

The common fire salamander *Salamandra salamandra* and invasive pathogen *Bsal*: a conservation strategy for a vulnerable species

Abel Koopman (s4775597)
a.m.koopman.1@student.rug.nl

Supervisor: Sebastian Lequime
Rijksuniversiteit Groningen



Abstract

The common fire salamander (*Salamandra salamandra*), native to Europe, is currently vulnerable to extinction, caused by habitat degradation and the introduction of the chytrid fungus *Batrachochytrium salamandrivorans* (*Bsal*). Since its introduction via the wildlife pet trade, *Bsal* has spread through multiple European countries, exhibiting high virulence and 100% host mortality, with a projected range expansion of 11 km per year. Although some population persistence in infected habitats has been observed, these populations exhibit long-term reductions in abundance and ecological functionality. Amphibians play an important role in their ecosystem and the extirpation of salamander populations can lead to a trophic cascade, which destabilizes their ecosystem. Possible conservation methods are evaluated using scientific, practical, and ethical considerations. This thesis proposes a conservation strategy based on endemic coexistence, by combining target-specific action with ecosystem restoration. The two-pronged strategy proposed consists of genetically engineered resilience to *Bsal*, accompanied by extensive habitat restoration and ecosystem improvements such as beaver reintroduction. *Ex situ* methods and human-mediated refugia are considered transitional measures. Empirical conservation research on the fire salamander and *Bsal* could in addition generate models for managing current and future infectious diseases and restoring ecosystems.

Table of contents

Abstract.....	1
Table of contents.....	2
Introduction.....	3
Legal status and applied conservation.....	4
Evaluation criteria for methods.....	5
Practical limitations.....	5
Ethics.....	5
Conservation methods.....	6
Pathogen in the environment.....	7
Wildlife trade ban.....	7
‘Clean trade’.....	7
Habitat restoration.....	8
Refugia.....	8
Fungicide.....	8
Public awareness.....	9
Infection.....	9
Vaccination.....	9
Relocation.....	9
Captivity.....	10
Treatment.....	10
Genetic engineering.....	10
Summary table methods.....	12
Discussion.....	13
Statement on the use of AI.....	16
References.....	16

Note: Cover image designed by the author, based on vector elements sourced from VectorStock (2025).

Introduction

The common fire salamander (*Salamandra salamandra*), native to Europe and occurring in wetlands and woodlands with ponds and streams, is currently at high risk for extinction within one hundred years (Gilbert et al., 2020). This is due to a combination of habitat loss, destruction and fragmentation, and the spread of chytrid fungus *Batrachochytrium salamandrivorans* (*Bsal*) (IUCN, 2023). In the Netherlands, increasing numbers of dead fire salamanders were observed from 2008 onwards, until 2013 when the population was nearly reduced to extirpation (local extinction) (Spitzen-van der Sluijs et al., 2013). Later that year, the novel, lethal fungus *Bsal* was discovered to be the cause of this rapid population decline. The pathogen ‘eats’ away the skin of its host, which creates lesions and eventually leads to death (Martel et al., 2013).

Bsal is native to eastern Asia, and was introduced to Europe through wildlife pet trade (Nguyen et al., 2017). *Bsal* has already invaded habitats in the Netherlands, Belgium, Germany, Luxembourg, and Spain (Spitzen-van der Sluijs et al., 2016, Porco et al., 2024, Ribas et al., 2022). Schmidt et al. (2017) have estimated a yearly advancement of *Bsal* through Europe of eleven kilometers per year. *Bsal* has a high virulence, active and passive modes of transmission, and infection always leads to death of the fire salamander, leading Stegen et al. (2017) to suggest that the fungus will behave as a ‘perfect storm’ able to rapidly extirpate salamander populations across Europe.

Fire salamanders reach reproductive maturity at the age of five years and have a generation time of seven to fifteen years. Using this information, the IUCN estimates a population decline of 30–49% in Europe in the next three generations (thirty years) (IUCN, 2023). There has been some evidence of population persistence in infected habitats, but with severely reduced abundances that do not recover, even over a decade (Erens et al., 2023). The closest related pathogen of *Bsal* is the well-studied *Batrachochytrium dendrobatidis* (*Bd*), dubbed the ‘amphibian plague’ for its role in the extirpation and extinction of amphibian species globally (Berger et al., 1998).

Salamander extirpation can lead to trophic cascades negatively impacting its entire ecosystem (Zipkin & DiRenzo, 2022). According to the IUCN Red List, 56% of the world’s 758 salamander species (Caudata) are currently vulnerable to extinction, and many are susceptible to *Bsal* (IUCN, 2024). A potential *Bsal* invasion into other continents could cause further global amphibian decline. In preparation, researchers in the Americas are already monitoring and preparing to prevent its establishment (Grant et al., 2016).

This thesis explores potential conservation approaches applicable to the fire salamander in Europe and will assess the quality of the various methods using practical and ethical considerations. A conservation strategy developed for the fire salamander could serve as a model for protecting other susceptible salamander species, and other amphibians.

Legal status and applied conservation

Before we describe the possible conservation methods, we will look at the legal protection of the fire salamander and the conservation that has already been applied.

Salamandra salamandra is protected by the Bern Convention of 1979. The Bern Convention is a binding legal instrument, with the aim to conserve European wildlife and promote collaboration between European countries in this field. Under it, the common fire salamander is categorized as a *protected species*, which are species that 'are to be protected, but a certain exploitation is possible if the population level permits.' (Council of Europe, 1979). The fire salamander is currently not a CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) species, which means the import and export of fire salamanders is not tracked (CITES, n.d.).

Bsal is included in the EU regulation of Animal Health Law since 2018, which categorizes *Bsal* as a disease for which 'measures are needed to prevent it from spreading' (Article 9(1)(d) of Regulation (EU) 2016/429) and 'there is need for surveillance'. (Article 9(1)(e) of Regulation (EU) 2016/429.) The European Commission has published a 'clean trade' policy in 2019 for the commercial movement of salamanders into and between EU member states. This policy states that all commercially traded salamanders have to be free of *Bsal* and accompanied by an animal health certificate that proves this (European Commission, 2018).

The European Commission has published a *Bsal* Action plan in 2020, which calls for the EU to establish a monitoring system, to implement the 'clean trade' policy, to fund research regarding *Bsal* mitigation and set up a workgroup. The call to the member states is similar, with an additional call for 'immediate and effective removal of any non-native amphibian species' (Gilbert, 2020). On the Action Plan's website (<http://bsaleurope.com/>), the EU provides information about the current status of *Bsal* spread, but a plan for monitoring is still being developed. There is a list with contact information and websites for ten member states to report the finding of dead salamanders, although to this date [04-05-2025], only two out of the five listed websites lead to a functioning form to report this.

The '*Bsal* Action Plan' (2020) legally binds the EU and its member states to establish monitoring of the spread. The Netherlands, with the Dutch non-profit organisation RAVON (Reptielen Amfibieën Vissen Onderzoek Nederland), is the only member state that communicated about the past monitoring efforts. RAVON detected *Bsal* in 3 out of 37 tested sites in 2021 and 2022 (Spitzen-van der Sluijs, 2022).

Concerning conservation efforts, only few initiatives could be found to date. In 2013, after the rapid fall of the Dutch fire salamander population, RAVON caught the remaining individuals and brought them to several zoos, which are now breeding individuals as a 'reserve population' (Van Santen, 2013). RAVON collaborates with commercial and noncommercial breeding advocacy groups to provide information on the mitigation of *Bsal* and has advocated for *Bsal*-free wildlife trade.

Evaluation criteria for methods

In this thesis, I will discuss the possible conservation methods for the fire salamander with regard to *Bsal*. Based on existing literature, I will briefly describe methods and evaluate their potential quality, based on several criteria. An ideal conservation method would be 1) effective for fire salamander protection, 2) low cost in labor and materials, 3) easy to execute, and 4) legal, safe, and ethical.

Practical limitations

There is a practical dimension to conservation methods, which this thesis cannot neglect. Some methods, while scientific marvels, are simply a poor choice, due to practical limitations. Although scientific research usually does not really discuss these issues around implementation, wildlife conservation has to function with very limited funds, while its needs are growing. Research into conservation methods that are impossible to execute would be a waste of time. Where applicable or especially notable, I will discuss practical limitations of the methods.

Ethics

When and whether to intervene in nature is a matter of philosophical stance. There is some literature on the ethics of nature conservation, but at its core, applied conservation biology is strewn with conflicting wants and needs that literature has no answers to (Minteer & Collins, 2008). This thesis does not aim to prescribe what is right or wrong in conservation, but will point out some of the ethical dilemmas concerning conservation methods.

In the case of conserving *Salamandra salamandra* against extinction, there are many stakeholders, with conflicting wants and needs. The first stakeholder, of course, is the fire salamander itself. Although an individual fire salamander probably does not care whether its species goes extinct or not, it is in their interest not to be infected by a lethal, skin-eating fungus.

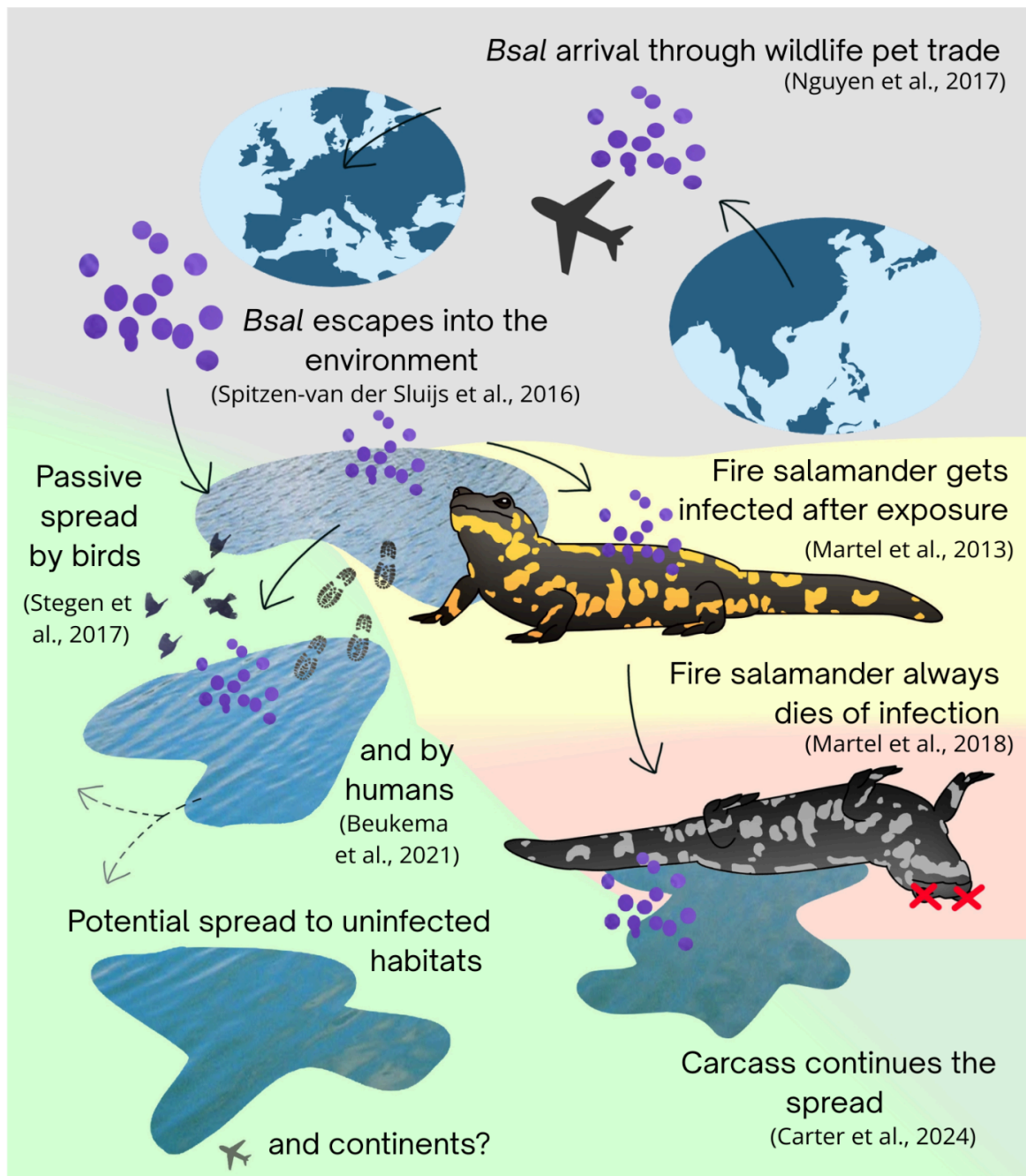
Another important stakeholder, philosophically the most interesting, is nature. But, what is nature? Does it have interests and needs? Any attempt to capture a definition of nature falls short. In the context of this thesis and to contrast it to human wants and needs, nature is defined as the global ecosystem of non-human life, which garners the interest of maintaining ecosystem stability and sometimes needs a little help to correct human-made mistakes. Written from the perspective of conservation biology, this thesis sides with the fire salamander and nature. Due to the practical nature of conservation biology, methods should be approached with some pragmatism. Therefore, the interests and concerns of other stakeholders such as local (human) inhabitants, researchers, hobbyist amphibian breeders and commercial wildlife traders, zoos, and farmers are also discussed when relevant to a conservation method.

Conservation methods

Disease is the interaction of three components: pathogen, host, and environment. Conservation action with the aim of protecting the fire salamander against *Bsal* should not merely be focused on the pathogen but on the interactions between these components. Conservation methods will be discussed grouped into two interactions: pathogen in the environment and infection of the host by the pathogen. A visual summary of these interactions is provided below (see Figure 1).

Figure 1

A visual summary of interactions between *Bsal*, the fire salamander and the environment. Figure designed by the author, based on vector elements sourced from VectorStock (2025).



Pathogen in the environment

Due to its environmental persistence, complete eradication of *Bsal* in Europe is found to be unlikely (Bletz & DiRenzo, 2025). Reducing the pathogen load in the environment could still slow down the spread and prevent infection of new habitats. Dead individuals need to be removed from the environment because they can continue to spread the pathogen (Carter et al., 2024). The spread of *Bsal* can be measured in the environment, which is a useful tool to direct conservation efforts. Measuring environmental DNA through droplet digital PCR is a highly sensitive method to monitor for *Bsal* in natural water (Porco et al., 2024). A CRISPR-based method can be applied to test individuals for *Bsal* infection via skin swabs (Hoenig et al., 2024). This method is cost- and time-efficient, but not as sensitive as PCR methods.

Even though *Bsal* is already present in Europe now, continued arrivals of the pathogen pose an additional threat, because these new arrivals can potentially harbor new genetic material. Preventative measures can prevent or limit the continued transport of *Bsal* into Europe through commercial trade.

Wildlife trade ban

The most effective solution to prevent arrival of *Bsal* would be to ban the import of all live *Bsal*-carrier species into Europe. Europe is the central hub of the international amphibian trade (Auliya, 2016). There is a large market for wildlife trade, the global market yielding 150 to 200 billion US dollars yearly (Andersson et al., 2021). This would mean no trade in salamander species, as well as a few anuran species (Nguyen et al., 2017, Chen et al., 2023). An additional argument for a wildlife trade ban is that salamander species that are imported from Asia for pet trade have become vulnerable to extinction by over-collection of the wild population (IUCN, 2024).

A trade ban would need to be enforced on EU-level and would be difficult to realize, due to the large commercial market of wildlife trade. Dutch non-profit RAVON collaborated with commercial and non-commercial interest parties on a statement (<https://www.ravon.nl/Bsal#7>), stating they are opposed to a complete trade ban on fire salamanders and show support for a 'clean trade' policy.

'Clean trade'

Regulations for a 'clean trade' policy that have been proven to reduce pathogen spread in other species and diseases are regular disinfection of the animal housing, restricted contact between animals, separation by species, sanitary handling of the animals, and tracking all traded species (Galindo-Bustos et al., 2013, Morales et al., 2021, Baláž et al., 2017). The current 'clean trade' policy focuses only on salamanders, but anurans and possibly other species can be silent carriers (Nguyen et al., 2017). It would be more effective to extend the 'clean trade' policy to all possible *Bsal* carriers, preferably all amphibians.

Habitat restoration

Alongside the threat of *Bsal*, habitat loss, destruction, and fragmentation are the main contributors to fire salamander population decline (IUCN, 2024). Habitat restoration has proven to be a successful strategy for the conservation of the crested newt (*Triturus cristatus*) and the common spadefoot toad (*Pelobates fuscus*) (Rannap et al., 2009). Restoration with enhancements to make the habitat less suitable for *Bsal* could relieve multiple threats in one method.

Larger habitat size tends to have a stabilizing effect on inhabiting populations (Greig et al., 2022). Extensive restoration by enlarging the habitat and improving breeding grounds has been shown to increase population numbers of the threatened natterjack toad (*Epidalea calamita*) (Rannap et al., 2024). Fragmentation of habitat can be relieved by reconnecting existing habitats: improved connectivity has been shown to fortify the local abundance of the fire salamander, but could also increase the likelihood of *Bsal* transmission (Bolte et al., 2023). However, a study conducted in the Netherlands found that a *Bsal*-infected subpopulation was not able to infect a subpopulation at only eight hundred meters distance, despite any obvious physical barriers (Spitzen-van der Sluijs et al., 2018). Land would need to be bought to enlarge or connect habitats, and farmers are unlikely to be willing to give up their land. In countries where *Bsal* occurs, about 50% of all land cover is in use for agricultural purposes (Food and Agriculture Organization, n.d.).

Beavers are keystone species for wetlands. Hossack et al. (2015) showed that the modification of wetlands by beavers increased the occupancy of amphibians by 34%. The introduction of beavers (*Castor fiber*) as ecosystem engineers could, through damming, create shallows with elevated water temperatures, which can limit the growth of *Bsal* (Blooï et al., 2015). Beaver-engineered wetlands tend to have improved water quality, which can promote predation on *Bsal* by the microcrustacean population (Smith et al., 2020, Beranek et al., 2020). The presence of *Bd* in the environment is positively correlated with vegetation cover and canopy density (Becker et al., 2012). Reducing canopy cover, for example, through beaver foraging (Zwolicki, 2025), could potentially limit *Bsal* growth by increasing the water temperature due to more exposure to sunlight. The fire salamander occurs along streams up to 2500 meters elevation, but prefers low elevation, and beavers occur up to 850 meters (IUCN, 2024).

Refugia

Instead of large-scale habitat restoration, refugia can prevent extirpation by providing a protected patch within the habitat that species can retreat to to survive (Heard et al., 2015). Human-mediated refugia for the fire salamander could be designed to be unsuitable to *Bsal*, regularly monitored for *Bsal* presence, and possibly artificially kept free of *Bsal*. Such refugia are easier to realize than large-scale projects and avoid the risk of promoting spread through connectivity.

Fungicide

Reducing or eliminating the presence of *Bsal* in the environment of the fire salamander could be an effective way to curb the spread. The chemical disinfection of infected ponds, in combination

with disease treatment of the amphibian inhabitants, has shown to be a low cost and somewhat effective method, but does not provide long-term protection (Bosch et al., 2015). The effect of using a non-specific disinfectant on microbial ecology was not investigated in this study.

Adding microbes that are antagonistic to *Bsal* to the habitat could be a less disruptive and more lasting method of curbing *Bsal* growth. Endemic microbes could be augmented to antagonise *Bsal* (Bletz et al., 2013).

Mycoparasites, either mycoviral or fungicolous fungal (fungus-eating fungus), can antagonise pathogenic fungi and could be a long-term method to reduce *Bsal* presence (Barge et al., 2022). It has not yet been researched whether *Bsal* has mycoparasites in its endemic range. It is difficult to predict the effectiveness of introducing mycoparasites to the environment; additionally, introducing them could have undesired side effects, such as infecting unintended hosts or spreading to the native range of *Bsal* and disrupting the microbial ecology there.

Public awareness

Beukema et al. (2021) found a positive correlation between the density of hiking trails and the presence of *Bsal*, suggesting that human foot traffic can increase the spread of the pathogen. RAVON has published a protocol for amphibian researchers and hobbyists instructing them to disinfect boots and tools to prevent *Bsal* spread (https://www.ravon.nl/Portals/2/Bestanden/Publicaties/Hygiene_protocol.pdf). There have been no public awareness campaigns yet to communicate the role of hikers and other casual visitors.

Infection

In the case of *Bsal* and the fire salamander, all individuals are susceptible to infection, which, without intervention, leads to certain death (Martel et al., 2018). Methods for preventing or treating infection can counter population decline. All subsequent methods involve capturing or handling wild animals, which is stressful for the animal (Bliley & Woodley, 2012). These methods and studies should adhere to the 3R principle: replace, reduce, and refine (Zemanova, 2020).

Vaccination

One of the most important interventions for human epidemics is the use of vaccinations. No research has yet been done on *Bsal* vaccines. Vaccine development is expensive and tends to take 10-20 years (Saleh et al., 2021). If a vaccine were to be developed, an effective and long-term vaccination campaign would need to be set up to vaccinate fire salamanders in the wild.

Relocation

If *Bsal* is detected in a known fire salamander habitat, it is an option to catch the remaining population before they all get infected. After capture, they can be relocated to a *Bsal*-free natural habitat (translocation) or held captive until such habitat is available (repatriation). Most amphibian relocations to new habitats are successful, with the most commonly reported

difficulties relating to the physical and biotic environment (Parker & Fitzgerald, 2024), as well as human-disturbance at the release site (Pellitteri-Rosa et al., 2008).

Captivity

Fire salamanders can be held in captivity by a research facility or zoo, if there are no suitable habitats available at the time of relocation. Captive animals have no added ecological value, but can act as a reserve population and be repatriated when circumstances allow. Keeping wild animals captive for a long time means that they cannot perform their natural behaviour as they would in the wild. Ideally, captivity is only a temporary situation. It could however take months or even years before suitable habitats are available for repatriation. In the meantime, wild animals are being kept and bred, not for their well-being but for the concept of biodiversity. An additional complicating factor in the case of zoos, is that they have a commercial interest in the animals they are safekeeping and might not want to give up their population after re-establishment of the species in the wild.

Treatment

There are multiple potential treatments against a *Bsal* infection. As *Bsal* disrupts the skin microbiome (Bletz et al., 2018), fortifying their natural microbiome or applying probiotics that are harmful to *Bsal* could prevent or treat infection (Rebollar et al., 2020, Bletz et al., 2013).

The antifungal drug itraconazole has proven effective against *Bsal* infections in fire salamanders, even in individuals with severe skin lesions and has already worked *in situ* for *Bd* (Plewnia et al., 2023, Hudson et al., 2016). Uncareful use, however, could lead to antifungal resistance. Itraconazole is not *Bsal*-specific and most likely disrupts the skin microbiome of the salamander.

Most ectothermic amphibians perform induced fever as a pathogen response, a behavior where they actively seek out a warm environment and raise their body temperature to fight the pathogen (Cabanzo-Olarte et al., 2024). In a study by Blooi et al. (2015) fire salamanders infected with *Bsal* were kept at 25°C for 10 days, which fully cleared the infection. A study done in Vietnam has found Tam Dao salamanders (*Paramesotriton deloustali*) infected with *Bsal*, in natural water with temperatures between 20–25 °C (Laking et al., 2017). It is unclear whether this was induced fever or whether *Bsal* could still grow under these conditions. The critical maximum (lethal) temperature of caudates is about 35°C (Hutchison, 1961). Placing *in situ* floor-level temperature baths at temperatures lethal to *Bsal* but safe for fire salamanders, could attract the animals to induce fever and clear themselves of infection. The bath water could be a suitable and non-invasive spot to monitor the presence of *Bsal*.

Genetic engineering

Natural selection can lead to population recovery if there is variation in susceptibility or mortality to a pathogen. The common fire salamander is 100% susceptible to *Bsal* upon interacting with the pathogen, with a hundred percent chance of death after infection (Martel et al., 2018). No increase in host tolerance or resistance has been measured so far (Erens et al., 2023). In native disease dynamics, the host and the pathogen often have an ‘arms race’, where neither can

eradicate the other due to competitive evolution (Van Valen, 1973). The fire salamander has had no evolutionary time to develop an effective immune reaction against *Bsal*. If the genetic component of the host response to *Bsal* could be more precisely pinpointed, it would be possible to perform transgenic germline editing on embryos to introduce resilience in wild populations. It would be preferable to introduce reduced mortality instead of resistance to infection. Increasing resistance can change the transmission dynamics and create an evolutionary pressure to 'overthrow' the resistance, which is less likely with tolerance (Venesky et al., 2012).

The variation in survival of *Bd* in the southern corroboree frog (*Pseudophryne corroboree*) was found to be linked to the major histocompatibility complex (Kosch et al., 2018). Similar research for *Bsal* and the fire salamander has not been done, but Verbrugghe, Pasmans, and Martel have found four stable reference genes that are active during *Bsal* infection, which could be helpful to further investigate the anti-*Bsal* response's genetics (Verbrugghe et al., 2019).

There are at least three true salamander species (Salamandridae) susceptible to *Bsal* but with a chance to recover without intervention (Martel et al., 2014). One of these species might be a suitable transgenic donor.

Instead of genetically engineering the salamanders, it could be possible to engineer the pathogen *Bsal* in a way that reduces the susceptibility or mortality rate. No research has been conducted yet on the possibilities of genetically altering chytrid fungi. Introducing a genetically modified fungus in the environment could affect local ecology if host specificity changes. It also has the potential to 'escape' to its native environment and impact ecosystem stability there.

Public opinion tends to be divided on the ethics of genetic engineering, and societal opposition might become an issue when policy is developed around the modification of wild animals (Busch et al., 2021). The modification of natural beings in accordance with human needs and beliefs brings about an array of philosophical questions about our place in the natural world, whether we are obliged to intervene if technology allows, or if problematic human domination is merely taking a new shape (Sandler, 2019).

Summary table methods

All methods discussed in the previous sections are summarised in the table below (see Table 1). None of the methods that were evaluated scored a 'yes' for each criterion.

Table 1 <i>Summary of evaluation criteria for methods in chapter 'Conservation Methods'.</i>							
Method	Protects the fire salamander	Short-term effect	Long-term effect	Relatively low cost	Easy to execute	Legal, safe and ethical	<i>In situ</i> applied
<i>Not doing anything</i>	no	no	no	yes	yes	no	no
Wildlife trade ban	maybe	no	yes	yes	no	yes	no
'Clean trade'	maybe	no	maybe	yes	yes	yes	no
Monitor	no	no	no	maybe	yes	yes	no
Increase habitat size	maybe	maybe	yes	no	maybe	yes	yes
Improve connectivity	maybe	maybe	maybe	no	maybe	maybe	yes
Introduce beavers	maybe	maybe	yes	maybe	maybe	yes	yes
Microcrusta. restoration	maybe	yes	yes	maybe	maybe	yes	yes
Reduce canopy cover	maybe	yes	no	yes	yes	maybe	yes
Refugia	yes	yes	yes	maybe	maybe	yes	yes
Chem. disinf. of environm.	yes	yes	no	yes	yes	no	yes
Probiotics in environm.	maybe	yes	maybe	no	maybe	maybe	yes
Introduce mycoparasites	maybe	yes	maybe	no	no	maybe	yes
Public awareness	no	maybe	maybe	yes	yes	yes	no
Vaccination	yes	yes	maybe	no	no	maybe	yes
Relocation	yes	yes	maybe	maybe	maybe	maybe	yes
Captivity	yes	yes	no	maybe	yes	maybe	no
Probiotic treatment	maybe	yes	no	maybe	maybe	maybe	maybe
Antifungal treatment	yes	yes	no	yes	maybe	maybe	maybe
Temperature treatment	yes	yes	no	yes	maybe	yes	maybe
Gen. en. fire salamander	yes	no	yes	no	no	maybe	yes
Genetic engineer. <i>Bsal</i>	maybe	maybe	yes	no	no	maybe	yes
Note. Methods are listed in order of appearance in the chapter 'Conservation Methods', except for <i>not doing anything</i> , which is included for the 'Discussion' chapter. Methods were evaluated according to criteria described in the section 'Evaluation criteria for methods'. Additional notes on whether the method is short- or long-term in effect and whether it is applied in situ are included to support the discussion. Each criterion is scored as 'yes' (green), 'maybe' (yellow), or 'no' (red), based on evidence from the 'Conservation Methods' chapter; if no literature was available, 'maybe' or personal judgement was used.							

Discussion

Considering the continued decline in population and the high likelihood of extinction of *Salamandra salamandra* within one hundred years, current conservation efforts are not sufficient to protect this species. As I presented before, there is no single, 'perfect' method to protect the fire salamander from *Bsal*. Full eradication of *Bsal* in Europe is unlikely at this point, thus, a conservation strategy needs to be geared towards endemic coexistence. A conservation strategy for coexistence should 1) make the fire salamander resilient to *Bsal* and 2) restore the habitat. Habitat restoration is both an ultimate necessity for the long-term conservation of fire salamanders, as well as a proximate solution to slow down the spread of *Bsal* and retain as much of the current metapopulation as possible, until resilience is achieved.

The most effective strategy to achieve resilience is through the synthetic introduction of variation in host response to *Bsal* infection, rather than through natural or artificial selection for tolerance or resistance. This is because the common fire salamander is 100% susceptible and suffers 100% mortality when interacting with the pathogen (Martel et al., 2018). Although there has been some fire salamander persistence in infected habitats, it is always accompanied by a severe reduction in abundance, which even a decade later showed no sign of recovery (Erens et al., 2023).

The fact that there is some level of population persistence is most likely due to anti-parasite behaviour or behavioural pathogen avoidance. However, populations with such reduced abundance are especially vulnerable to extirpation and cannot effectively perform their ecological role. This means intervention by genetic engineering is the only remaining option to facilitate durable persistence. Genetically modified individuals can be introduced to infected habitats to recover the population, but they should also be introduced to uninfected habitats. By introducing them multiple generations before *Bsal* arrival, resilience can spread through the population and prevent genetic deterioration from a selective sweep. Further research on synthetic variation in immune response could include comparative infection transcriptomics with related species, developmental effects of major histocompatibility complex gene multiplication, and microbiome immune response interactions.

Obtaining resilience to *Bsal* includes not disrupting the salamander's natural immune defense and skin microbiome. Methods which are dysregulatory to the microbial ecosystem, such as the introduction of mycoviruses, fungicidal fungi, genetically modified *Bsal*, chemicals, or fungicides should therefore be avoided. Any method that requires repeated capture and handling of wild fire salamanders, such as vaccinations and *in situ* medical intervention, should be avoided due to the intensive labor, short-term effects, and stress for the animals. Captivity effectively protects the fire salamander against *Bsal* but removes it from its ecological role. It should only be considered when extirpation is at hand, and then only with the aim of repatriation. Translocation to an unoccupied *Bsal*-free habitat or a refugium combined with *ex situ* treatment should be preferred.

Fire salamander resilience to *Bsal* is an essential step for non-threatening host-pathogen coexistence, but does not eliminate the risk of extinction. A resilient population will still have increased mortality compared to the pre-*Bsal* situation and needs habitat restoration to obtain population stability. Increased habitat connectivity could promote spread from infected habitats, but fortifies local abundance (Bolte et al., 2023). Habitat connectivity is an important aspect of

ecosystem restoration, and where possible, should be applied, despite the risk of increasing spread. In places where connectivity cannot be improved, enlargement could still help to increase the population size. Habitat enlargement is expensive, but should be included in long-term plans. In the meantime, improvement of existing habitat could slow down the spread of *Bsal* by reducing pathogen load in infected habitats and slowing down the spread to uninfected habitats.

Beaver introduction is another promising avenue within habitat restoration, since all known *Bsal*-infected habitats are within the native range of the beaver. Beavers create more shallow waters for fire salamanders to breed in and elevate water temperatures by reducing canopy cover. Improved water quality restores microcrustaceans that prey on *Bsal*. Elevated water levels could even help against human-mediated spread by submerging hiking routes. Although beaver introduction would be beneficial for the fire salamander, conservation efforts will have to contend with resistance from farmers and nature recreationists.

Large-scale habitat restoration is a marathon, not a sprint. In this context, human-mediated refugia can provide a temporary safe haven from *Bsal*. As with beaver introduction, a reduction of canopy density and microcrustacean restoration may reduce *Bsal* prevalence, with systematic monitoring of pathogen presence further complementing these effects. Human-mediated refugia need management, and although it is not a long-term solution, it could support fire salamander populations until durable habitat restoration and genetic resilience are achieved. Human access to the refugium should be restricted to prevent human-mediated *Bsal* spread.

Science tends to view itself as separate from politics, but especially in urgent conservation problems such as the fire salamander and *Bsal*, our political reality must be considered. There is a lack of political commitment for the conservation of the fire salamander at the level of policy, implementation, and execution. The 'clean trade' policy, public awareness, and captive breeding are indirect, low-effect efforts, which are executed poorly, despite the legal obligation by the EU to limit the spread of *Bsal*. Effective legislative tools such as a wildlife trade ban are not even being considered, due to political prioritization of free market values over nature conservation.

Conservation science cannot wait on political will but must take the lead. The cause of the fire salamander population decline and subsequent risk of extinction is anthropogenic, which means that not doing anything is morally not permissible. Conservation should not be contingent on policy and political processes, because these tend to be volatile and subject to change. Research on genetic resilience to *Bsal* can be conducted independently of political commitments. Habitat restoration has repeatedly been hypothesised and proven to be effective for species conservation and should be applied for the fire salamander to prove its practical value (Rannap et al., 2009, Rannap et al., 2024).

As long as wildlife trade continues, the threat of disruptive, invasive disease looms, driving native species to extinction, and triggering cascading ecological collapse. There are very few *in situ* studies on fire salamander conservation or *Bsal*. Testing methods that can be executed as a singular intervention in the field could effectively contribute to conservation and provide valuable information that lab studies cannot recreate. By leveraging ecological and evolutionary processes such as stabilisation through biodiversity and introducing genetic variation, singular interventions can create a positive feedback loop that simultaneously protects

salamanders and ecosystems, leading to lasting recovery. This also means applied conservation methods should be ecologically considerate and not be at the expense of cohabiting species, but either target-specific or focused on ecosystem restoration.

Although political will for conservation may be absent today, generating overwhelming, field-based proof of what works can provide future generations with compelling evidence on effective restoration methods. By conducting practical conservation research on *Bsal* and the fire salamander, ecosystems could be restored through research and, in the future, serve as a model for both invasive disease management and habitat restoration.

Statement on the use of AI

Artificial Intelligence (AI) was used to assist with language translation and text formatting.

References

Andersson, A. A., Tilley, H. B., Lau, W., Dudgeon, D., Bonebrake, T. C., & Dingle, C. (2021). CITES and beyond: Illuminating 20 years of global, legal wildlife trade. *Global Ecology and Conservation*, 26, e01455. <https://doi.org/10.1016/j.gecco.2021.e01455>

Auliya, M., García-Moreno, J., Schmidt, B. R., Schmeller, D. S., Hoogmoed, M. S., Fisher, M. C., Pasmans, F., Henle, K., Bickford, D., & Martel, A. (2016). The global amphibian trade flows through Europe: The need for enforcing and improving legislation. *Biodiversity and Conservation*, 25, 2581–2595. <https://doi.org/10.1007/s10531-016-1206-9>

Baláž, V., Gortázar Schmidt, C., Murray, K., Carnesecchi, E., Garcia, A., Gervelmeyer, A., Martino, L., Munoz Guajardo, I., Verdonck, F., Zancanaro, G., Fabris, C., & European Food Safety Authority (EFSA). (2017). Scientific and technical assistance concerning the survival, establishment and spread of *Batrachochytrium salamandrivorans* (Bsal) in the EU. *EFSA Journal*, 15(2), e04739. <https://doi.org/10.2903/j.efsa.2017.4739>

Barge, E. G., Leopold, D. R., Rojas, A., Vilgalys, R., & Busby, P. E. (2022). Phylogenetic conservatism of mycoparasitism and its contribution to pathogen antagonism. *Molecular Ecology*, 31(10), 3018–3030. <https://doi.org/10.1111/mec.16436>

Becker, C. G., Rodriguez, D., Longo, A. V., Talaba, A. L., & Zamudio, K. R. (2012). Disease risk in temperate amphibian populations is higher at closed-canopy sites. *PloS one*, 7(10), e48205. <https://doi.org/10.1371/journal.pone.0048205>

Beranek, C. T., Clulow, J., & Mahony, M. (2020). Wetland Restoration for the Threatened Green and Golden Bell Frog (*Litoria aurea*): Development of a Breeding Habitat Designed to Passively Manage Chytrid-Induced Amphibian Disease and Exotic Fish. *Natural Areas Journal*, 40(4), 362–374. <https://doi.org/10.3375/043.040.0409>

Berger, L., Speare, R., Daszak, P., Green, D. E., Cunningham, A. A., Goggin, C. L., Slocombe, R., Ragan, M. A., Hyatt, A. D., McDonald, K. R., Hines, H. B., Lips, K. R., Marantelli, G., & Parkes, H. (1998). Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences of the United States of America*, 95(15), 9031–9036. <https://doi.org/10.1073/pnas.95.15.9031>

Beukema, W., Erens, J., Schulz, V., Stegen, G., Spitzen-van der Sluijs, A., Stark, T., Laudelout, A., Kinet, T., Kirschey, T., Poulain, M., Miaud, C., Steinfartz, S., Martel, A., & Pasmans, F. (2021). Landscape epidemiology of *Batrachochytrium salamandrivorans*: Reconciling data limitations and conservation urgency. *Ecological Applications*, 31(5), e02342. <https://doi.org/10.1002/eap.2342>

Bletz, M. C., Grant, E. H. C., & DiRenzo, G. (2025). Quantitative support for the benefits of proactive management for wildlife disease control. *Conservation Biology*, 39(1), e14363. <https://doi.org/10.1111/cobi.14363>

- Bletz, M. C., Kelly, M., Sabino-Pinto, J., Bales, E., Van Praet, S., Bert, W., Boyen, F., Vences, M., Steinfartz, S., Pasmans, F., & Martel, A. (2018). Disruption of skin microbiota contributes to salamander disease. *Proceedings of the Royal Society B: Biological Sciences*, 285(1885), 20180758. <https://doi.org/10.1098/rspb.2018.0758>
- Bletz, M. C., Loudon, A. H., Becker, M. H., Bell, S. C., Woodhams, D. C., Minbiole, K. P. C., & Harris, R. N. (2013). Mitigating amphibian chytridiomycosis with bioaugmentation: Characteristics of effective probiotics and strategies for their selection and use. *Ecology Letters*, 16(6), 807–820. <https://doi.org/10.1111/ele.12099>
- Bliley, J. M., & Woodley, S. K. (2012). The effects of repeated handling and corticosterone treatment on behavior in an amphibian (*Ocoee salamander: Desmognathus ocoee*). *Physiology & Behavior*, 105(5), 1132–1139. <https://doi.org/10.1016/j.physbeh.2011.12.009>
- Blooi, M., Martel, A., Haesebrouck, F., Vercammen, F., Bonte, D., & Pasmans, F. (2015). Treatment of urodelans based on temperature dependent infection dynamics of *Batrachochytrium salamandrivorans*. *Scientific Reports*, 5, 8037. <https://doi.org/10.1038/srep08037>
- Bolte, L., Goudarzi, F., Klenke, R., Steinfartz, S., Grimm-Seyfarth, A., & Henle, K. (2023). Habitat connectivity supports the local abundance of fire salamanders (*Salamandra salamandra*) but also the spread of *Batrachochytrium salamandrivorans*. *Landscape Ecology*, 38, 1537–1554. <https://doi.org/10.1007/s10980-023-01636-8>
- Bosch, J., Sanchez-Tomé, E., Fernández-Loras, A., Oliver, J. A., Fisher, M. C., & Garner, T. W. J. (2015). Successful elimination of a lethal wildlife infectious disease in nature. *Biology Letters*, 11(11). <https://doi.org/10.1098/rsbl.2015.0874>
- Cabanzo-Olarte, L. C., Cardoso Bicego, K., & Navas Iannini, C. A. (2024). Behavioral responses during sickness in amphibians and reptiles: Concepts, experimental design, and implications for field studies. *Journal of Thermal Biology*, 123. <https://doi.org/10.1016/j.jtherbio.2024.103889>
- Carter, E. D., DeMarchi, J. A., Wilber, M. Q., Miller, D. L., & Gray, M. J. (2024). *Batrachochytrium salamandrivorans* is necronotic: carcasses could play a role in Bsal transmission. *Frontiers in Amphibian and Reptile Science*, 2. <https://doi.org/10.3389/famrs.2024.1284608>
- Chen, G., Lau, A., Wan, B., Poon, E. S. K., Fung, H. S., Lee, W. H., Sung, Y.-H., & Sin, S. Y. W. (2023). Occurrence of pathogenic chytrid fungi *Batrachochytrium salamandrivorans* and *Batrachochytrium dendrobatidis* in the Hong Kong newt (*Paramesotriton hongkongensis*) and other wild and imported amphibians in a subtropical Asian region. *Journal of Wildlife Diseases*, 59(4), 709–721. <https://doi.org/10.7589/JWD-D-22-00145>
- CITES. (n.d.). *Species database*. Convention on International Trade in Endangered Species of Wild Fauna and Flora. Accessed May 4, 2025, from <https://cites.org/eng/disc/species.php>
- Council of Europe. (1979). *The Bern Convention: Presentation*. Accessed May 4, 2025, from <https://www.coe.int/en/web/bern-convention/presentation>
- Erens, J., Preissler, K., Speybroeck, J., Beukema, W., Spitzen-van der Sluijs, A., Stark, T., Laudelout, A., Kinet, T., Schmidt, B. R., Martel, A., Steinfartz, S., & Pasmans, F. (2023). Divergent population responses following salamander mass mortalities and declines driven by the emerging pathogen *Batrachochytrium*

salamandrivorans. *Proceedings. Biological sciences*, 290(2007), 20230510.
<https://doi.org/10.1098/rspb.2023.0510>

European Commission. (2018). *Commission Implementing Decision (EU) 2018/320 of 28 February 2018 on measures to prevent the introduction into the Union of the fungus *Batrachochytrium salamandrivorans* (Bsal)*. Official Journal of the European Union, L 62, 18–23. Retrieved from <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A02018D0320-20191202>

Food and Agriculture Organization. (n.d.). *Agricultural land (% of land area) – European Union*. <https://www.fao.org/>

Galindo-Bustos, M. A., Brousset Hernandez-Jauregui, D. M., Cheng, T., Vredenburg, V., & Parra-Olea, G. (2014). Presence and prevalence of *Batrachochytrium dendrobatidis* in commercial amphibians in Mexico City. *Journal of Zoo and Wildlife Medicine*, 45(4), 830–835. <https://doi.org/10.1638/2014-0023.1>

Gilbert, M. J., Spitzen-van der Sluijs, A. M., Canessa, S., Bosch, J., Cunningham, A. A., Grasselli, E., Laudelout, A., Lötters, S., Miaud, C., Salvidio, S., Veith, M., Martel, A., & Pasmans, F. (2020). *Mitigating Batrachochytrium salamandrivorans in Europe: Batrachochytrium salamandrivorans action plan for European urodeles*. European Commission, Directorate-General Environment. <http://bsaleurope.com/wp-content/uploads/2021/03/Bsal-Action-Plan.pdf>

Grant, E. H. C., Muths, E. L., Katz, R. A., Canessa, S., Adams, M. J., Ballard, J. R., Berger, L., Briggs, C. J., Coleman, J. T. H., Gray, M. J., Hopkins, M. C., Harris, R. N., Hossack, B., Huyvaert, K., Kolby, J. E., Lips, K. R., Lovich, R. E., McCallum, H. I., Mendelson, J. R. III, ... White, C. L. (2016). *Salamander chytrid fungus (Batrachochytrium salamandrivorans) in the United States—Developing research, monitoring, and management strategies* (Open-File Report No. 2015–1233). U.S. Geological Survey. <https://doi.org/10.3133/ofr20151233>

Greig, H. S., McHugh, P. A., Thompson, R. M., Warburton, H. J., & McIntosh, A. R. (2022). Habitat size influences community stability. *Ecology*, 103(1), e03545. <https://doi.org/10.1002/ecy.3545>

Heard, G. W., Thomas, C. D., Hodgson, J. A., Scroggie, M. P., Ramsey, D. S. L., & Clemann, N. (2015). Refugia and connectivity sustain amphibian metapopulations afflicted by disease. *Ecology Letters*, 18(8), 853–863. <https://doi.org/10.1111/ele.12463>

Hester van Santen. (3 september 2013 dinsdag). Nieuwe schimmel vernietigt salamander. *NRC Handelsblad*. <https://advance-lexis-com.proxy-ub.rug.nl/api/document?collection=news&id=urn%3acontentItem%3a598-P-63B1-JC8W-Y263-00000-00&context=1519360&identityprofileid=Z3QWZ756943>.

Hoenig, B. D., Böning, P., Plewnia, A., & Richards-Zawacki, C. L. (2024). A Simplified, CRISPR-Based Method for the Detection of *Batrachochytrium salamandrivorans*. *EcoHealth*, 22(1), 161–171. <https://doi.org/10.1007/s10393-024-01690-x>

Hossack, B. R., Gould, W. R., Patla, D. A., Muths, E., Daley, R., Legg, K., & Corn, P. S. (2015). Trends in Rocky Mountain amphibians and the role of beaver as a keystone species. *Biological Conservation*, 187, 260–269. <https://doi.org/10.1016/j.biocon.2015.05.005>

Hudson, M. A., Young, R. P., Lopez, J., Martin, L., Fenton, C., McCrea, R., Griffiths, R. A., Adams, S.-L., Gray, G., Garcia, G., & Cunningham, A. A. (2016). In-situ itraconazole treatment improves survival rate

during an amphibian chytridiomycosis epidemic. *Biological Conservation*, 195, 37–45. <https://doi.org/10.1016/j.biocon.2015.12.041>

Hutchison, V. H. (1961). Critical Thermal Maxima in Salamanders. *Physiological Zoology*, 34(2), 92–125. <http://www.jstor.org/stable/30152688>.

IUCN. (2024). *The IUCN Red List of Threatened Species*. Version 2024-3. Accessed on May 4, 2025, from <https://www.iucnredlist.org>

IUCN SSC Amphibian Specialist Group. (2023). *Salamandra salamandra*. *The IUCN Red List of Threatened Species* 2023: e.T59467A219148292. <https://dx.doi.org/10.2305/IUCN.UK.2023-1.RLTS.T59467A219148292.en> Accessed on 04 May 2025.

Kosch, T. A., Silva, C. N. S., Brannelly, L. A., Roberts, A. A., Lau, Q., Marantelli, G., Berger, L., & Skerratt, L. F. (2018). Genetic potential for disease resistance in critically endangered amphibians decimated by chytridiomycosis. *Animal Conservation*, 22(3), 238–250. <https://doi.org/10.1111/acv.12459>

Laking, A. E., Ngo, H. N., Pasmans, F., Martel, A., & Nguyen, T. T. (2017). *Batrachochytrium salamandrivorans* is the predominant chytrid fungus in Vietnamese salamanders. *Scientific Reports*, 7, Article 44443. <https://doi.org/10.1038/srep44443>

Martel, A., Blooi, M., Adriaensen, C., Van Rooij, P., Beukema, W., Fisher, M. C., Farrer, R. A., Schmidt, B. R., Tobler, U., Goka, K., Lips, K. R., Muletz, C., Zamudio, K. R., Bosch, J., Lötters, S., Wombwell, E., Garner, T. W., Cunningham, A. A., Spitzen-van der Sluijs, A., Salvidio, S., ... Pasmans, F. (2014). Wildlife disease. Recent introduction of a chytrid fungus endangers Western Palearctic salamanders. *Science (New York, N.Y.)*, 346(6209), 630–631. <https://doi.org/10.1126/science.1258268>

Martel, A., Spitzen-van der Sluijs, A., Blooi, M., Bert, W., Ducatelle, R., Fisher, M. C., Woeltjes, A., Bosman, W., Chiers, K., Bossuyt, F., & Pasmans, F. (2013). *Batrachochytrium salamandrivorans* sp. nov. causes lethal chytridiomycosis in amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, 110(38), 15325–15329. <https://doi.org/10.1073/pnas.1307356110>

Minteer, B. A., & Collins, J. P. (2008). From Environmental to Ecological Ethics: Toward a Practical Ethics for Ecologists and Conservationists. *Science and Engineering Ethics*, 14(4), 483–501. <https://doi.org/10.1007/s11948-008-9087-0>

Morales, A., Sibrián, X., & Porras, F. D. (2021). Survey of Beak and Feather Disease Virus (BFDV) in Guatemalan Neotropical Psittacine Birds. *Journal of Avian Medicine and Surgery*, 35(3), 325–332. <https://doi.org/10.1647/20-00042>

Nguyen, T. T., Nguyen, T. V., Ziegler, T., Pasmans, F., & Martel, A. (2017). Trade in wild anurans vectors the urodelan pathogen *Batrachochytrium salamandrivorans* into Europe. *Amphibia-Reptilia*, 38(4), 554–556. <https://doi.org/10.1163/15685381-00003125>

Parker, M. R., & Fitzgerald, L. A. (2024). Using life history to predict outcomes of conservation translocations of herpetofauna. *Animal Conservation*. <https://doi.org/10.1111/acv.13009>

Pellitteri-Rosa, D., Gentili, A., Sacchi, R., Scali, S., Pupin, F., Razzetti, E., Bernini, F., & Fasola, M. (2008). Factors affecting repatriation success of the endangered Italian agile frog (*Rana latastei*). *Amphibia-Reptilia*, 29(2), 235–244. <https://doi.org/10.1163/156853808784124910>

- Plewnia, A., Lötters, S., Veith, M., Peters, M., & Böning, P. (2023). Successful drug-mediated host clearance of *Batrachochytrium salamandrivorans*. *Emerging Infectious Diseases*, 29(2), 411–414. <https://doi.org/10.3201/eid2902.221162>
- Porco, D., Purnomo, C. A., Glesener, L., Proess, R., Lippert, S., Jans, K., Colling, G., Schneider, S., Stassen, R., & Frantz, A. C. (2024). eDNA-based monitoring of *Batrachochytrium dendrobatidis* and *Batrachochytrium salamandrivorans* with ddPCR in Luxembourg ponds: taking signals below the Limit of Detection (LOD) into account. *BMC Ecology and Evolution*, 24(1), 4. <https://doi.org/10.1186/s12862-023-02189-9>
- Rannap, R., Kübarsepp, K., Lepik, I., & Rannap, J. (2024). Extensive restoration of the entire habitat complex is key to the successful recovery of threatened species: The case of the natterjack toad *Epidalea calamita* at the northern range margin. *Journal for Nature Conservation*, 82. <https://doi.org/10.1016/j.jnc.2024.126707>
- Rannap, R., Lõhmus, A., & Briggs, L. (2009). Restoring ponds for amphibians: A success story. In B. Oertli, R. Céréghino, J. Biggs, S. Declerck, A. Hull, & M. R. Miracle (Eds.), *Pond conservation in Europe* (pp. 297–316). Springer. https://doi.org/10.1007/978-90-481-9088-1_20
- Rebollar, E. A., Martínez-Ugalde, E., & Orta, A. H. (2020). The Amphibian Skin Microbiome and Its Protective Role Against Chytridiomycosis. *Herpetologica*, 76(2), 167–177. <https://doi.org/10.1655/0018-0831-76.2.167>
- Ribas, M. P., Cabezón, O., Velarde, R., Estruch, J., Serrano, E., Bosch, J., Thumsová, B., & Martínez-Silvestre, A. (2022). Coinfection of Chytrid Fungi in Urodeles during an Outbreak of Chytridiomycosis in Spain. *Journal of Wildlife Diseases*, 58(3), 658–663. <https://doi.org/10.7589/JWD-D-21-00170>
- Saleh, A., Qamar, S., Tekin, A., Singh, R., & Kashyap, R. (2021). Vaccine Development Throughout History. *Cureus*, 13(7), e16635. <https://doi.org/10.7759/cureus.16635>
- Sandler, R. (2020). The ethics of genetic engineering and gene drives in conservation. *Conservation Biology*, 34: 378–385. <https://doi.org/10.1111/cobi.13407>
- Schmidt, B. R., Bozzuto, C., Lötters, S., & Steinfartz, S. (2017). Dynamics of host populations affected by the emerging fungal pathogen *Batrachochytrium salamandrivorans*. *Royal Society Open Science*, 4(3), 160801. <https://doi.org/10.1098/rsos.160801>
- Smith, A., Tetzlaff, D., Gelbrecht, J., Kleine, L., & Soulsby, C. (2020). Riparian wetland rehabilitation and beaver re-colonization impacts on hydrological processes and water quality in a lowland agricultural catchment. *The Science of the Total Environment*, 699, 134302. <https://doi.org/10.1016/j.scitotenv.2019.134302>
- Spitzen – van der Sluijs, A., Gilbert, M., Lambriks, N., & Herder, J. (2022, August 22). *Inventarisatie aanwezigheid B. salamandrivorans in Nederland op basis van eDNA*. Nederlandse Voedsel- en Warenautoriteit (NVWA). <https://www.nvwa.nl/binaries/nvwa/documenten/dier/dierziekten/overige-dierziekten/publicaties/verspreidingsonderzoek-salamanderschimmel-bsal/verspreidingsonderzoek-salamanderschimmel-bsal.pdf>

Spitzen-van der Sluijs, A., Martel, A., Asselberghs, J., Bales, E. K., Beukema, W., Bletz, M. C., ... & Lötters, S. (2016). Expanding distribution of lethal amphibian fungus *Batrachochytrium salamandrivorans* in Europe. *Emerging infectious diseases*, 22(7), 1286. <https://doi.org/10.3201/eid2207.160109>

Spitzen-van der Sluijs, A., Spikmans, F., Bosman, W., de Zeeuw, M., van der Meij, T., Goverse, E., Kik, M., Pasmans, F., & Martel, A. (2013). Rapid enigmatic decline drives the fire salamander (*Salamandra salamandra*) to the edge of extinction in the Netherlands. *Amphibia-Reptilia*, 34(2), 233-239. <https://doi.org/10.1163/15685381-00002891>

Spitzen-van der Sluijs, A., Stegen, G., Bogaerts, S., Canessa, S., Steinfartz, S., Janssen, N., ... & Martel, A. (2018). Post-epizootic salamander persistence in a disease-free refugium suggests poor dispersal ability of *Batrachochytrium salamandrivorans*. *Scientific reports*, 8(1), 3800. <https://doi.org/10.1038/s41598-018-22225-9>

Stegen, G., Pasmans, F., Schmidt, B. R., Rouffaer, L. O., Van Praet, S., Schaub, M., Canessa, S., Laudelout, A., Kinet, T., Adriaensen, C., Haesebrouck, F., Bert, W., Bossuyt, F., & Martel, A. (2017). Drivers of salamander extirpation mediated by *Batrachochytrium salamandrivorans*. *Nature*, 544(7650), 353–356. <https://doi.org/10.1038/nature22059>

Van Valen L (1973) A new evolutionary law. *Evol Theory* 1:1–30

VectorStock. (2025). *Various vector images*. <https://www.vectorstock.com>

Venesky, M. D., Mendelson, J. R. III, Sears, B. F., Stiling, P., & Rohr, J. R. (2012). Selecting for tolerance against pathogens and herbivores to enhance success of reintroduction and translocation. *Conservation Biology*, 26(4), 586–592. <https://doi.org/10.1111/j.1523-1739.2012.01854.x>

Verbrugghe, E., Pasmans, F., & Martel, A. (2019). Reference gene screening of *Batrachochytrium dendrobatidis* and *Batrachochytrium salamandrivorans* for quantitative real-time PCR studies. *Scientific Reports*, 9, Article 18534. <https://doi.org/10.1038/s41598-019-54582-4>

Zemanova, M. A. (2020). Towards more compassionate wildlife research through the 3Rs principles: moving from invasive to non-invasive methods. *Wildlife Biology*, 2020(1). <https://doi.org/10.2981/wlb.00607>

Zipkin, E. F., & DiRenzo, G. V. (2022). Biodiversity is decimated by the cascading effects of the amphibian-killing chytrid fungus. *PLoS pathogens*, 18(7), e1010624. <https://doi.org/10.1371/journal.ppat.1010624>

Zwolicki, A. (2025). Can beavers canopy alterations affect managed forests more than natural forests?. *Forest Ecology and Management*, 577, 122407. <https://doi.org/10.1016/j.foreco.2024.122407>