E., DiRenzo, G. V., Zamudio, K. R., Toledo, L. F., James, T. Y., & Lips, K. R.	2019	x				
Muletz-Wolz, C. R., Fleischer, R. C., & Lips, K. R.	2019					x
Murray, K. A., Skerratt, L. F., Speare, R., & McCallum, H.	2009		x		x	x
Murrieta-Galindo, R., Parra-Olea, G., González-Romero, A., López-Barrera, F., & Vredenburg, V. T.	2014		x	x	x	
Mutschmann, F.	2015	x				
Nava-González, B. A., Suazo-Ortuño, I., Parra-Olea, G., López-Toledo, L., & Alvarado-Díaz, J.	2019		x	x	x	x
Oevermann, A., Robert, N.	2004	x				
Ohst, T., Gräser, Y., Mutschmann, F., & Plötner, J.	2011		x			
Olson, D. H., Aanensen, D. M., Ronnenberg, K. L., Powell, C. I., Walker, S. F., Bielby, J., ... & Fisher, M. C.	2013					x
Parrott, J. C., Shepack, A., Burkart, D., LaBumbard, B., Scimè, P., Baruch, E., & Catenazzi, A.	2017		x	x		
Pasmans, F., Muijsers, M., Maes, S., Van Rooij, P., Brutyn, M., Ducatelle, R., ... & Martel, A.	2010		x			x
Pasmans, F., Van Rooij, P., Blooi, M., Tessa, G., Bogaerts, S., Sotgiu, G., ... & Beukema, W.	2013				x	x
Perez, R., Richards-Zawacki, C., Krohn, A. R., Robak, M., Griffith, E. J., Ross, H., ... & Voyles, J.	2014					x
Pessier, A. P.	2002, 2014	x				
Puschendorf, R., Bolaños, F., & Chaves, G.	2006a		x		x	x
Puschendorf, R., Carnaval, A. C., VanDerWal, J., Zumbado-Ulate, H., Chaves, G., Bolaños, F., & Alford, R. A.	2009		x	x	x	
Puschendorf, R., Castaneda, F., & McCranie, J. R.	2006b		x		x	x
Rollins-Smith, L. A.	2009					x
Rollins-Smith, L. A.	2017					x
Rollins-Smith, L. A., & Conlon, J. M.	2005					x

Rollins-Smith, L. A., Carey, C., Longcore, J., Doersam, J. K., Boutte, A., Bruzgal, J. E., & Conlon, J. M.	2002				x	
Ron, S. R.	2005			x		
Ruggeri, J., Toledo, L. F., & de Carvalho-e-Silva, S. P.	2018					x
Rumschlag, S. L., Boone, M. D., & Fellers, G.	2014	x		x		x
Russell, R. E., Halstead, B. J., Mosher, B. A., Muths, E., Adams, M. J., Grant, E. H., ... & Honeycutt, R. K.	2019					x
Ryan, M. J., Lips, K. R., & Eichholz, M. W.	2008		x		x	x
Sauer, E. L., Cohen, J. M., Lajeunesse, M. J., McMahon, T. A., Civitello, D. J., Knutie, S. A., ... & Delius, B. K.	2019					x
Sauer, E. L., Cohen, J. M., Lajeunesse, M. J., McMahon, T. A., Civitello, D. J., Knutie, S. A., ... & Delius, B. K.	2020				x	x
Savage, A. E., Becker, C. G., & Zamudio, K. R.	2015					x
Scheele, B. C., Driscoll, D. A., Fischer, J., Fletcher, A. W., Hanspach, J., Vörös, J., & Hartel, T.	2015			x		
Scheele, B. C., Foster, C. N., Hunter, D. A., Lindenmayer, D. B., Schmidt, B. R., & Heard, G. W.	2019			x		
Scheele, B. C., Guarino, F., Osborne, W., Hunter, D. A., Skerratt, L. F., & Driscoll, D. A.	2014				x	x
Scheele, B. C., Hunter, D. A., Skerratt, L. F., Brannelly, L. A., & Driscoll, D. A.	2015	x		x	x	x
Schmeller, D. S., Blooi, M., Martel, A., Garner, T. W., Fisher, M. C., Azemar, F., ... & Loyau, A.	2014					
Silva, S., Matz, L., Elmassry, M. M., & San Francisco, M. J.	2019	x				
Sonn, J. M., Berman, S., & Richards-Zawacki, C. L.	2017	x				x
Spangler, M.	2015		x			
Spitzen, A.	No date	x				
Spitzen-van der Sluijs, A., Martel, A. N., Hallmann, C. A., Bosman, W., Garner, T. W., Van Rooij, P., ... & Pasmans, F.	2014			x		
Stegen, G., Pasmans, F., Schmidt, B. R., Rouffaer, L. O., Van Praet, S., Schaub, M., ... & Haesebrouck, F.	2017	x	x			x
Stockwell, M. P., Clulow, J., & Mahony, M. J.	2010	x				x
Stockwell, M. P., Clulow, J., & Mahony, M. J.	2015			x		
Sztatecsny, M., & Glaser, F.	2011		x			
Van Kessel, A.	2012	x				
Van Rooij, P., Martel, A., Haesebrouck, F., & Pasmans, F.	2015	x				x
Velo-Antón, G., Rodríguez, D., Savage, A. E., Parra-Olea, G., Lips, K. R., & Zamudio, K. R.	2012		x			
Venesky, M. D., Raffel, T. R., McMahon, T. A., & Rohr, J. R.	2014					x
Voyles, J.	2011	x				x
Voyles, J., Johnson, L. R., Briggs, C. J., Cashins, S. D., Alford, R. A., Berger, L., ... & Rosenblum, E. B.	2012	x				

Voyles, J., Johnson, L. R., Rohr, J., Kelly, R., Barron, C., Miller, D., ... & Rosenblum, E. B.	2017	x				
Voyles, J., Rosenblum, E. B., & Berger, L.	2011	x				x
Voyles, J., Young, S., Berger, L., Campbell, C., Voyles, W. F., Dinudom, A., ... & Speare, R.	2009	x				x
Vredenburg, V. T., Knapp, R. A., Tunstall, T. S., & Briggs, C. J.	2010	x				x
Whitfield, S. M., Kerby, J., Gentry, L. R., & Donnelly, M. A.	2012		x	x	x	x
Wilber, M. Q., Knapp, R. A., Toothman, M., & Briggs, C. J.	2017			x		x
Woodhams, D. C., Barnhart, K. L., Bletz, M. C., Campos, A. J., Ganem, S. J., Hertz, A., ... & Tokash-Peters, A. G.	2001	x		x		
Woodhams, D. C., Bosch, J., Briggs, C. J., Cashins, S., Davis, L. R., Lauer, A., ... & Voyles, J.	2011					x
Woodhams, D. C., Kilburn, V. L., Reinert, L. K., Voyles, J., Medina, D., Ibánez, R., ... & Rollins-Smith, L. A.	2008		x		x	
Zumbado-Ulate, H., Bolanos, F., Gutiérrez-Espeleta, G., & Puschendorf, R.	2014		x	x	x	
Zumbado-Ulate, H., García-Rodríguez, A., Vredenburg, V. T., & Searle, C.	2019		x	x	x	x