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The current state of research on the global amphibian epidemic, chytridiomycosis: A systematic literature review and view into the future of the field

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ABSTRACT

Recent years have shown a rapid decline in global frog populations. Among other issues, one main cause of these declines has been linked to chytridiomycosis, a disease caused by the fungus *Batrachochytrium dendrobatidis,* or *Bd*. The discovery of this fungus is relatively recent in the field of herpetology, and thus there is much still unknown about the disease such as its distribution and what causes certain areas and species to be more susceptible to it. A systematic literature review was conducted to see where the state of the research is currently, in order to gain a better view of the possibilities for future management of the disease. This paper reviewed the research that has been done so far, taking note of geographical ranges studied, species studied, age of individuals studied, and methodology of studies, including ethical considerations. Gaps in the research include effective mitigation methods to be used *in situ,* leading to a suggestion for potential future research in this realm.

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INTRODUCTION

Worldwide, biodiversity has been greatly impacted by a variety of factors, often coming from anthropogenic influences. Loss of biodiversity is a critical topic, as the Earths biosphere is seemingly approaching a sixth mass extinction, as extinction rates continue to reach higher and higher levels (Blaustein et. al., 2018). These losses have been seen over all kingdoms of the biosphere, however, amphibians have become key indicators for the health of ecosystems, as they are highly susceptible to environmental change (Rooij et. al., 2015). With porous skin, amphibians are very easily affected by changes to their ideal ecosystem. One threat that has been identified as a key cause of the decline of amphibians are emerging infectious diseases.

The discovery of *Batrachochytrium dendrobatidis*, or *Bd,* has shed light on many of the intense negative trends in amphibian populations seen over all continents where amphibians are found. Since its discovery in the 1980s, *Bd* is now known to be the fungus that causes chytridiomycosis, a disease that affects the production of keratin in frogs' skin, leading to loss of ability to breath properly through the newly less porous skin (Berger et. al., 2016). Chytrid has also been known to cause defects in affected tadpoles' mouths, but usually not enough to cause death (Sauer et. al., 2020). Chytridiomycosis can lead to death of individuals, usually adults and metamorphs, and great loss of populations in some areas, and thus eventual extinction.

Since its original identification, chytridiomycosis has been linked to the decline of 200 frog species globally and has influenced at least 350 species (Fisher et. al., 2009). With shockingly high numbers like these that are only continuing to grow, research on this novel infectious disease within the amphibian world is crucial to prevent further extinction.

Previous research on chytrid fungus has identified that, the effectiveness of the fungus is highly determined by temperature and precipitation of the environment, limiting it to cooler areas such as temperate and montane biomes, as the general consensus has found its ideal temperature range to be 17−25°C (Cohen et. al., 2017). *Bd* is also restricted to mainly wet areas, as its life history includes an infectious aquatic zoospore stage, making water necessary in order to infect its host (Ruggeri et. al., 2018). This has made stream breeding amphibians most commonly affected and studied in research of the disease.

Much about the distribution of *Bd* globally as well as what environmental and immunological factors make certain areas or species more susceptible to the disease, or potentially more resistant to the disease than other species is unknown to date. This information is important as it will lead to better understanding of the pathology of the disease and thus lead to more efficient methods of management of the spread of chytridiomycosis among amphibian populations. This systematic literature review focused on the research that has been done of chytridiomycosis in the past by looking at the distribution of *Bd* globally and within countries, as well as the research done on environmental susceptibility to the disease and individual frogs' differences in susceptibility to the disease. Over 1,000 abstracts were reviewed for relevancy to the literature review topic, and a total of 159 papers were chosen as relevant studies to the review. It is important to take note of the research that has been done in the past in order to identify where gaps may lie in the research field. This can then help scientists to work to bridge these gaps, leading to deeper understanding of the devastating disease of chytridiomycosis, and possibly control the spread of *Bd* through various methods found possibly effective in practice so far. Additionally, this review looks at an emerging topic in the field of chytrid disease research and possible mitigation strategies.

METHODS

2.1 Methodology

This systematic literature review was conducted using Web of Science as search parameters. A number of searches were done using variations of predetermined key words in various forms, using Boolean notations for more effective searching practices. Key words used included: “frog”, “amphibian”, “distribution”, “chytrid”, “Bd”, “*Batrachochytrium dendrobatidis”,* and “global”, in various combinations in order to maximize search result relevancy to the literature review topic. From these searches, a total of 1,159 papers were reviewed by reading their titles first, then reading their abstracts. Relevant papers were then exported to EndNote for organizational purposes. A total of 476 papers were deemed relevant. Due to time constraints, the number of papers to be reviewed was dropped down to 124, prioritizing highly cited studies, and by determining which studies used results found in other relevant papers in their own analysis. Utilizing EndNote software, relevant references were then grouped for analysis based on the locations of the study, the species studied, and other parameters discussed in this review. Papers were reviewed for overall focus and results.

2.2 Searches

<u>Search 1:</u> ecological threats AND frogs

97 results, 80 relevant

<u>Search 2:</u> Chytrid* AND Bd AND *Batrachochytrium dendrobatidis* AND Frogs

515 results, 210 relevant

<u>Search 3:</u> Chytrid* AND Bd AND *Batrachochytrium dendrobatidis* AND Global

214 results, 37 relevant

Search 4: Chytrid* AND Bd AND *Batrachochytrium dendrobatidis* AND distribution

137 results, 73 relevant

Search 5: Suscept* AND chytrid* AND Bd AND *Batrachochytrium dendrobatidis*

196 results, 76 relevant

2.3 Search Results

See Appendix 1 for a complete list of studies used in this Literature Review.

RESULTS

3.1 General Findings

3.1.1 Optimal thermal range

There is a general consensus in the literature that *Bd* has an optimal thermal range in which it is most often found in nature. This temperature is a relatively cool range of 17-25 °C (Cohen et. al., 2017), leading to *Bd* to be most often found in temperate or montane regions (Flechas et. al., 2017). This leaves some amphibian species more susceptible to *Bd* simply due to environmental factors. Frogs that inhabit cooler areas, such as temperate or montane areas, have been found to be more likely to be affected by the disease, as it is more prevalent in these areas. Additionally, some focus has been made in the literature on the microhabitats that frogs often inhabit during different parts of the day. Some species, such as *Eleutherodactylus coqui*, will nocturnally live in trees, where there are slightly warmer temperatures and lower humidity, making them less susceptible to chytrid than those that sleep on the forest floor (Burrowes et. al., 2017). However, not much research has been done in this area, leading to a gap in the knowledge within the field.

3.1.2 Association with water

Another factor that is highlighted in the research done is that chytrid is highly associated with high precipitation rates and consistent water supply, due to their motile aquatic zoospore stage. This fact has put stream breeding frogs at higher risk for becoming in contact with *Bd* thus making them more susceptible (Kriger et. al., 2007). One study done in California by Briggs *et. al.* (2010) found that populations of stream breeding frogs such as *Rana muscosa and Rana sierra* will be more highly affected by *Bd* when the population is dense and when the water is still, allowing for *Bd* load to increase at a much higher rate due to continual reinfection.

3.1.3 Snout Vent Length

Thirdly, chytrid disease has been found to be negatively correlated with individuals body size. In the literature, size is often equivalated with snout vent length (SVL), and studies has shown that there is an association between presence of *Bd* on an individual and having shorter than average SVL. One study by Kriger *et. al.* (2007) found that SVL was actually a consistently better predictor of the presence of *Bd* infection and the resulting intensity of the infection than climatic variables such as temperature or precipitation, though these variables are also still good indicators. There is debate as to whether this correlation is because smaller or younger individuals are more susceptible to infection by the fungus, or if infection leads to slower growth rates of individuals, meaning that those that are infected at the juvenile stage will be smaller in their adult stage. One study done by Lamirande and Nichols (2002) found a higher resistance to chytridiomycosis with increasing age and size of individuals. Another study by Parris and

Cornelius (2004) argues the opposite hypothesis, stating that chytrid disease causes stress on developmental processes in individuals, leading to a smaller SVL.

3.2 Study Site

Batrachochytrium dendrobatidis has been linked to the decline of amphibian species populations on a global scale. The sampling of studies used in this systematic literature review are indicative of this fact, as studies have been done in all continents but one, and a great variety of areas have been studied within each continent. No studies reviewed were done in Antarctica, as there are not any amphibians found in Antarctica, and chytrid has not yet been found in Antarctica (Fisher et. al., 2009). However, there has definitely been bias in the literature towards certain areas over others, as can be seen in the data collected through this review. The highest number of studies were done in North America, with a total of 33 of the reviewed studies taking place in either Canada, the United States, Mexico, Cuba, or Central America. The majority of these studies were done in California in the US. The second highest was Australia/New Zealand, with 25 studies being done there. The third highest was South America, with 12 studies being done in 7 countries, including Argentina, Brazil, Chile, Colombia, Peru, Uruguay, and Venezuela (Figure 1). The continents with high numbers of studies all contain biodiversity hotspots, such as the Amazon rainforest in South America, and the Wet Tropics Bioregion in Australia, making them more likely to be affected by an amphibian epidemic. High levels of biodiversity means higher levels of species to be negatively influenced by disease. All other studies in this review not included in this counting took a global approach to their study by using previously collected data resources or were also a literature review.

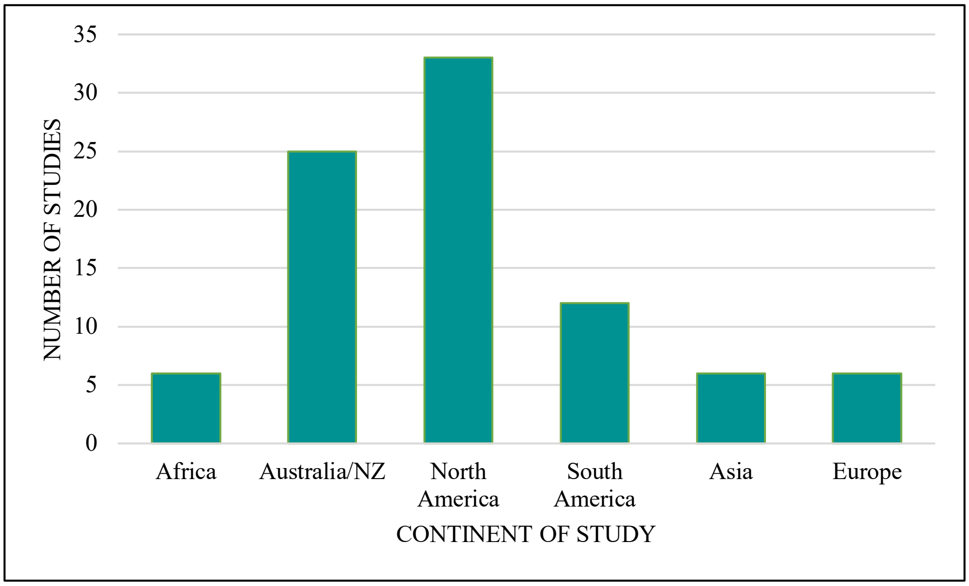

Figure 1: The number of studies on *Bd* separated by geographic location

3.3 Species studied

There is great variety seen in the species selected by researchers to study the effects and distribution of *Bd.* Species selected varied among each continent, as different frogs are native to different ecosystems. Within studies done in Australia, a total of 24 different species were used among 17 studies. The remaining studies in the Australia group were reviews, looking at data collected from previous studies in order to create a broader understanding of the literature so far. These reviews utilize data on multiple species, for example, one utilized previously collected data from 213 species (Hero et. al., 2004). Of the species used in studies done in Australia, 13 were of the genus *Litoria*. The remaining studies each had a focus on a different genus, including *Crinia, Hyla, Limnodynastes, Mixophyes, Pseudophyrne, Rhinella, Adelotus, Uperoleia,* and *Assa*. The genus *Litoria* is under the family *Pelodryadidae*, which includes mainly tree frogs found in Australia and New Guinea. These frogs are usually stream breeders making them a good choice of study in chytridiomycosis research (Mattison, 2011) Genus *Litoria* includes over 150 different species of frogs, all native to Australasia. This genus not only contained the largest number of species studied, but was also most highly represented across the literature, appearing in 8 of the 20 Australian papers reviewed. All other genera were less highly represented, appearing only once or twice with one or two species within each genus being studied (Figure 2).

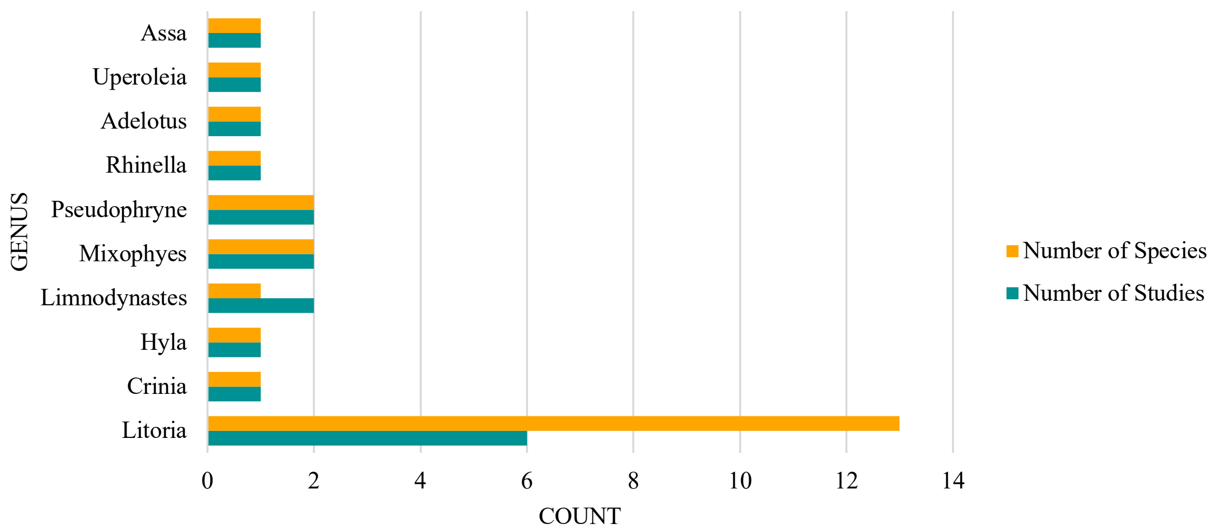

Figure 2: The distribution of genera of frogs studied in Australian studies of chytridiomycosis

3.4 Number of species studied

Throughout the literature, there is a large range in the number of species studied. Some papers took a larger scope approach by reviewing previously collected data, such as a 2015 paper done by James et. al., which overviewed the research that has been done since the discovery of chytridiomycosis and utilized previous studies in order to map its range in terms of environmental suitability, as well as the evolution of the *Bd* fungus and other commonly researched factors. Studies such as these use an innumerable amount of species in their analysis, as they are on such a large scale. A total of 6 papers took a global scale or review approach to their study. Most of the research done chose to perform studies by collecting samples from *in situ* or raising *in vitro* one to a few species. Within studies done in Australia, 11 of the 16 studies chose only one species to focus on. Studies such as these most commonly used swabbing methods *in situ*, targeting one species while surveying in the field. The remaining studies took samples from 2 or 3 species, or were a review, taking data from previous research, leading to a higher number of species studied.

3.5 Ages of individuals studied

Amphibians have a unique life history in that it includes a larval stage, metamorphic/juvenile stage, and adult stage, post metamorphosis (Waddle et. al., 2019). Within studies done on the presence of chytridiomycosis within amphibian communities, studies have focused on a variety of ages, depending on the goal of the study. Some studies collected eggs from the field and then raised them in a laboratory setting in order to be inoculated with *Bd* once they were adults. Utilizing this method allows for control of the husbandry of each individual, reducing secondary variables that could affect the results of the study. It has been found that tadpoles affected by chytrid fungus are less likely to die of the disease but will be affected in their growth in later stages of life (Waddle et. al., 2019). When tadpoles are affected by chytrid disease, there are visual deformities in their mouth parts, making them recognizable (Kadekaru et. al., 2017). Studies on the differences in susceptibility at each stage of life have shown that premetamorphs are the most likely to be severely affected by the disease and more likely to experience mortality (Sauer et al., no date).

Other studies chose to only take samples from adult individuals. Adults are more likely to be found in breeding areas, where a high percentage of chytridiomycosis cases are begun. Chytrid disease has been linked to stream breeding amphibian species due to its high correlation with permanently wet areas. Because of this, it makes sense for researchers to select adult individuals, as they are of reproductive age and are more likely to be found in these breeding streams.

Of the studies done in Australia, 11 chose to only select adult individuals. The remaining studies focused on juveniles or took samplings all throughout the life of each individual by raising them in lab setting.

3.6 Sampling methods

There is variation seen in terms of methodology chosen to sample individual amphibians for presence of chytrid. The two main methods used in the literature are swabbing and histological sampling. There is also a mixture in the literature between use of *in vitro* vs *in situ* sampling for chytrid fungus.

3.6.1 Histology vs. swabbing

Histology involves taking a tissue sample from the individual and then running diagnostic tests to determine in *Bd* is present or not (Kriger et. al., 2006). This method is much less favorable and less used in the field (Figure 3). The much more common method of sampling, used in 10 of the 17 of the studies, is swabbing. This method involves performing multiple swipes across various surfaces of the individual frogs' skin, using a sterile swab for each new swipe. For example, a study done in Australia describes swabbing multiple areas of each individual multiple times. Each individual was swabbed on their side from groin to armpit, the undersides of feet and thighs, and the ventral surface, eventually adding up to a total of 70 strokes (Kriger et. al., 2007). These swabs are then used to extract DNA of the fungus and processed through a TaqMan real time PCR assay to determine if it is present in the skin. Studies have shown that swabbing is the more effective method of identifying the presence of *Bd* on an individuals' skin, and additionally is more humane as it does not require euthanasia or the mutilation of any individuals.

3.6.2 in situ vs. in vitro

Another difference seen between studies was the choice of either utilizing an *in situ* or *in vitro* method of sampling for presence of *Bd* and other elements. Some studies chose to sample individuals found directly in the field, such as one done in Venezuela, in which sampled a critically endangered toad, *Atelopus cruciger*, by observing population dynamics between the toad and *Bd* fungus. The methodology of this study included mark and recapture of individuals and swabbing each one for *Bd* zoospores to then be further analyzed in a laboratory setting (Lampo et. al., 2017).

Other studies collected individuals or larvae to be reared in a laboratory setting and then inoculated with *Bd,* most often to test for variations in susceptibility. A study of how individual's size affects their susceptibility to chytrid utilized this method, collecting *Anaxyrus americanus* egg masses and then raised the toads through metamorphosis until the start of the experiment (Burrow et. al., 2016). Individuals were then given *Bd* treatments in a controlled setting.

Other studies utilized *in vitro* methods to avoid unnecessary infection of any frogs in the study. One study from California focusing on how temperature fluctuations affects *Bd* in terms of the virulence of the fungus (Linduaer et. al., 2020). This experimentation required a controlled laboratory environment in order to control these temperature fluctuations. They sampled daily temperatures found at a toad breeding pool in Yosemite and then grew *Bd* cultures at these fluctuating temperatures and compared them to cultures grown at a constant temperature. Within studies done in Australia, a majority used an *in situ* sampling method, and utilized swabbing over histological analysis (Figure 3).

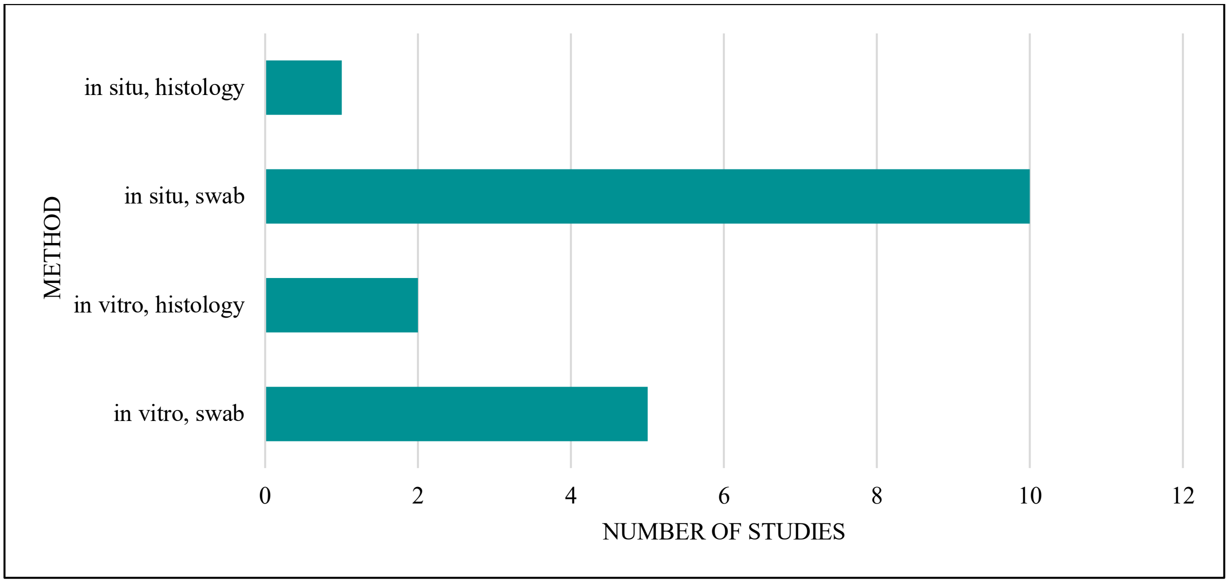

Figure 3: Number of Australian studies of *Bd* utilizing each sampling method described.

4. DISCUSSION

4.1 Emerging topics

Among the literature, there are some new focuses that have emerged in the field of chytridiomycosis research. One new theme seen in recent literature is microhabitats and their possible role in aiding amphibians at risk for chytridiomycosis. Microhabitats are small regions within a larger habitat area in which individuals will perform much of their daily routine in, including where they eat, reproduce, and rest (Burrowes et al., 2017). Microhabitats may have different abiotic characteristics than the general ecosystem they are a part of, such as temperature or amount of moisture, which leads to variation in *Bd*'s pathogenicity and the hosts susceptibility to the fungus within the microhabitat. It has been seen that *Bd*'s success in an environment is highly dependent on being within its optimal thermal range of 17-25 °C (Altman et. al., 2019) and having enough water for its zoospores to be motile and spread among a population(Ruggeri et. al., 2018). This has led to a focus in the literature on stream breeding frog species (Kriger et. al., 2007). However, there is a subsect of species that breed out of the water, called direct-developers, and do not have a tadpole stage, (Longo et. al., 2010). These individuals are usually less susceptible to chytrid disease as they spend more time in microhabitats unsuitable for *Bd*, however, there are some species found to be affected by the disease.

One study done in Puerto Rico conducted a study on *Eleutherodactylus coqui,* a frog that utilizes multiple microhabitats, none of which are in a body of water (Burrowes et al., 2017). The study observes differences in susceptibility to *Bd* through differences in levels of infection intensity among microhabitats inhabited by individuals. The results of the study found variation in prevalence of chytrid fungus zoospores among different microhabitats, leading to differences in susceptibility among individuals that spend time in each microhabitat. Arboreal microhabitats, mostly including tree trunks where adult males would call for mates, were found to have lower amounts of *Bd* zoospores. This is attributed to the warmer temperatures and lower moisture levels found higher up in the canopy. Juveniles were found to spend more time in forest floor microhabitats, possibly due to inability to climb up into arboreal habitats, where it is much cooler and wetter, making them more susceptible to a higher *Bd* load.

Another study took this same idea of microhabitats and proposes that this emerging focus could lead to possible remediation of the chytrid epidemic (Hettyey et. al., 2019). Previous studies on management of the disease have found remedies that must be done in a controlled laboratory setting (Woodhams et al., 2011). Some possible methodology includes utilizing antifungals, microscopic aquatic predators of *Bd* zoospores, and elevating ecosystem temperatures, however these methods are difficult to rationalize using in a field setting, as they could cause damage to the natural ecosystem. Hettyey et. al. looks to relieve populations *in situ* in a more effective and less invasive way*,* leading to reliable remediation. Taking advantage of microhabitats with higher temperatures that already exist in the environment could allow for individuals to avoid the fungus. This study suggests that utilizing the difference between the critical thermal maximum of *Bd* zoospores and that of warm adapted frog species could lead to effective *in situ* remediation of chytridiomycosis. Rather than altering the entire environment of these species by decreasing canopy cover in order to raise temperatures in breeding pools or other lowland areas, they suggest that making microhabitats with warmer temperatures will be enough to reduce *Bd* load in individuals, given enough exposure to these warm areas. Warm adapted species will seek after these warm microhabitats as amphibians are ectotherms.

Research into microhabitats and their possible use in aiding in the current amphibian decline crisis that is occurring globally could lead to new methodology in mitigating the disease. Studies like these bring new ideas to light that have not been thoroughly investigated in the literature so far.

4.2 Ethics

An important consideration of any environmental research is the possible outcomes an experiment can have on individuals or their ecosystem. Within the field of chytridiomycosis research, there are considerations to be taken in not only experimentation but also possible mitigation strategies for the disease.

As previously discussed, ethical considerations are important in experiments. The use of more ethical techniques such as swabbing for *Bd* presence and prevalence rather than euthanasia and histological techniques has been studied and noted for its more humane nature. One study compared these two methods and found swabbing to be more effective at producing reliable results than histology as well (Kriger et al., 2006). The development of the real-time TaqMan

PCR assay for histological techniques was seemingly beneficial to the field, allowing for quantitative detection of zoospores from toe clips. However, this methodology requires a toe clip, which has been found to reduce survivorship in individual frogs, thus decreasing its ethical value. Swabbing frogs with sterile cotton swabs has not been linked to any further effects on the individual upon release, making it a much safer and ethical choice in practice. This method is effective as chytridiomycosis effects the skin of the frogs, thus taking sampling from areas other than the skin is unnecessary. The study by Kriger et. al. (2006) proves this point as well as the fact that swabbing is actually more effective at gathering quantitative data on zoospore load on individuals.

Another issue of ethics that must be considered in the field of chytrid disease is the possibilities of disease management. One review of developing mitigation strategies for chytridiomycosis discusses the main approaches that have been identified in the literature (Woodhams et. al., 2010). These actions include treatment and release, pond treatment with fungicides or drying, and biocontrol. With all of these methods comes consideration for the possible threats to the organisms and study area. For example, the use of fungicides could be found effective in a laboratory setting, however, these fungicides may have unintended impacts on the ecosystem should they be used *in situ*. Fungi other than *Bd* play important roles in pond ecology, as decomposers and primary producers (Woodhams et. al., 2011), and their elimination will inevitably have downstream effects. Treatment and release programs have found some success in previous experimentation with tadpoles, as they have been found to survive through metamorphosis (Bosch et. al., 2001). However, the consideration that individuals may become re-infected upon release or that *Bd* may become resistant to treatment prevents this type of mitigation from being used on a large scale. It is however, promising that studies such as these are happening, broadening the possibility of eventual large scale remediation of chytrid disease in global amphibian populations.

4.3 Australia vs the rest of the world

Looking at the progress made in the field of chytridiomycosis research, it seems that research has been well spread throughout the world. As seen in the results, research has been done on all continents, save Antarctica, as there are no frogs found there. While a majority of studies were done in North America, these studies are spread across multiple countries. Australia has had a large focus on the disease due to the high number of endemic amphibian species found there. One review of Australian frog declines noted that 55 of 213 frog species studied are recognized as threatened, no longer found in nature, or completely gone from their historical range (Hero et. al., 2004). A total of 18.8% of frogs were listed as endangered at the time of this study, in 2004. Today these numbers are increasing still, especially with the bush fires that occurred in late 2019 to early 2020. These fires caused further damage to habitats of frogs already declining due to chytrid, such as the corroboree frog in the Australian alps, a cool environment prime for *Bd* growth (Scheel et. al., 2019). These high rates of population decline put Australia at a higher level than most other countries, which in 2004 was 10% of species being threatened.

Globally, there is stress put on tropical areas as they contain high levels of biodiversity. This is a good thing for Australia, as it contains the Wet Tropics Bioregion and other highly diverse ecosystems. This does also mean that other countries see similarly intense declines in a great number of frog population sizes as well, such as Japan, Venezuela, and other hot spots for biodiversity. Numbers such as these are shocking, creating a high pressure on Australian scientists to work rapidly towards a solution.

CONCLUSION

This systematic literature review took a closer look into the current crisis within the world of amphibians that a new emerging disease, chytridiomycosis, has caused since its discovery. This disease, caused by the fungus *Batrachochytrium dendrobatidis,* has influenced more than 350 species and has led to the decline of at least 200 species of frogs, as far as is known today. Due to its relatively recent discovery, there is much unknown about the disease and how it comes to be so lethal and fast moving in its hosts, however, this review has brought to light some main points seen in the literature of chytridiomycosis research today.

Chytrid has been highly linked to its optimal thermal range of 17-25 °C. This range has made *Bd* limited in its growth abilities outside of this range, thus it is primarily found in temperate and montane regions or lowland areas of tropical regions. Chytrid disease is also highly associated with persistently wet environments as their zoospores have an aquatic phase, necessitating a consistent source of water in order to continue spreading. In terms of age distribution, *Bd* most remarkably affects juveniles, decreasing their overall growth and eventually causing death. Tadpoles are now known to be able to live through metamorphosis with the disease, but it will cause deformities in their mouth parts and likely have later affects on their growth and development.

Research in the field has taken form in various ways, with various focuses. Most studies have been researching the distribution of the fungus, what causes differences in susceptibility of individuals, or the susceptibility of the environment to high levels of *Bd* growth. The literature shows that susceptibility of the individual is highly dependent on their environment. *In vitro* experimentation has been successful in finding possible mitigation strategies for infected individuals, however most of these strategies have not been approved for use in the field, due to possible downstream effects on the environment or frog individuals. New emerging ideas include the use of natural microhabitats in order to reduce the impact of *Bd* prevalence in an area, monopolizing on the small areas of higher temperatures and less water to rid individuals of their current *Bd* load. The results of this literature review emphasize the importance of continuing the research in the field in order to develop new mitigation ideas that can be effectively implemented *in situ*. Gaps in the research seem to mostly be in the area of managing the disease, and as frog populations continue to decline at the rapid rates they currently are, it is critical that action is taken quickly.

APPENDIX 1: Complete List of all Sources in Systematic Literature Review

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