



## Review Paper

## Towards a food web based control strategy to mitigate an amphibian panzootic in agricultural landscapes



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## ABSTRACT

While the emerging amphibian disease chytridiomycosis is causing dramatic and ongoing biodiversity losses worldwide, sustainable strategies to mitigate this global threat to amphibians are currently missing. We here propose a conceptual framework for a novel biological mitigation strategy based on the increasing evidence that naturally occurring micropredators, such as protists, rotifers and crustaceans, are capable of using zoospores of the chytrid pathogens *Batrachochytrium dendrobatidis* (Bd) and *Batrachochytrium salamandrivorans* (Bsal) as a food source under controlled laboratory conditions. Pathogen predation may serve as a cost-efficient way to prevent chytridiomycosis outbreaks under natural conditions by reducing zoospore densities and thereby infection loads. This predator-pathogen relationship is not an isolated interaction, but is embedded in the aquatic food web structure that interacts with a wide range of environmental factors. Amphibian breeding ponds are increasingly associated to agricultural landscapes due to ongoing land use occupancy for food production, exposing these water bodies to a variety of environmental stressors such as agrochemical pollution, nutrient enrichment and cattle trampling. Environmental stressors may affect the composition and abundance of aquatic communities, while they can also exert sublethal effects that may reduce the zoospore removal efficiency of micropredators. By carefully controlling environmental stressors, trophic interactions may be steered to optimize chytrid predation with the aim of reducing zoospore densities to such extent that hosts and pathogens can sustainably coexist. We present a scientific outline of this novel concept and provide a framework for ongoing research to develop a complete mitigation strategy against chytridiomycosis based on such food web control.

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## 1. Introduction

Environmental pressures such as overexploitation of species, introduction of invasive alien species, pollution, climate change, habitat degradation and spread of diseases are causing dramatic biodiversity losses worldwide (Rands et al., 2010). Since amphibians are declining more rapidly than any other group of vertebrates, they are generally considered as a key indicator for the environmental health status of an ecosystem (Wake and Vredenburg, 2008). The emerging disease chytridiomycosis, caused by the chytrid pathogen *Batrachochytrium dendrobatidis* (*Bd*), is affecting species of all three orders of amphibians (Anura, Urodela and Gymnophiona) and is threatening worldwide biodiversity by ongoing declines and extirpations of amphibian populations. Its sister species, *Batrachochytrium salamandrivorans* (*Bsal*), causes salamander population declines across Europe (Martel et al., 2013, 2020; Spitzen-van der Sluijs et al., 2016). These amphibian chytrid fungi have contributed to the decline of at least 501 amphibian species over the last 50 years, including 90 presumed extinctions (Scheele et al., 2019). Control strategies to prevent chytridiomycosis-driven biodiversity losses are mainly focusing on biosecurity to prevent the introduction of the pathogens into naïve amphibian populations (Roy et al., 2017) or on small scale management actions such as fungicide treatment (Bosch et al., 2015; Hudson et al., 2016), bioaugmentation experiments with antifungal microbiota (Bletz et al., 2013; Rebollar et al., 2016) and reintroduction programs (Brannelly et al., 2016). However, these strategies were only partially successful and amphibian species that are not susceptible to chytridiomycosis can serve as a reservoir for the pathogen, compromising reintroduction efforts for lost species and posing a continuous risk for further dispersal of the pathogen (Lips et al., 2006). Structural mitigation strategies that are long-term effective and widely applicable are currently missing. Considering the latter aspect, these strategies need to be environmentally responsible, cost-effective and easily applicable in a wide range of habitats.

Free living stages of pathogens also serve as prey within food webs, and such predator-pathogen interaction may have implications for the outcome of wildlife diseases (Johnson et al., 2010; Frenken et al., 2019). While research on the relevance of this interaction for tempering wildlife diseases is currently rare or even missing, this is not the case for human infectious diseases. Martínez Pérez et al. (2004) and Schallenberg et al. (2005) showed a significant reduction of the human-pathogenic bacteria *Vibrio Cholerae* and *Campylobacter jejuni* through grazing by a protozoan and cladocerans, respectively, in simulated natural conditions. Food web biomanipulation could thereby enhance *Daphnia* abundance and consequently reduce pathogen density and the risk of contracting waterborne diseases (Schallenberg et al., 2005). Stimulating copepod predation, among other predators, on aquatic vectors of mosquito borne viruses has been proved to be an effective control strategy for human diseases such as dengue fever, malaria and chikungunya (Nam et al., 1998, 2012; Moore et al., 2010; Baldacchino et al., 2015). Weterings et al. (2018) showed the importance of *Aedes* predation and the interaction of landscape, abiotic and biotic factors with the complex food web structures of the terrestrial and aquatic life stages of the mosquito to control dengue fever.

Members of the zooplankton community have been shown to be capable of reducing *Bd* zoospore densities in lab conditions (Buck et al., 2011; Hamilton et al., 2012a; Searle et al., 2013; Schmeller et al., 2014; Blooi et al., 2017). In a natural situation, however, this predator-pathogen interaction is embedded in the aquatic food web structure and its complex interplay with abiotic and biotic factors (Sánchez-Carrillo et al., 2018). For instance, the infectivity of *B. dendrobatidis* and population density and metabolic activity of aquatic communities, including amphibian's immunity and zooplankton dynamics, typically follow seasonal fluctuations steered by environmental conditions such as temperature, light and nutrient availability, affecting aquatic food web functioning and disease outbreaks (Claska and Gilbert, 1998; Berger et al., 2004; Sommer et al., 2012; Daversa et al., 2018; Campbell et al., 2019). Moreover, the increasing conversion of natural areas into agricultural landscapes strongly associates amphibian breeding ponds with agricultural activities in many regions (Foley et al., 2005). Cattle trampling and exposure to agrochemicals, such as chemical fertilizers, pesticides and veterinary pharmaceuticals, might affect aquatic communities and trophic relationships (Relyea, 2009; Smalling et al., 2012). Close monitoring and control of abiotic factors in the aquatic environment steering food web interactions to optimize chytrid predation is a promising mitigation strategy for chytridiomycosis. In this paper, we review the opportunity of using pathogen predation as a biological control strategy for chytridiomycosis and how agricultural activities might affect this strategy. We also provide a framework with future research perspectives and actions that are needed to further develop a scientifically based mitigation strategy based on these principles of optimized pathogen predation.

## 2. Biological control through chytrid predation in agricultural landscapes

Biological control through pathogen predation implies that naturally occurring aquatic organisms are consuming free living zoospores of the chytrid causative agents (*B. dendrobatidis* and *B. salamandrivorans*) to such extent that infection prevalence and infection loads are reduced to levels that allow coexistence between host and pathogen. These chytrid consuming planktonic organisms are further referred to as micropredators, since free swimming zoospores are filtered and intercepted out of the water phase. While pathogen eradication is highly unlikely via this strategy, this may not be required for the purpose of controlling population level effects of chytridiomycosis in nature owing to the dose-dependent nature of the disease (Garner et al., 2009; Woodhams et al., 2011). In this situation, infections are still present without causing mass mortality events or extirpations, which is characteristic for an endemic situation.

*Bd* zoospores have a diameter of 3–5  $\mu\text{m}$  (Longcore et al., 1999), which is well within the preferred food size range of major filter feeding zooplankton groups such as rotifers (Wallace et al., 2006) and cladocerans (Geller and Müller, 1981). However, most zooplankton groups are able to selectively feed upon particles and may give priority to other food sources such as

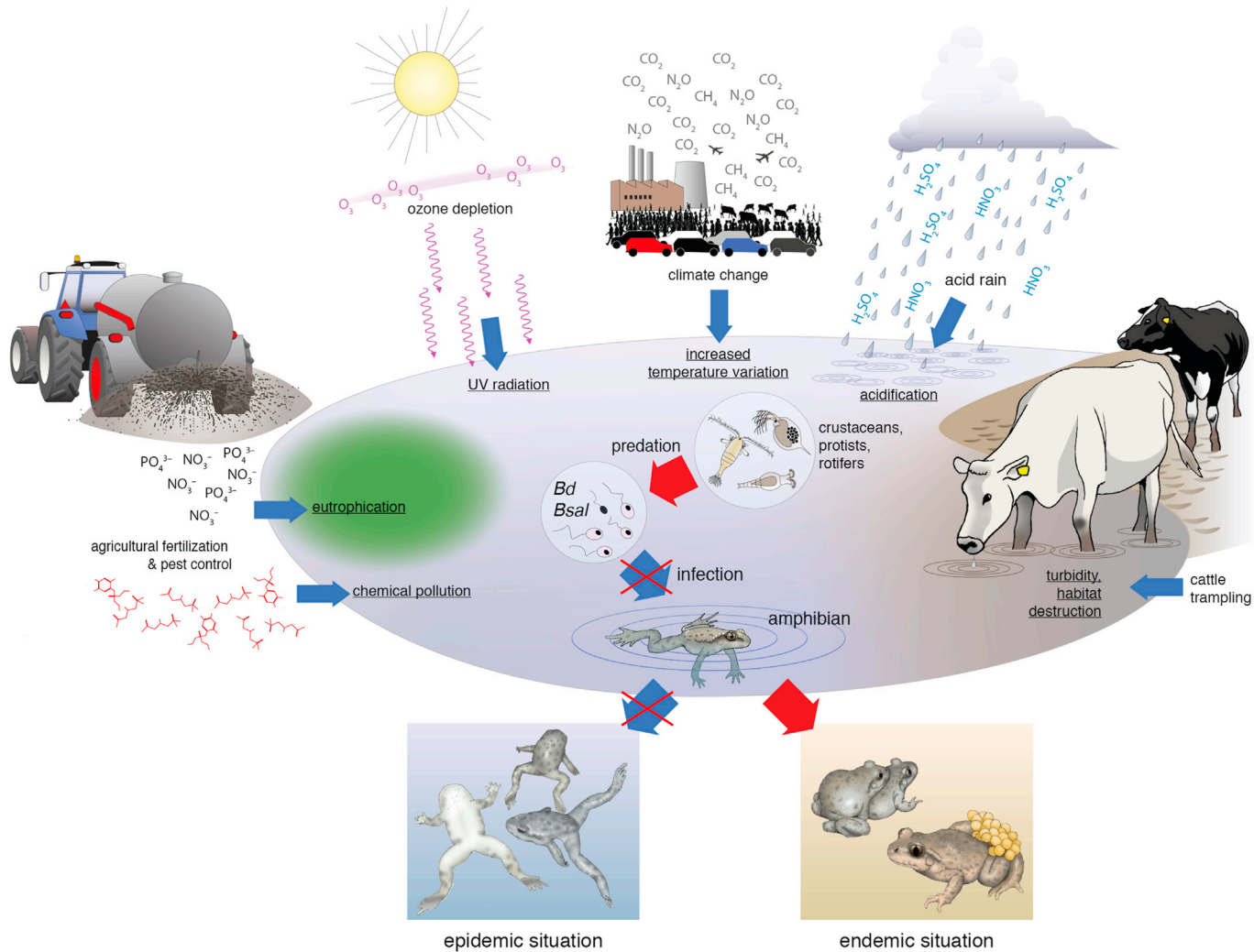
phytoplankton (Sailley et al., 2015). Nevertheless, several studies have proven that various micropredators (e.g. ciliates, rotifers, *Daphnia* sp.) are capable of using *Bd* zoospores as a food source (Buck et al., 2011; Hamilton et al., 2012a; Searle et al., 2013; Schmeller et al., 2014; Blooi et al., 2017). Schmeller et al. (2014) showed that the density of aquatic micropredators determined the survival of *Bd* zoospores, and was correlated with *Bd* prevalence in anuran tadpoles in natural ponds. Additional circumstantial evidence for the role of aquatic micropredators in steering *Bd* infection and disease dynamics was provided by Blooi et al. (2017), who correlated the presence of abundant and diverse communities of *Bd* ingesting organisms in Central American bromeliad phytothelmata with protection against chytridiomycosis driven declines. All micropredators described in this context belong to the hyper diverse zooplankton community with, for example, approximately 170 euplanktonic ciliate species, more than 1900 rotifer species, about 620 cladoceran species and over 2800 copepod species that have been described to inhabit freshwater environments around the world and these numbers are expected to be an underestimation since many species are yet to be discovered (Berger et al., 2000; Boxshall and Defaye, 2008; Forró et al., 2008; Segers, 2008). Individual water bodies are also typically characterized by high zooplankton species richness. Kuczyńska-Kippen (2020) identified up to 65 rotifer species, 21 cladoceran species and 9 copepod species in rural field ponds in Poland and Forró et al. (2003) found 7 cladoceran species and 9 copepod species in temporary waters of Belgium, which are both considered as important breeding habitats for amphibians. Since each of these taxa has its own behavior and feeding traits, it is crucial to identify the components of the zooplankton community that serve as effective micropredators and deserve the focus for conservation management actions.

Environmental stressors, such as chemical pollution, acidification, elevated exposure to UV-radiation, habitat destruction and increased temperature variations, may induce adverse effects in aquatic communities, affecting trophic interactions, pathogen predation dynamics and disease outcome. Fig. 1 shows a conceptual overview of abiotic stress factors that may interact with the predator-pathogen interaction and associated control strategy for chytridiomycosis in an amphibian breeding pond. In this review, we focus on the adverse effects of agricultural activities, since small water bodies located in agricultural areas (e.g. cattle drinking ponds) are important breeding habitats for many amphibians (Knutson et al., 2004; Swartz and Miller, 2019). These ponds are commonly exposed to at least some degree of agrochemical contamination, that may have direct implications for the health and survival of amphibian populations (Mann et al., 2009; Goessens et al., 2020). Contaminant exposure may also have an indirect effect, by affecting the chytridiomycosis disease course. Some chemical compounds are known to induce immunosuppressing effects in host amphibians, for instance by altering their skin microbiomes, making them more susceptible to infection and disease (Rohr et al., 2017; McCoy and Peralta, 2018). The pathogen can also be affected by pollutants, such as fungicides or disinfectants used in agriculture, lowering infection pressure (Hanlon et al., 2012). Finally, micropredator communities may suffer either lethal effects, sublethal behavioral changes or indirect effects via trophic cascades, altering their grazing capacity on chytrid zoospores (Hanazato, 2001; Groner and Relyea, 2011; Hasenbein et al., 2016). Besides agrochemical pollution, the frequent use of amphibian breeding ponds as drinking pools for cattle can also affect the ecological structure and functioning of the pond. Grazing of aquatic vegetation, nutrient redistribution through defecation and urination and disturbance by trampling of large animals may directly affect amphibians reproductive success (Knutson et al., 2004). On the other hand, this may lead to eutrophication events and destruction of crucial microhabitats for micropredators (Declerck et al., 2006; Stein et al., 2014), reducing their potential to eliminate chytrid pathogens.

### 3. Anthropogenic impact on chytrid predation in agricultural landscapes

Contamination of amphibian breeding ponds by anthropogenic pollutants and associated toxic effects on aquatic communities may affect the abundance and diversity (species richness and evenness) of micropredators (Relyea, 2005, 2009; Hasenbein et al., 2016). For example, larger zooplankton species that often outcompete smaller species tend to be more vulnerable to pesticide pollution (Hanazato, 2001). Increased toxicity to larger species and a consecutive reduction of competition effects will result in a zooplankton community dominated by smaller groups, such as rotifers and small cladocerans (Hanazato, 1998). Zooplankton community changes may have strong implications for pathogen eradication since micropredators can be outcompeted and replaced by less effective groups or vice versa.

Besides direct lethal effects, zooplankton species can experience several sublethal effects induced by agrochemicals. The insecticide metabolite dichlorodiphenyldichloroethylene (DDE) and the herbicide glyphosate caused reduced grazing rates of a *Daphnia* species on algae (Bengtsson et al., 2004), whereas the antimicrobial drug sulfamethazine reduced the feeding rates and body sizes of the rotifer species *Brachionus calyciflorus* (Yan et al., 2019). Andrade et al. (2018) showed increased predator avoidance in zooplankton communities caused by a herbicide mixture (glyphosate and 2,4-D), since these active ingredients mimic predator cues on the nervous system of the organisms. Such maladaptive responses cause unnecessary energy consumption (Andrade et al., 2018), that may result in reduced foraging activities and thus lower feeding rates. On the other hand, behavioral changes caused by pollution may also increase their susceptibility for predators (Dodson et al., 1995). Reduced swimming activities were observed in a rotifer species caused by exposure to the organophosphorus insecticide dimethoate (Guo et al., 2012) and in *Daphnia magna* due to environmentally relevant concentrations of the pyrethroid insecticide cypermethrin, resulting in a lower feeding efficiency (Christensen et al., 2005). Flaherty and Dodson (2005) observed a significant mortality and malformed carapaces and swimming setae in *D. magna* caused by a mixture of two pharmaceuticals (clofibric acid and fluoxetine), whereas these two products showed no effects when tested individually. Finally, some contaminants (e.g. pesticides and pharmaceuticals) have also been shown to alter sex ratios in cladoceran populations. Increased



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**Fig. 1.** Conceptual overview of the biological control strategy based on pathogen predation in an amphibian breeding pond. Infection of amphibians with *Batrachochytrium dendrobatidis* (Bd) or *Batrachochytrium salamandrivorans* (Bsal) causes the fungal disease chytridiomycosis, potentially leading to mass mortality events and population extinctions (epidemic situation). Predation by naturally occurring micropredators on free-living zoospores of Bd and Bsal reduces zoospore densities, tipping the host-pathogen interaction to coexistence in the absence of mass mortality events (endemic situation). Amphibian breeding ponds are frequently exposed to a wide range of anthropogenic pressures, causing environmental stress. These stressors may interact with the aquatic food web structure and infection dynamics, thereby steering the biological control strategy. Note that disease dynamics and trophic interactions are following seasonal fluctuations steered by temperature, light and nutrient availability.



production of males can interfere with the parthenogenic life cycle of these species that allows for high fecundity and rapid population growth (Olmstead and LeBlanc, 2003; Flaherty and Dodson, 2005).

Phytoplankton biomass and diversity may also be affected by pollution, leading to indirect effects on micropredators since this is the main food source for the zooplankton community (Brett et al., 2009; Striebel et al., 2012). Increased phytoplankton biomass, following high nutrient loads (Smith, 2003), may result in an oversupply of alternative food sources which lowers the importance of chytrids in the micropredator's diet. On the other hand, eutrophication events reduce biodiversity resulting in a phytoplankton community that is typically dominated by large diatoms and filamentous or toxic cyanobacteria (Downing et al., 2001; Dignum et al., 2005). These algae are poor food sources for most zooplankton, followed by reduced zooplankton biomass through bottom-up regulation (Hessen et al., 2006). Similar bottom-up processes may occur after herbicide pollution, for example simetryn lowered phytoplankton density causing a reduction in herbivorous zooplankton abundance (Kasai and Hanazato, 1995). Exposure of the green algae *Raphidocelis subcapitata* to the herbicide pendimethalin lowered its nutrition value for grazers and the chemical was shown to accumulate in the bodies of *D. magna* by feeding on contaminated *R. subcapitata*, leading to a decreased reproduction rate of 16% in *D. magna* (Bessa da Silva et al., 2016). Lower nutritional quality of phytoplankton cells, e.g. due to a changed composition in their unsaturated fatty acid content, for secondary producers has also been observed during algal blooms after nutrient enrichment, inducing a decrease in zooplankton abundance (Müller-Navarra et al., 2004). The availability of chytrid zoospores, having a significant energetic and nutritional value, may serve as an alternative food source in these situations (Kagami et al., 2007; Johnson et al., 2010; Frenken et al., 2018). Finally, algal blooms can outcompete macrophyte vegetation that serves as an important habitat for many micropredator species (shelter, foraging, ...) (Scheffer et al., 1993; Declerck et al., 2007). Direct access of cattle, e.g. in drinking pools, enhances this effect by causing eutrophication events due to increased nutrient input by defecation and urination, especially when it is combined with trampling (Declerck et al., 2006; Van den Broeck et al., 2019). Trampling by large animals also causes destruction of microhabitats resulting in lower species richness (Stein et al., 2014). Van den Broeck et al. (2019) observed a change in crustacean communities in mesocosms from filter-feeding cladocerans towards higher abundances of calanoid copepods and *Triops* after disturbance caused by nutrient input and simulated trampling, since the latter groups are more able to cope with higher turbidity. Since each zooplankton taxa has its own food niche and metabolic traits, these community changes may again have implications for the pathogen removal efficiency.

#### 4. Perspectives towards a biological control strategy

Using pathogen predation as a biological mitigation strategy for chytridiomycosis requires detailed identification of effective micropredators and a thorough knowledge of the seasonal fluctuations of pathogen, host and micropredator dynamics and the abiotic and biotic factors interacting with the predator-pathogen interaction. However, numerous gaps in our understanding of these relationships and how they are embedded in the aquatic food web are still existing. Amphibian breeding ponds typically have a trophic structure with a high degree of complexity. An environmental stressor (e.g. pollutant) affecting one trophic level may have implications for the whole aquatic community. For instance, a herbicide that directly affects the phytoplankton community, may cause nutrition stress in zooplankton communities, which are in turn a critical food source for higher trophic levels (Bessa da Silva et al., 2016; Hasenbein et al., 2017). As another example, the impact of an insecticide on the zooplankton community can cause shifts in the phytoplankton composition by affecting top-down regulation, that may induce changes in the whole pond community by modified food web interactions, competition for nutrients and light and oxygen dynamics (Mills and Semlitsch, 2004; Relyea and Hoverman, 2008). Both chytrid pathogens and amphibian hosts can also directly be affected by certain types of stress, such as pesticide exposure or temperature changes, that may cause zoospore mortality or reduced zoospore production and increased host susceptibility for infection and disease (Hanlon and Parris, 2012; Voyles et al., 2012; McMahan et al., 2013). Therefore, it is crucial to not only focus on the interaction between micropredators and chytrid zoospores as such when investigating potential management actions to mitigate chytridiomycosis, but to incorporate the whole aquatic food web and the abiotic variables that influence it to assess the final impact of environmental factors on the elimination of chytrid zoospores (Buck et al., 2015). Examples of management actions towards food web control in amphibian breeding ponds include an alternative pesticide management system and fertilizer program in the vicinity of amphibian breeding ponds, fencing of ponds to prevent direct access of cattle and creating more suitable habitat conditions for micropredators (e.g. macrophytes). According to the authors, a triptych of field monitoring, integrated laboratory experiments and ecological modelling is needed to gain full insights about the potential of these measures to mitigate chytridiomycosis in nature. A flowchart of these consecutive research steps, including research objectives and proposed methodology, is provided in Fig. 2.

##### 4.1. Field monitoring

Strict monitoring of the abiotic and biotic state of amphibian breeding ponds is the first critical step in understanding the ecological mechanisms driving biological control of chytridiomycosis. Extended data collection is crucial as input for the ecological modelling stage that will be discussed later. Detailed knowledge and insights in the trophic structure, including the diversity of potential micropredator species, infection status and exposure to environmental stressors, is needed to estimate the elimination efficiency of chytrid zoospores. A detailed protocol for determining chytridiomycosis infections on amphibian skin is provided in Hyatt et al. (2007). Basic monitoring methods supplemented with state-of-the-art techniques, such as

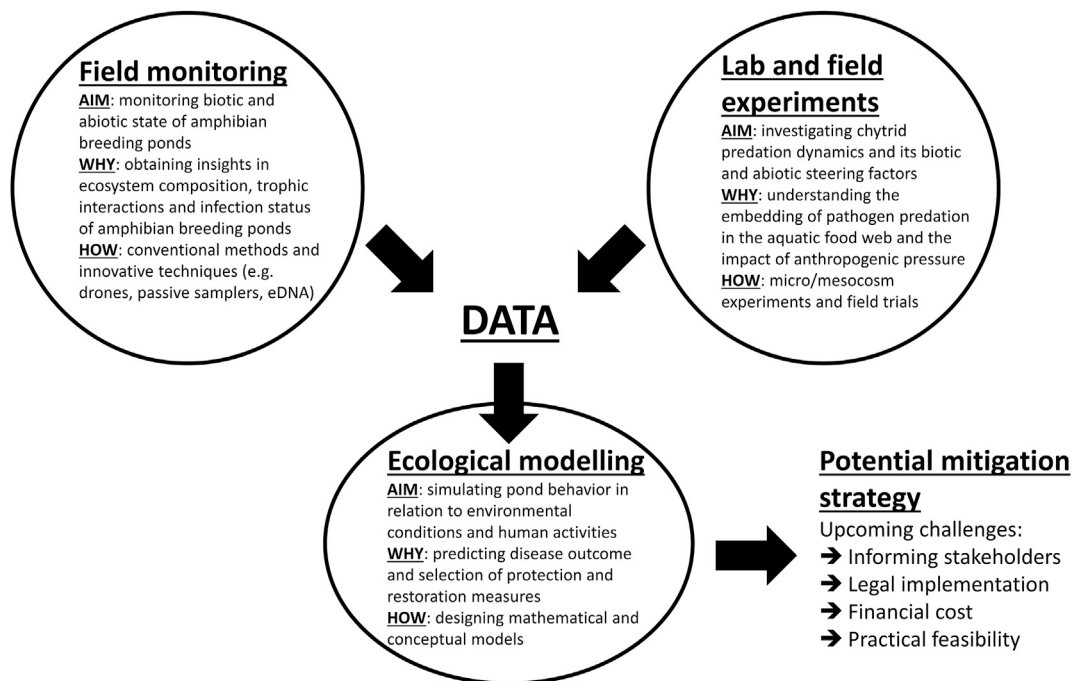


Fig. 2. Research perspective flowchart needed to develop a scientifically proven food web based strategy to mitigate chytridiomycosis in amphibians.

biomolecular technologies using environmental DNA (eDNA), drone technology and passive samplers, can provide highly accurate and complete information of the geographical, physical, chemical and biological state of the pond under investigation (Thomsen and Willerslev, 2015; Lally et al., 2019; Valenzuela et al., 2019).

#### 4.2. Integrated laboratory experiments

It has been proved in laboratory experiments that several zooplankton species are capable of using *Bd* zoospores as a food source (Buck et al., 2011; Hamilton et al., 2012a; Searle et al., 2013; Schmeller et al., 2014). However, crucial information about this predator-pathogen interaction in natural situations is still unrevealed today. Identification of effective micropredators within the zooplankton community with the potential to efficiently remove chytrid pathogens has poorly been elucidated yet. Moreover, knowledge on how the predator-pathogen interaction is embedded in natural food webs and how it is affected by environmental factors is also still very limited. It has been shown, for instance, that *Daphnia* are able to distinguish between different types of food and select particles that are given priority as a food source (Brett et al., 2009). The preferences of consuming zoospores in the availability of other food sources has poorly been investigated so far, although Searle et al. (2013) showed less reduction of *Bd* zoospores by a *Daphnia* sp. when the green algae *Ankistrodesmus falcatus* was present. Insights concerning the food preferences of micropredator species are crucial for optimizing pathogen eradication in nature. Moreover, exposure of amphibian breeding ponds to anthropogenic pollutants, e.g. agrochemicals, may affect micropredator communities and disrupt this predator-pathogen interaction. A wide body of literature is available on investigating the acute and chronic toxic effects of chemicals on aquatic organisms and communities, including potential micropredator communities (Hanazato, 2001; Fleeger et al., 2003; Van Wijngaarden et al., 2005; Peters et al., 2013; Nys et al., 2018). However, embedding the predator-pathogen interaction in the aquatic food web and unravelling its abiotic and biotic steering variables requires a more integrated approach.

Mesocosm setups are powerful systems to mimic the natural environment in controlled conditions to perform integrated experiments. This experimental design has been useful to examine the effects of environmental factors on the dynamics of chytrid infections, such as temperature (Hamilton et al., 2012b), pesticide pollution (Edge et al., 2013) or aquatic invertebrate activity (Betancourt-Román et al., 2016). Besides investigating the impact of environmental factors on pathogen behavior and disease dynamics, mesocosm studies can provide highly valuable information and perspectives about the potential of biological control of chytridiomycosis by identifying effective micropredator species and providing insights in the environmental factors steering chytrid predation. Hamilton et al. (2012a) performed mesocosm and microcosm experiments to examine the removal capacity of *Bd* zoospores by the freshwater crustacean *Daphnia*. They concluded that *Daphnia* served as an important food source for tadpoles, and that *Daphnia* were able to significantly reduce the number of *Bd* zoospores in the water column of the microcosms. However, more integrated experiments incorporating multiple trophic levels, such as primary producers that serve as an alternative food source for micropredators or macroinvertebrates and fish inducing predation stress on

micropredators, are lacking. Finally, the impact of environmental stressors in an agricultural landscape, such as agrochemical exposure or cattle trampling, on the removal efficiency of *Bd* zoospores is still unknown. Using integrated mesocosm experiments, crucial knowledge to optimize chytrid predation by controlling steering variables of aquatic food webs can be obtained. Based on this knowledge, a selection of management actions can be made to be further investigated in natural pond studies.

#### 4.3. Ecological modelling

The development and use of mathematical and conceptual models (e.g. food web models, migration models, habitat suitability models, ...) to predict how environmental factors are affecting disease dynamics is the last crucial step before stakeholders and authorities can take appropriate measures to mitigate chytridiomycosis. These models are based on data gathered from field monitoring, laboratory experiments (e.g. mesocosm studies) and basic ecological concepts. Thereby, associated variables and processes need to be carefully selected in a context of biodiversity conservation, water management and sustainable development (Goethals and Forio, 2018; de Vries et al., 2020; Forio and Goethals, 2020). Species distribution models and habitat suitability models can be used to evaluate the effect of abiotic factors on pathogens, amphibian hosts and micropredator populations (Lenhardt et al., 2013; Bennetsen et al., 2015). These models are powerful tools to estimate the risk of chytridiomycosis spreading to unexposed areas (Seimon et al., 2015; Flechas et al., 2017; Yap et al., 2018). Food web models, describing the flows of energy and biomass between different trophic levels within an ecosystem, can be used to predict the impact of environmental stressors on trophic interactions between aquatic communities (Gotelli and Ellison, 2006). These kind of ecological models are inevitable tools to predict the outcome of mitigation measures to control aquatic food webs, such as stricter regulations regarding agrochemical application and habitat restoration measures. For example, Ambelu et al. (2014) used ecological models to identify environmental and biological factors affecting the occurrence of blackfly larvae in aquatic ecosystems in Ethiopia. These models can then be used to develop ecological management strategies to control the distribution of blackflies, since this is a major disease vector for river blindness (Ambelu et al., 2014).

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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