Title: Proactive management outperforms reactive strategies for wildlife disease control

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All authors contributed to project development and design and facilitation of expert elicitation. GD and EHCG wrote the original occupancy model. MCB updated model code, wrote simulation code, and ran all models. MCB wrote first draft of manuscript, created figures and tables, and shiny app. GD & EHCG assisted with writing and editing of the manuscript. GD & EHCG obtained funding for the project.

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Abstract
Finding effective pathogen mitigation strategies is one of the biggest challenges humans face today. In the context of wildlife, emerging infectious diseases have repeatedly caused widespread host morbidity and population declines of numerous taxa. In areas yet unaffected by a pathogen, a proactive management approach has the potential to minimize or prevent host mortality. However, we typically lack critical information on the disease dynamics in a novel host system, have limited empirical evidence on efficacy of management interventions, and lack validated predictive models. As such, quantitative support for identifying effective management interventions is largely absent, and the opportunity for proactive management is often missed. Here, we consider the potential invasion of the chytrid fungus, *Batrachochytrium salamandrivorans*, whose expected emergence in North America poses a severe threat to hundreds of salamander species in this global salamander biodiversity hotspot. We developed and parameterized a dynamic multi-state occupancy model to forecast host and pathogen occurrence, following expected emergence of the pathogen, and evaluated the response of salamander populations to different management scenarios. Our model forecasts that taking no action is expected to be catastrophic to salamander populations. We also show that proactive action is expected to maximize host occupancy outcomes compared to 'wait and see' reactive management, thus providing quantitative support for proactive management opportunities. Additionally, we found that Bsal eradication is unlikely under any evaluated management options. Contrary to our expectations, even early pathogen detection had little effect on Bsal or host occupancy outcomes. Our analysis provides quantitative support that proactive management is the optimal strategy for promoting persistence of disease-threatened salamander populations. Our approach fills a critical gap by defining a framework for evaluating management options prior to pathogen invasion and can thus serve as a template for addressing novel disease threats that jeopardize wildlife and human health.

Introduction

The Anthropocene can be succinctly characterized by the sentiment expressed in Joni Mitchell's song, Big Yellow Taxi (1970): "We don't know what we've got, til it's gone." While efficiency in identifying threats to biodiversity has improved (Langwig et al. 2015; Harfoot et al. 2021; Sutherland et al. 2022) and there is often the desire to prevent species and population declines, reactive responses have been the status quo for conservation management (Lindenmayer et al. 2013). This has taken many forms: recovery plans are developed and enacted after species are on the brink of extinction (e.g., (Lindenmayer et al. 2013; Nelson et al. 2019)), corridors are built to reestablish connectivity after habitat is fragmented (e.g., (Haddad et al. 2015; McGuire et al. 2016; Watson et al. 2018)), and restoration activities are undertaken to improve habitat quality that has been degraded by land-use change or pollution (e.g.(Palmer et al. 2016)). The same delays have occurred in disease-related conservation crises; monitoring, research, and mitigation efforts begin only after a pathogen has invaded, caused disease, and jeopardized population persistence (e.g., bats – (Foley et al. 2011), amphibians - (Woodhams et al. 2011; Scheele et al. 2014; Skerratt et al. 2016), plants – (Ristaino et al. 2021)).

During these conservation crises, it is often presumed that reducing risk may be more effective than mitigating the impacts after manifestation of the problem (Drechsler et al. 2011; Martin et al. 2012b; Bloom et al. 2017; Mamo et al. 2020). Quantitative support for this expectation, however, is largely absent from the conservation literature and thus proactive management is rarely implemented (Lindenmayer et al. 2013; Walls 2018; Mamo et al. 2020). Often, before any management action is taken, there is a desire for more field- or lab-based research to reduce uncertainty due to limited empirical data on efficacy of management actions (Bernard & Grant 2019), an inability to precisely predict outcomes for management of a novel threat (Russell et al. 2017), or an imprecise understanding of the decision context (Grant et al. 2017; Canessa et al. 2019). However, delaying management until uncertainty is reduced can curtail opportunities to proactively reduce risk and protect susceptible systems; furthermore, resolving such uncertainties may not affect the best-supported decision in a formal decision analysis (Runge et al. 2011; Canessa et al. 2015). When the primary roadblocks to rapidly addressing a disease threat are knowledge gaps, accommodating all sources of uncertainty in an analysis can provide quantitative evidence for optimizing management decisions in a timely manner. Ahead of a conservation crisis, such estimates can provide the ability to formally compare the relative value of a full set of both proactive and reactive management actions, that is both actions implemented before arrival of the threat as well as those implemented after.

A major emerging issue for natural (and human) systems is the increase in hypervirulent pathogens. Diseases caused by these pathogens pose a substantial threat to worldwide biodiversity and the functioning of human and natural systems (Daszak et al. 2000; Fisher et al. 2020). The global decline of amphibians is a prime example (Scheele et al. 2019; Fisher & Garner 2020); *Batrachochytrium dendrobatidis* (Bd) is suspected to have led to the decline and extinction of hundreds of amphibian species (Scheele et al. 2019). In many systems, the threat was not identified until after declines were documented. For others, declines occurred after the threat was identified and despite there being improved knowledge of the threat to the system; many amphibian species are still at risk of extinction from chytridiomycosis despite decades of research (Lips et al. 2006; Bower et al. 2019; Fisher & Garner 2020). Even when there has been advanced knowledge of the risk to naïve populations, management is typically undertaken reactively (i.e., after Bd has been detected and has impacted a region; e.g., (Zippel et al. 2011; Gratwicke & Murphy 2016; Harding et al. 2016; McFadden et al. 2018), foregoing an opportunity to implement proactive management (i.e., actions implemented to reduce or mitigate the disease threat before it is introduced into a naïve system).

In 2013, a new pathogenic chytrid fungus of amphibians, *Batrachochytrium salamandrivorans* (Bsal), was identified when it invaded and decimated European salamander populations (Stegen et al. 2017; O'Hanlon et al. 2018; Lötters & Vences 2020). To date, Bsal has not been detected in the highly susceptible salamander populations in North America (Klocke et al. 2017; Waddle et al. 2020), a hotspot of global salamander diversity (AmphibiaWeb 2023). Thus, North America has a unique opportunity to proactively manage populations and habitats to prepare susceptible amphibian communities for the imminent invasion of Bsal (Grant et al. 2016; Grear et al. 2021; Gray et al. 2023). Since 2013, the scientific community has invested in learning about the biology of Bsal and has explored several management actions that could mitigate the effects of Bsal in laboratory settings (Van Rooij et al. 2015; Woodhams et al. 2018). Although our knowledge of this biothreat has advanced, the same challenges to initiating management exist. Given the high biodiversity and susceptibility of North American amphibians, there is no direct analog for how a Bsal invasion can be addressed. In this "pre-invasion" period, we cannot precisely predict how Bsal will impact North American amphibian communities, and how management actions will perform in natural ecosystems. Despite this severe uncertainty, managers must still decide how to address this impending disease threat. Deciding how to mitigate Bsal risk (including a decision to delay action) should be based on sound science.

Here, we estimate the potential impacts of Bsal and the outcome of different management interventions on naïve North American amphibian communities in the face of multiple large uncertainties using a novel formulation of a dynamic multi-state occupancy model. Parameterization was possible using a combination of field-derived empirical data and expert elicitation when data were absent. We used our model to (Figure 1A): (i) quantify the risk that Bsal poses to highly susceptible North American amphibian communities, (ii) predict the host-pathogen outcomes of 20 possible management actions under a variety of Bsal invasion scenarios (Table 1), (iii) compare proactive (i.e., implementation prior to pathogen invasion) and reactive (i.e., implementation after pathogen invasion and establishment) management intervention strategies, (iv) estimate the consequences of early vs. late Bsal detection combined with reactive management on host and pathogen occupancy, (v) assess the value of managing different proportions of sites, and (vi) assess the value of switching to a different type of management action after Bsal detection. These quantitative estimates of the system response to a diverse set of possible management actions allow decision-makers across eastern North America to understand the relative effectiveness of proactive management against wait-and-see responses.

Materials and Methods

Methods overview

To evaluate the efficacy of management actions aimed to (i) maximize host persistence and (ii) maximize pathogen-free space, our dynamic multi-state occupancy model tracked six host-pathogen states (SI Appendix Table S1); we parameterized the model using existing data along with best practices and established protocols for formal elicitation of expert judgement (Hanea et al. 2017; Hemming et al. 2018). We ran simulations using the full aggregated probability distributions for all parameters (Table 1) to forecast occupancy of both susceptible host populations and the lethal fungal pathogen 20 years after pathogen invasion under multiple management scenarios: (i) no management, (ii) proactive management (n = 10 actions, SI Appendix, Table 2), (iii) reactive management (n = 10 actions, SI Appendix, Table 2) under four different invasion-response timelines (i.e., the elapsed time between Bsal invasion and management intervention), and (iv) combinations of proactive and reactive management (n = 193) (Figure 1A&B). We also used probabilistic decision trees to compare reactive management outcomes under scenarios of early vs. late detection of the pathogen. The evaluated actions focused on actions that target the host amphibian or the system environment and have been proposed as potential management actions by the North American Bsal Task Force. Visualizations of all aggregate parameter estimates for each action can be found in the SI Appendix.

Dynamic multi-state occupancy model

We assessed the expected impact of Bsal and potential management interventions on populations of susceptible pond-dwelling salamander populations using a novel formulation of a dynamic multi-state occupancy model (see SI Appendix for full model details). We formulated our model and parameter estimate elicitation considering one of the most susceptible and widespread species in eastern North America – the eastern newt (*Notopthalmus viridescens*; (Gray et al. 2023). Eastern newts have one of the largest ranges of North American amphibians –from Canada, south to Florida and west through the Great Lakes and Texas; they are also one of the most abundant amphibians in pond and wetland habitats across its distribution, so estimating the effects and evaluating management responses to Bsal will have implications for temperate forest ecosystems.

Dynamic multi-state occupancy models allow us to predict the annual changes in occurrence of multiple states (i.e., combinations of host and pathogen presence) at a collection of sites (e.g., Miller et al. 2012)). A site, in our model, was defined as an aquatic habitat (e.g., a wetland, pond or pool) inhabited by eastern red-spotted newts. Our model has six combinations of host and pathogen occupancy states (i.e., multiple 'states' of occupancy; Figure 1, Table S1), including two host states (host present or host absent), and three pathogen states (pathogen absent, pathogen present at low prevalence, or pathogen present at high prevalence). The model is also dynamic, meaning it predicts transitions between states through time; nine parameters (Table 1) describe the transitions among the six states from one timestep to the next. These nine parameters include host and pathogen colonization rate, host persistence rates under different pathogen states, pathogen growth rate, pathogen decline rate, and pathogen extinction rates (See Table 1 for details). We assumed that all transition probabilities are constant across all timesteps within a simulation, except host colonization (c_t^H) which is defined by an autologistic function (SI Appendix, Eq. 1). This function makes host colonization probability at a given time *t* dependent on the occupancy of the previous timestep (following Yackulic et al. 2012), which accommodates the site fidelity of the focal host species, eastern newts.

The duration of our simulations was 28 years. In the SI Appendix, we outline transition matrices, equations, and how model details vary among the five main time periods and for the different management scenarios. For the purposes of our model the processes of pathogen invasion and establishment are grouped together, which we refer to as 'invasion' hereafter. A conceptual model of the pathogen invasion and management scenarios (i.e., no management action, only proactive action, only reactive action, and the combination of proactive and reactive management) is presented in Fig. 1.

Management scenarios

We incorporated management via effects on parameters in the transition matrix. We considered four scenarios for the timing of management interventions on host and pathogen persistence: (i) <u>no management scenario</u>, where no action is implemented prior to or after Bsal invasion, (ii) <u>proactive management scenario</u>, where a proactive action is implemented prior to Bsal invasion and continued through the Bsal invasion process until the final timestep, (iii) <u>reactive management scenario</u>, where a reactive action is implemented after Bsal invasion at one of four time intervals (2, 4, 8, or 16 years after Bsal arrival) to evaluate different invasion-response timelines, and (iv) <u>proactive + reactive management scenario</u>, where a proactive action is implemented prior to Bsal arrival and continued through the Bsal invasion process until Bsal is detected at one of the four time intervals, at which time treatment with a different reactive action commences and continues through the final timestep (i.e., we are evaluating the impact of switching actions after Bsal emergence). Note that proactive management scenarios do not switch to become reactive following Bsal invasion. Management scenarios are defined once based on when the implementation of an action started relative to Bsal's presence in the system. (i.e., before or after invasion). Additionally, please note we evaluated a 1-year invasion-response timeline for reactive management for use in two instances: the decision tree analysis (details below) and evaluation of initial invasion dynamics. Details on management simulations are in SI Appendix.

Management actions

We considered 20 management actions (Table 2) that have been proposed as options for Bsal management by the North American Bsal Task Force and amphibian disease researchers (Woodhams et al. 2018; Thomas et al. 2019). Management options included actions that target the host (e.g., vaccination or probiotics) and the environment (e.g., salinity or environmental micropredators). Seven of these actions were considered in both a proactive and reactive context, three were considered solely in a proactive context, and three were considered solely in a reactive context (Table 1). Please note that a given action that has both proactive and reactive implementation has a different definition based on this distinct timing of implementation and parameter rates were elicited independently. We considered some actions (e.g., host probiotic or environmental salinity) as both proactive and reactive due to the possibility of different efficacies depending on the timing of implementation. Others are considered only in one timing or the other (e.g., vaccination and environmental fungicide) because they are unlikely to be implemented in the alterative timing context.

Parameter values and assumptions

Parameter values were obtained from two main sources: empirical data and expert elicitation. Empirical data of newt occupancy from the Chesapeake & Ohio Canal National Historic Park, MD, U.S.A, collected between 2005-2021 were used to inform the autologistic function for host colonization rate (c^H) in our model (data available from https://irma.nps.gov/NPSpecies/). For three 'base' rates (e.g., rates under no management) parameters (d^L, e^S , and e^L), we assumed these probabilities would be close to zero as we have no expectation that Bsal will decline in prevalence (d^L) or become extinct (e^S, e^L) without active management. As such, for d^L and e^S, we assumed a mean of 0.05 (on the logit scale a mean of -2.94 ±0.25 SD), and for e^L, we assumed a mean of 0.01 (on the logit scale a mean of -4.59 ±0.25 SD). Expert elicitation was used to obtain estimates for the remainder of the parameters given the limited empirical data available (explained below). Select reactive management actions (environmental fungicide, hydrological manipulation, and host antifungal), were assumed to have no effect on Bsal colonization rate (c^S) and therefore base rate values for c^S were used during reactive management scenarios for these actions.

Expert elicitation & parameter aggregation

Often, especially in responding to emerging infectious diseases, decisions must be made before empirical data are available, creating a need to estimate model parameters in alternative ways. Ideally, we would use parameter estimates from empirical data and mathematical models to understand the impact that Bsal presents to native North American amphibians, and project the expected system response to management actions. However, when such information is not yet available, expert elicitation is well-suited to scenarios in which uncertainty impedes the decision-making progress, such as in identifying optimal strategies for emerging infectious disease in complex systems (Gustafson et al. 2018; Cook et al. 2021).

We used a formal process of expert elicitation to obtain parameter estimates for our model under no management, proactive, and reactive management strategies. Using standardized protocols, elicitation of expert judgement produces reliable predictions and has been used in a variety of applications (e.g., (O'Hagan et al. 2006; Speirs-Bridge et al. 2010; Runge et al. 2011; Martin et al. 2012a; Adams-Hosking et al. 2016)). Expert elicitation is conducted in a way that reduces bias and fully characterizes uncertainty (Morgan 2014; Sutherland & Burgman 2015). Elicitation is governed by specific protocols that help to avoid inherent biases resulting from cognitive traps including anchoring, availability bias, over confidence, representativeness bias and motivational bias (O'Hagan, 2019). Importantly, we asked about each parameter of the model (Table 1) not the overall expect outcome of an action, which helps limit biases. Following best practices in expert elicitation (Hanea et al. 2017; Hemming et al. 2018), we recruited a diverse set of experts (n = 35), with expertise in amphibian ecology, disease ecology, pathogen biology, and wildlife disease. We divided the experts into four groups composed of eight to ten experts, and we asked each expert group questions associated with four to six distinct management actions; each group answered questions about the base rates with no management and one reactive action (host antifungal treatment) to allow across-group comparison. We conducted two rounds of elicitation to obtain estimates for 158 parameters, following the IDEA ("Investigate, Discuss, Estimate, Aggregate") protocol (Hanea et al. 2017; Hemming et al. 2018) which uses a four-point elicitation method (Speirs-Bridge et al. 2010) and modified Delphi approach for revision (Burgman et al. 2011). This approach allows for linguistic uncertainty to be resolved and experts' unique knowledge to be shared during the discussion phase. Importantly, with expert elicitation, we are not seeking consensus among members but looking to capture the true range of uncertainty for a given parameter. This expert judgement process allowed us to obtain a quantitative expression of an expert's belief for the probabilistic distribution of each of nine model parameters under implementation of a specific action (Table 1).

The four point estimates were used to generate a distribution for each question (i.e., each parameter for a given action) for each expert using quantile matching methods using R (R Core Team, 2022) and package 'fitdistplus' (Delignette-Muller & Dutang 2015). Individual distributions are presented in the SI Appendix – Elicitation distribution plots. An aggregated distribution for each management action-parameter combination, which incorporates both within- and among-expert uncertainty, was calculated using median quantile aggregation (Moore et al. 2022). More specifically, we took the median of the lower bound (2.5% quantile), the median (50% quantile), and the upper bound (97.5%) from the calculated individual-expert distributions. Experts were weighted equally for aggregation (Hemming et al. 2022). Additional details on elicitation and aggregation procedures, including all materials used for the expert elicitation and provided to experts, are available in the SI Appendix.

Simulations

We ran simulations for each of four scenarios: (i) no management, (ii) proactive management (before Bsal invasion), (iii) reactive management under different invasion response timelines (2, 4, 8, and 16 years after Bsal invasion) which represents when a manager commences management intervention in response to pathogen detection that can vary as a result of surveillance intensity, and (iv) combination of proactive and reactive management. Parameter estimates were drawn from the aggregated distributions of each of the nine parameters (Table 1) that govern our dynamic multi-state occupancy model for simulations. In all management model simulations, we used two different Bsal seeding approaches. Under the first approach, Bsal is seeded to one randomly selected site in timestep eight; in the second Bsal seeding approach, Bsal was allowed to stochastically arrive in the system beginning at year eight; that is, we no longer 'seeded' Bsal into the system directly at timestep eight but allow Bsal to arrive based on the Bsal colonization rate to any naïve site. This was carried out to evaluate how proactive management actions may affect initial pathogen establishment dynamics. Simulations for each action or action combination, as well as a baseline simulation of no management action, were run with 100 iterations to predict salamander occupancy 20 years after Bsal invasion. We evaluated ten proactive actions, ten reactive actions, and the combination scenario where different combinations of proactive and reactive actions were implemented sequentially (n=93 total combinations evaluated) to assess the value of switching the type of management after Bsal detection.

Surveillance scenarios with decision trees

Surveillance is required for state-dependent management. The robustness of a surveillance program influences the likelihood of pathogen detection (Heisey et al. 2014). We define a robust surveillance program as one that results in detection within 2 years post pathogen arrival (i.e., early detection) and a limited surveillance program which fails to detect Bsal until 8 years post arrival (i.e., late detection). To quantify the relative benefit of different surveillance intensities, we combined our simulation output with a probabilistic description of the detection and response process (i.e., a decision tree, Figure 1C). To explore different surveillance scenarios, we used this decision tree (Figure 1C) to evaluate the expected values (i.e., weighted averages of a given host and pathogen occupancy outcome) of management actions under different surveillance scenarios: (i) robust surveillance leading to early detection (2 years after Bsal invasion) and (ii) limited surveillance leading to late detection (8 years after invasion). We also evaluated a robust surveillance scenario with the management response implemented 1 year after Bsal invasion (the earliest possible in our yearly model). Decision trees incorporate uncertainty in the likelihood of both Bsal invasion and detection. Because we used an expected value approach, we assumed a risk-neutral profile and results may vary under risk-adverse and risk-seeking profiles.

Final occupancy estimates from the management simulations (i.e., year 28) were used in decision tree calculations. In our expected value calculations, we assumed the probability of Bsal arrival by time t = [2,8] to be 0.60, and the probability of early or late detection was 0.80 under the respective scenarios. These values were not elicited from experts and were used to represent conservative estimates of likelihood of Bsal arrival and successful detection. More details on decision trees and how expected values were calculated can be found in the SI Appendix.

Results

Finding 1: Doing nothing jeopardizes host persistence and leads to high pathogen prevalence

We found that 20 years after Bsal invasion, in the absence of any management, host occupancy is expected to be extremely low (0.15,0-0.72 CI, Figure 2A), and Bsal is expected to occur at a substantial number of sites at high prevalence (0.81,0.55-0.94 CI, Figure 2B). This represents an average loss of over 50% of the newt-occupied sites, and a potential loss of 100% of the newt-occupied sites (lower CI).

Finding 2: Preventing and eliminating Bsal is unlikely

Our model results show that no single management action, proactive or reactive, has the capacity to fully prevent invasion or eradicate Bsal (Figure 3A); thus, achieving "pathogen-free" space is an unrealistic expectation. Both proactive and reactive actions reduced the proportion of Bsal high-prevalence sites compared to no management, but the relative difference varied across management actions (SI Appendix Figure S1, S2). In general, reactive actions (when considering the 2-year invasion-response timeline) resulted in a lower proportion of sites with high Bsal prevalence compared to proactive actions (Figure 3A). However, when we allowed stochastic invasion of Bsal (i.e., Bsal was not seeded into the system– see *Simulation* section in the Methods), proactive actions reduced the proportion of Bsal-occupied sites early in the invasion (i.e., number of sites colonized by Bsal after 3 years) compared to reactive actions (Figure 3B). This suggests that while proactive management cannot protect a system from Bsal invasion, it can slow the invasion process, reducing spread across the habitat network.

Finding 3: Proactive management maximizes host occupancy

In our model simulations, proactive management led to higher host occupancy rates than reactive management 20 years after Bsal invasion (Figure 4). This was true regardless of which proactive management action was used; almost all proactive actions had higher mean host occupancy rates 20 years after Bsal invasion than any reactive action. Two actions – proactive pond pH and high host thinning – which were the worst-performing [proactive] actions were the exception (SI Appendix Figure S3 & S4). While proactively increasing pond pH and implementing high host thinning performed poorly, these actions were still marginally better than nearly all reactive actions, with the exception of reactive implementation of environmental heat and hydrologic manipulation when implemented after 2 years of Bsal invasion. Furthermore, the outcomes of proactive actions had lower uncertainty in predictions of future host occupancy (i.e., narrower confidence intervals) than reactive actions (SI Appendix Figure S3 & S4). Vaccination had the highest estimated mean host occupancy (0.68), and seven of the proactive actions had estimated outcomes greater than 0.50 (SI Appendix Figure S3).

We also explored multiple scenarios relevant for manager decision making as they consider common trade-offs (e.g., the potential of ecological harm, impacts to recreational opportunities, and financial costs), including: (1) evaluating host outcomes across invasion-response timelines for reactive management actions, which is important in contexts (e.g., legal or statutory requirements) that may limit the ability to implement proactive options (SI Appendix Figure S5) and (2) understanding what proportion of sites need be treated to meet desired outcomes for maximizing amphibian persistence (SI Appendix Figure S6-8). Detailed results are in the SI Appendix, but in general, delaying action and failing to manage all host populations is expected to result in reduced host occupancy.

Finding 4: Robust surveillance only marginally improves outcomes under reactive management

Using decision trees, we found that early pathogen detection (i.e., within 2 years after Bsal invasion) had negligible effects on expected Bsal occupancy outcomes (Figure 5A). This was true across management actions and early detection never resulted in greater than a 2.5% reduction in expected Bsal occupancy (Figure 5C). Furthermore, early detection only marginally increased expected host occupancy outcomes (Figure 5B), but the relative benefit did vary across actions (Figure 5D). Even an extremely robust surveillance program, where Bsal is detected within the first invasion year, did not meaningfully improve expected outcomes (SI Appendix Figure S10).

We also compared management scenarios with both proactive and reactive management with decision trees, incorporating uncertainty in the likelihood of both Bsal invasion and detection. This allowed calculation of expected values for all combinations of proactive and reactive actions. Overall, we found that proactive action led to higher expected host occupancy outcomes than reactive action under any detection timeline (SI Appendix Figure S9). This was true even when we considered a rapid reactive response within 1 year of Bsal invasion (SI Appendix Figure S10). See SI Appendix for these results and discussion.

Discussion

Emerging infectious diseases have led to the decline and extinction of a diversity of wildlife species. The increasing number of ecosystems threatened by fungal pathogens present a particularly formidable challenge when it comes to mitigation (Langwig et al. 2015; Fisher et al. 2020). Reducing a novel disease threat is hindered by uncertainty in when and where the pathogen will arrive and compounded by uncertainty in the effectiveness of untested management actions. Despite the common sentiment that acting early for pathogen management may improve host population outcomes, uncertainties often lead to management delays which imperil biodiversity. Using a robust quantitative framework and full accounting of uncertainty, we demonstrate that acting ahead of a disease outbreak is always optimal, providing quantitative evidence to the hypothesis that proactive action may maximize conservation of host populations. We also demonstrate the negative consequences for host persistence when no management occurs and show that early pathogen detection, an often-quoted priority for response (Langwig et al. 2015; MacAulay et al 2022), is not a sufficient wait-and-see compromise for biodiversity conservation.

For North American salamanders, we found that doing nothing jeopardizes host persistence and leads to high pathogen prevalence at infected sites, which aligns with the known high susceptibility of North American salamander species to Bsal (Martel et al. 2014; Gray et al. 2023). The high rate of Bsal occurrence is likely a result of the small Bsal decline probabilities absent any intervention; this stems from pathogen traits such as its ability to infect alternative amphibian and non-amphibian hosts (Martel et al. 2014; Van Rooij et al. 2015; Gray et al. 2023), as well as the ability for the pathogen to persist in the environment (Stegen et al. 2017; Kelly et al. 2021). Our focal species, eastern red-spotted newt, is currently an abundant and widespread keystone predator (Kurzava & Morin 1994; Smith 2006). Based on other systems where abundant and keystone amphibians have precipitously declined, we may anticipate consequences of an unmanaged Bsal invasion of eastern newt communities to include reduced nutrient cycling (e.g.,(Whiles et al. 2006; Capps et al. 2015)), reduced wetland respiration (e.g.,(Whiles et al. 2013)), and cascading bottom-up (e.g., Zipkin et al. 2020) and top-down (e.g.,(Colón-Gaud et al. 2009; Colón-Gaud et al. 2010; Frauendorf et al. 2013; Connelly et al. 2014; Rantala et al. 2015)) effects on ecosystem processes.

Both proactive and reactive management improved host outcomes compared to no action, highlighting the importance of addressing disease threats via management in highly susceptible amphibian communities. Proactive actions, however, are expected to largely outperform nearly every reactive action; this was true when considering reactive management in both early and late detection scenarios. Our results resonate with the finding of others - that the window for effective intervention shrinks rapidly when Bsal outbreaks are not detected quickly or when response is delayed (e.g. Bozutto et al. 2020), and also extend this a step further in that enacting management proactively can substantially increase the potential benefit of management to host populations. While proactive actions often lack quantitative evidence in conservation decisions impeded by uncertainty, our findings address that directly; our results provide strong support to the benefit of implementing proactive actions. Surprisingly, relatively simple proactive actions (e.g., increasing habitat complexity), are expected to outperform even quickly implemented, and more intensive, reactive actions (e.g., environmental fungicide). Proactive actions have the potential to impact system dynamics in the early stages of the invasion, which could in part explain our findings.

It may be possible to improve host outcomes by performing multiple management actions simultaneously that target different aspects of the disease-host-environment interaction, including multiple proactive actions. For example, combining environmental heat, which targets the environment, and host probiotics, which targets modulation of host immunity, could achieve additive or synergistic benefits. Such combinations, however, may also increase the potential for harm to non-target parts of the system, and increase uncertainty in projecting the population outcomes. For example, each action may include potential impacts to (1) other components of the ecosystem, (2) recreational opportunities, and (3) financial costs of management. Additionally, the limited understanding of the potential additive or synergistic impacts of simultaneous action can increase uncertainty in projecting potential population outcomes, which makes identifying the best strategy challenging. Here we have evaluated single actions and shown a clear advantage of proactive action; additional work would need to be undertaken to find which combinations of actions may synergistically improve the host and Bsal outcomes.

While there was a clear advantage of acting proactively for host population outcomes, this was not the case for pathogen occupancy. Preventing establishment or eliminating Bsal - regardless of management timing - was highly improbable. Thus, achieving "pathogen-free" space (an often-cited priority; e.g., (Mack et al. 2000; Pluess et al. 2012; Klepac et al. 2013) is extremely unlikely. This aligns with empirical evidence for the effectiveness of Bsal mitigations that have been initiated reactively in Spain, where the implemented mitigation actions failed to eradicate Bsal (Martel et al. 2020). Eradication of wildlife pathogens is indeed rare, though some human and agriculture pathogens have been successfully eradicated with substantial management investments (e.g., Foot and Mouth Disease – (Naranjo & Cosivi 2013)). Difficulty in creating pathogen-free space may not be surprising for reactive actions occurring after pathogen invasion (Langwig et al. 2015). It is, however, more unexpected that proactive actions, which are expected to reduce initial pathogen colonization rates and therefore reduce invasion, were also unlikely to achieve 'pathogen-free' space. With that said, proactive actions did reduce the intensity of early invasion (i.e., number of sites colonized by Bsal after 3 years) compared to reactive actions. This suggests that while proactive management cannot eliminate the arrival of Bsal, it can slow the invasion process, reducing spread across the habitat network and potentially minimize rapid landscape-level spread to new areas – and host mortality. Slowing the spread can allow initiation of management action across the landscape, which can in turn curb disease-associated declines across the range of susceptible amphibian species and reduce cascading ecosystem-level effects.

Implementation of proactive actions may come with tradeoffs (Converse et al. 2013; Grant et al. 2017; Wilson et al. 2019). Indeed, tradeoffs between focal species conservation and other important resource management objectives are central in most wildlife and natural resource management decisions (e.g. Aenishaenslin et al. 2013; Mitchell et al. 2013; Sells et al. 2016; Walter et al. 2021; Hemming et al. 2022). Tradeoffs arise as managers balance multiple objectives – for example, the potential of ecological harm, impacts to recreational opportunities, and financial costs (Gerber et al. 2018; Bernard et al. 2019; Bozzuto et al. 2020). Therefore, while proactive actions maximize host occupancy, it is possible that managers may delay action, e.g., due to fear of unintended consequences to non-target parts of the system or to reduce the costs of management. In such situations, reactive, state-dependent management requires pathogen surveillance and is expected to accommodate these tradeoffs and allow for disease mitigation. Management efficacy is typically linked to the robustness of a surveillance program, which influences the likelihood of pathogen detection (Heisey et al. 2014) as well as cost. While early pathogen detection (i.e., a robust surveillance program) is typically thought to improve outcomes (Miller et al. 2022), we found little evidence for this. Early pathogen detection had negligible effects on Bsal outcomes and only marginally improved host outcomes even when considering scenarios of rapid pathogen detection within the first invasion year. Given the minimal benefit of robust surveillance and likely high price tag of such a program, it will be important to explicitly incorporate cost related objectives in a full decision analysis. Early action may be considerably more cost effective than approaches taken later (McCallum & Jones 2006; Bozzuto et al. 2020). In some cases, proactive actions may 'relieve' the cost burden of a robust and intensive surveillance program when a 'cheap' proactive management outweighs the cost of a robust surveillance program (e.g., Heisey et al. 2014); however, the total cost of proactive management depends on which action is used, and the cost of surveillance depends on how robust it is. Such considerations of economic costs of surveillance vs. management actions have been explore in the invasion species management decision space; and the optimal allocation can depend on spatial pattern, detection rates of the invader, speed of invasion, and other factors (e.g. Chadès et al. 2011; Guillera-Arroita et al. 2014; Rout et al. 2014; Yemshanov et al. 2017). We find that in the case of Bsal, the optimal allocation of resources – when the objective is to maximize host occupancy – may be to initiate proactive management ahead of a pathogen's invasion, instead of a robust surveillance program.

Conservation of biodiversity, now and in the future, will likely always be plagued with high uncertainty. It is important to acknowledge that we have largely used expert elicited values in our model simulations, which should serve as placeholders for field-based empirical data. Indeed, our main goal was to leverage this tool of expert elicitation in the absence of empirical data and couple it with quantitative approaches that accommodate large uncertainties to enable and improve time-sensitive decision making. By leveraging models and accommodating uncertainty, we quantify the critical need for immediate and sustained proactive actions and demonstrate their benefit over reactive management. This robust framework and crucial insights can help support management strategies to safeguard imperiled, disease-threatened wildlife communities.

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Figures and Tables

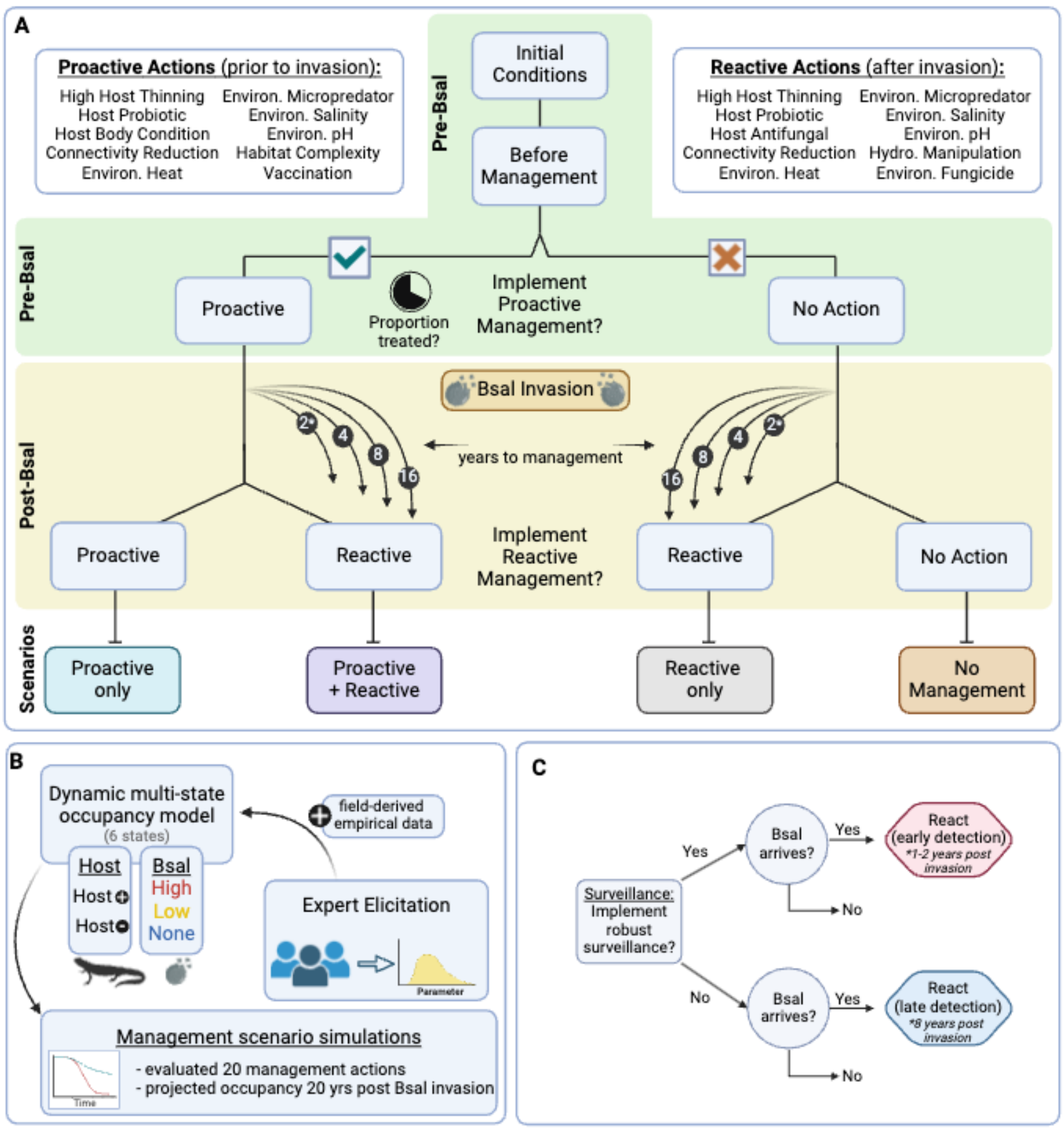

Figure 1. Schematic of quantitative framework. (A) diagram of the four management scenarios for which we ran simulations with the dynamic multi-state occupancy model: no management, reactive only, proactive only, and the combination of proactive and reactive management. Colored background boxes denote the different time periods of the model. Note that proactive management begins prior to Bsal invasion and continues through Bsal invasion and reactive management begins after Bsal invasion. Years

to management are depicted in the Post-Bsal section to represent the invasion-response timelines. There is an asterisk on the 2-year timeline to highlight that we also evaluated a 1-year response timeline (used in the decision trees). Checks and Xs signify implementation (or lack thereof) of the management action, respectively. (B) Flow diagram of steps within our quantitative framework for evaluating the impact of management interventions. The model as six states depicted graphically representing two host states of host present and host absent, and three pathogen states – Bsal at high prevalence (~ 70%), Bsal at low prevalence (~30%), and Bsal absent. (C) Visualization of the decision tree used to estimate the expected value of early versus late detection, which provides a probabilistic description of the detection-response process. Decision tree estimates were done with two scenarios of early detection including 1 year and 2 years post invasion.

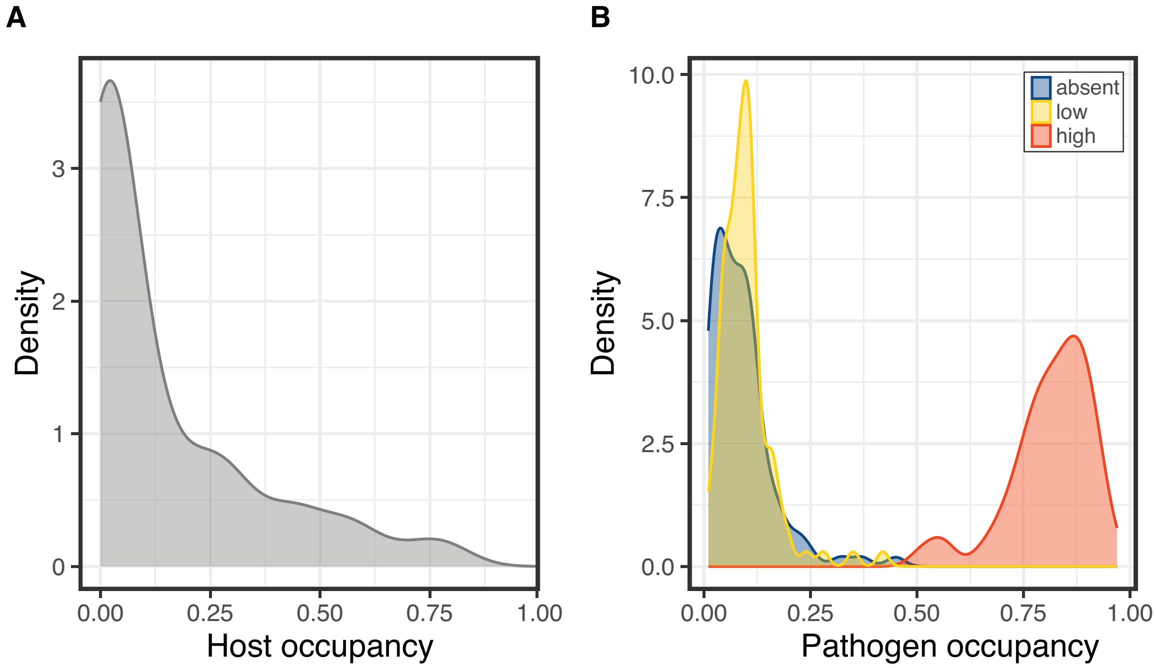

Figure 2. **Host occupancy is greatly reduced and pathogen occupancy at high prevalence is large with no management intervention.** Density plot of expected host occupancy (A) and pathogen occupancy (B) from no management scenario simulations. Colors in B denote three distinct Bsal states of absent (blue), low prevalence (yellow), and high prevalence(red).

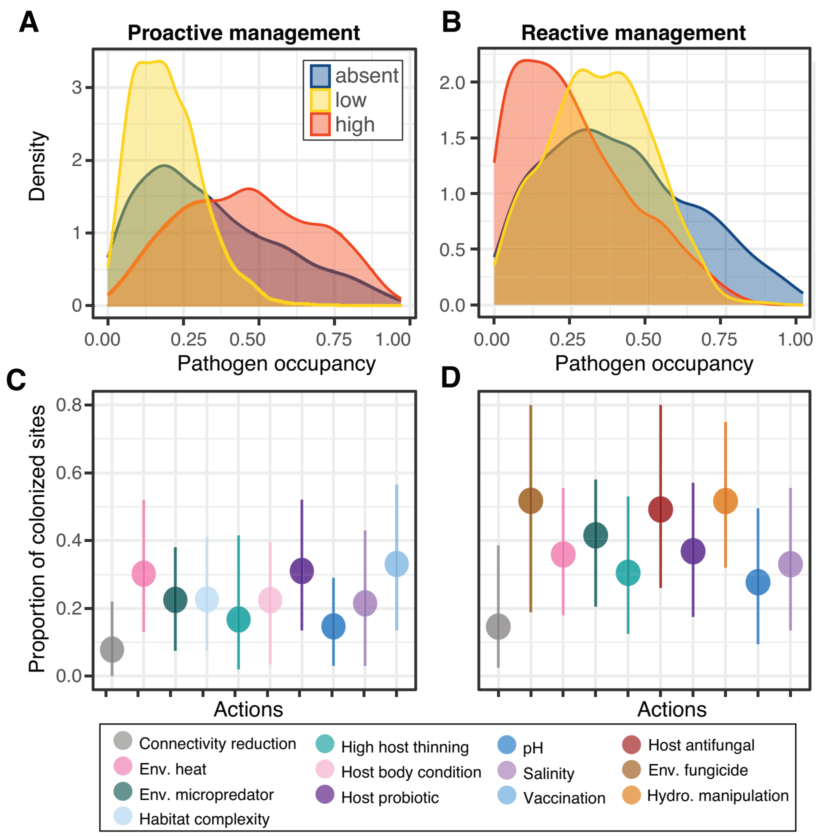

Figure 3. Effects of management on pathogen occupancy. Bsal occupancy 20 years after invasion for proactive (A & C) and reactive (B & D) management scenarios. A & B present average density plots across actions considering treatment of 100% of sites. Colors denote three distinct Bsal states of absent (blue), low prevalence (yellow), and high prevalence (red). Initial colonization of Bsal under individual proactive (C) and reactive (D) management actions. These estimates are from the simulations run to allow stochastic establishment of Bsal based on the annual Bsal colonization rates (i.e., no Bsal seed). Colors represent actions defined in the legend below the plots. Initial colonization estimates are defined as the proportion of sites with Bsal present at low prevalence 2 years after Bsal invasion (i.e., year 11 in the simulations), based on a colonization process described by the annual Bsal colonization rate.

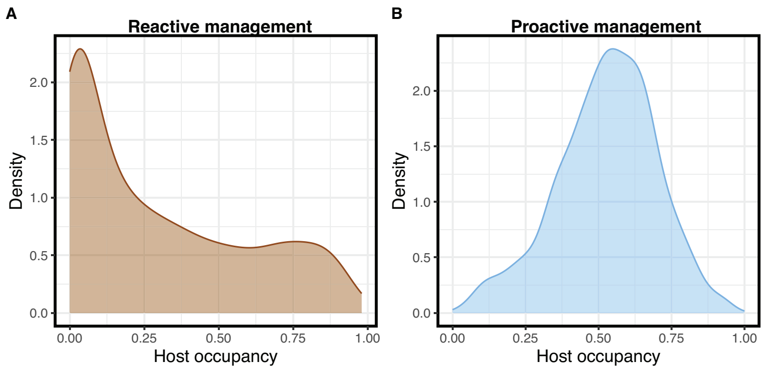

Figure 4. Proactive management yields higher host occupancy outcomes than reactive management. Density plots of host occupancy under (A) reactive and (B) proactive management intervention. Plots present average values across all management actions considering treatment of 100% of sites within the proactive (A) and reactive (B) management scenario. Reactive management here is the 2-year response timeline.

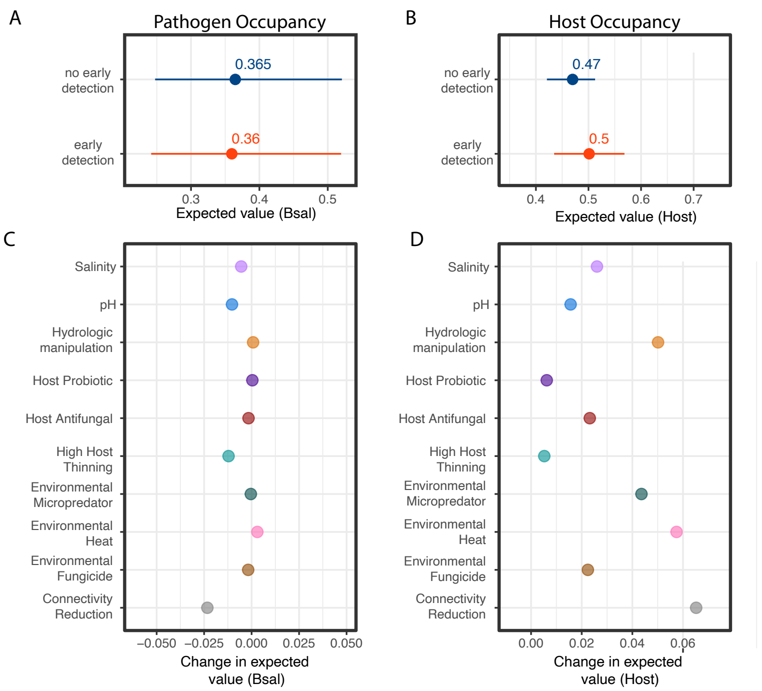

Figure 5. Expected pathogen and host occupancy under different surveillance scenarios (A) Average expected Bsal (A) and host (B) occupancy values under different surveillance scenarios that allow for early (red) vs late (blue) detection. Note that early detection (red) outperforms late detection (blue) when only considering reactive management for host occupancy. Expected change in Bsal (C) and host (D) occupancy when early detection and response occurs for each individual reactive management action. Note for Bsal occupancy there is little change in occupancy with early detection, and for host occupancy (D) for all actions there is an increase (positive value) when early detection and response occurs. All decision tree calculations are performed with outputs from the simulations of treatment of 100% of sites.

Table. 1 Parameters used to estimate initial conditions (psi) and changes between site states through time in our multi-state model.

Parameter	**Description**	**Source**
ψ^{H}	Occupancy of host	Timestep 1 = value was seeded Timestep 2 - 20 = Estimated by the model
c^{H}	The probability the host colonizes a site from t to t+1	Estimated from data Autologistic function
ϕ^{Hb}	The probability the host persists at an uninfected site from t to t+1	Elicited from experts
ϕ^{Hs}	The probability the host persists at an infected site with a small Bsal prevalence from t to t+1	Elicited from experts
ϕ^{HL}	The probability the host persists at an infected site with a large Bsal prevalence from t to t+1	Elicited from experts
g^{S}	The probability Bsal grows from a small to large prevalence at a site from t to t+1	Elicited from experts
c^{s}	The probability Bsal colonizes a site	Elicited from experts
e^{S}	The probability Bsal goes extinct at a site where there is small prevalence from t to t+1	Elicited from experts
e^{L}	The probability Bsal goes extinct at a site where there is large prevalence from t to t+1	Elicited from experts for actions
d^{L}	The probability Bsal declines from large to small prevalence at a site from t to t+1	Elicited from experts for actions

Table 2. Proposed management actions for Bsal and associated definitions and action timings based on the North American Bsal Task Force recommendations. An 'XX' indicates that we did not consider that action-timing combination.

Action Name	Proactive Description	Reactive Description
High host thinning	Removal & euthanasia of >90% of competent amphibian hosts at a site *prior to the arrival of Bsal and during the invasion year*	Removal & euthanasia of >90% of competent amphibian hosts at a site *after Bsal has arrived and established.*
Host probiotic	Augment abundance of local live beneficial bacteria or fungi (1000 – 1M cells) with anti-fungal properties on >80% of competent amphibian hosts; implemented once per month throughout the active season (March - July) *prior to the arrival of Bsal at a site and during the invasion year*	Augment abundance of local live beneficial bacteria or fungi (1000 – 1M cells) with anti-fungal properties on >80% of competent amphibian hosts; implemented once per month throughout the active season (March - July) at a site *after Bsal has arrived and established*
Connectivity reduction	Create barriers via drift fence and netting at a site *prior to the arrival of Bsal and during the invasion year* to limit movement of competent amphibian hosts and other organisms (assume implementation after breeding migration has occurred)	Create barriers via drift fence and netting at a site *after Bsal has arrived and established* to limit movement of competent amphibian hosts and other organisms
Environmental heat	Raise and maintain temperature of water to >25C for at least 10 days in spring *prior to the arrival of Bsal at a site and during the invasion year*. Temperature is raised gradually to allow for acclimation. (Assume the entire amphibian population is present within the aquatic habitats when treatment is implemented either because they are permanent residents or spring migrations have already occurred).	Raise and maintain temperature of water to >25C for at least 10 days in spring at a site *after Bsal has arrived and established*. Temperature is raised gradually to allow for acclimation. (Assume the entire amphibian population is present within the aquatic habitats when treatment is implemented either because they are permanent residents or spring migrations have already occurred.)
Environmental micropredator	Increase abundance of zooplankton by 400% through spring and summer each year *prior to the arrival of Bsal at a site and during the invasion year*	Increase abundance of zooplankton by 400% through spring and summer at a site *after Bsal has arrived and established.*
Salinity	Change salinity of pond (>8 ppt) throughout spring (when ambient and pond conditions are optimal for amphibian activity and Bsal growth) *prior to the arrival of Bsal at a site and during the invasion year.* (Assume the entire amphibian population is present within the aquatic habitats when treatment is implemented either because they are permanent residents or spring migrations have already occurred.)	Change salinity of pond (>8 ppt) throughout spring (when ambient and pond conditions are optimal for amphibian activity and Bsal growth) at a site *after Bsal has arrived and established.* (Assume the entire amphibian population is present within the aquatic habitats when treatment is implemented either because they are permanent residents or spring migrations have already occurred.)
pH	Change pH of pond <5 or >9.5 throughout spring (when ambient and pond conditions are optimal for amphibian activity and Bsal growth) *prior to the arrival of Bsal at a site and during the invasion year* (Assume the entire amphibian population is present within the aquatic habitats when treatment is implemented either because they are permanent residents or spring migrations have already occurred.)	Change pH of pond <5 or >9.5 throughout spring (when ambient and pond conditions are optimal for amphibian activity and Bsal growth) at a site *after Bsal has arrived and established.* (Assume the entire amphibian population is present within the aquatic habitats when treatment is implemented either because

		they are permanent residents or spring migrations have already occurred.)
Habitat complexity	Increase habitat complexity in aquatic sites to affect contact rates *prior to the arrival of Bsal at a site and during the invasion year*	XX
Vaccination	Vaccinate >80% of competent amphibian hosts via a series of four exposure/clearance regimes with live Bsal; implemented once per year at the start of the active season *prior to the arrival of Bsal at a site and during the invasion year*	XX
Host body condition	Improve body condition of competent amphibian hosts, i.e., by continuous food supplementation or habitat improvement to increase invertebrate abundance *prior to the arrival of Bsal at a site and during the invasion year*	XX
Host antifungal	XX	A course of topical itraconazole treatments applied to 80% of competent amphibian hosts at a site *after Bsal has arrived and established*. Assume a course of itraconazole bath treatments follows methods and concentrations found effective for Bd [e.g. 5 min baths with 0.25 ug/mL (0.0025 %) itraconazole for 5 consecutive days]
Hydrologic manipulation	XX	Capture and remove all amphibians; remove water from ponds to completely dry the substrate at a site *after Bsal has arrived and established*; allow to refill naturally. Reintroduce Bsal-free amphibians after ponds refill (assume captured amphibians are uninfected or cleared of Bsal infection prior to release).
Environmental fungicide	XX	Capture and remove all amphibians and complete a course of fungicide applications (e.g. Virkon) in aquatic habitat substrate, including in water, sediment and submerged aquatic vegetation at a site *after Bsal has arrived and established.* Reintroduce Bsal-free amphibians once Virkon has biodegraded to a safe level (assume captured amphibians are uninfected or cleared of Bsal infection prior to release)