Conservation translocations for amphibian species threatened by chytrid fungus: A review, conceptual framework, and recommendations

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Abstract
Emerging infectious diseases are an increasingly prominent threat to biodiversity. However, traditional methods in conservation generally have limited efficacy in the face of disease threats. Ironically, although unintentional human movement of species has facilitated the spread of pathogens, intentional conservation translocations are a promising approach to combatting disease threats under certain circumstances. Here, we summarize two decades of published literature on translocations of Australian frogs threatened by chytridiomycosis—a fungal disease that has caused amphibian declines and extinctions globally. We identify key motivations, considerations, and factors associated with outcomes, including the role of chytridiomycosis in failures. In an effort to improve success, we then propose a conceptual framework for determining when conservation translocations may be both feasible and beneficial, with a focus on understanding mechanisms favoring host persistence. Lastly, we build on our findings from the review and the conceptual framework to develop a set of recommendations to guide practitioners aiming to translocate amphibians as a conservation strategy in the face of chytridiomycosis. Although diseases pose a unique set of challenges for managing declining species in the wild, we argue that progress is likely with careful and well-informed adaptive management experiments to refine reintroduction and translocation efforts.

KEYWORDS
adaptive management, anurans, Batrachochytrium dendrobatidis, disease, endangered species, mitigation translocation, population augmentation, reintroduction
1 | INTRODUCTION

Since the mid-20th century, there has been a major increase in the volume and speed at which biological materials are transported across the world, with the unintended consequence of facilitating the introduction of pathogens into naïve environments (Fisher et al., 2012). Pathogen emergence has been associated with dramatic and sometimes catastrophic species die-offs. Emerging pathogens pose a major management challenge because traditional approaches to conserve biodiversity are often ineffective in the face of disease threats (Mendelson et al., 2006). For example, many conservation strategies focus on habitat protection or directly reducing human impact (e.g., preventing overharvesting; Diaz et al., 2019). Similarly, pathogen eradication and classic disease control measures (e.g., vaccination) are often impractical for mitigating infectious diseases of wildlife where multiple host species, often with short generation times, interact over broad geographic ranges (Garner et al., 2016; Scheele et al., 2014; Woodhams et al., 2011). Ironically, despite the role of human-facilitated dispersal in disease emergence, where pathogen eradication is impossible and traditional disease control measures fail, animal translocations may have an essential role in assisting in the long-term conservation of biodiversity.

At a global scale, the most notable example of pathogen-driven declines in wildlife is the amphibian disease chytridiomycosis, which is implicated in the decline of at least 501 species (Scheele et al., 2019). Chytridiomycosis results from infection with one of two species of pathogenic fungi, *Batrachochytrium dendrobatidis* (hereafter *Bd*, discovered in 1998; Berger et al., 1998; Longcore, Pessier, & Nichols, 1999) and *Batrachochytrium salamandrivorans* (hereafter *Bsal*, discovered in 2013; Martel et al., 2013). Both chytrid species are thought to have originated in East Asia (O’Hanlon et al., 2018) and have been spread by humans, particularly through wildlife trade (Martel et al., 2014). Ninety species are presumed extinct (Scheele, Pasmans, et al., 2019), and many more species are at risk of extinction in coming decades as a result of ongoing disease impacts in populations that survived initial epidemics (Scheele et al., 2017; Scheele, Pasmans, et al., 2019; Skerratt et al., 2016). These catastrophic amphibian declines have had a range of cascading ecosystem effects, such as declines in snakes in the Neotropics (Zipkin, DiRenzo, Ray, Rossman, & Lips, 2020).

*Batrachochytrium dendrobatidis* is now endemic across most environmentally suitable regions (Fisher, Garner, & Walker, 2009; Murray et al., 2011), meaning that amphibian conservation efforts must be planned in the context of *Bd*. A broad range of management actions have been proposed in response to chytridiomycosis (reviewed in Garner et al., 2016; Scheele et al., 2014; Woodhams et al., 2011). One set of actions that holds substantial promise are conservation translocations (Scheele et al., 2019). We consider conservation translocations as “the deliberate movement of organisms from one site to another where the primary objective is a conservation benefit” (Berger-Tal, Blumstein, & Swaisgood, 2020; IUCN/SSC, 2013). Under the umbrella term “conservation translocations,” we include (a) reintroduction of animals into areas from which they have been extirpated with the goal of establishing a population; (b) population augmentation, where animals are released into areas supporting conspecifics to increase population viability; (c) assisted colonization, where animals are released outside their indigenous range with the goal of establishing a population; and (d) mitigation translocation, where animals are relocated from habitat slated for destruction and released to an alternative site. In the first three cases, source animals may come directly from extant wild populations or captive breeding efforts.

The amphibian decline crisis has led to the establishment of numerous captive breeding programs for species at risk of extinction caused by chytridiomycosis (Harding, Griffiths, & Pavajeau, 2016). Following the development of the global Amphibian Conservation Action Plan in 2007 (Gascon et al., 2007), there has been a substantial increase in the total number of captive breeding programs, and a greater focus on threatened species (Harding et al., 2016). Many of these captive breeding programs have multiple goals, including the short-term goal of establishing a captive insurance population—which can be aided by combining captive breeding efforts with biobanking (Howell et al., 2021)—and the longer-term goal of releases to the wild (Zippel et al., 2011). Although translocations are popular conservation actions, they generally have low success rates and require considerable resources (Armstrong & Seddon, 2008; Berger-Tal et al., 2020; Griffiths & Pavajeau, 2008). Yet, as our understanding of both amphibian and *Bd* ecology increases, new approaches to conservation translocations for *Bd*-threatened species hold promise (Mendelson III, Whitfield, & Sredl, 2019).

Herein, we first present a brief review of two decades of translocation efforts for Australian frogs threatened by chytridiomycosis, identifying key factors associated with translocation success or failures, including the role of *Bd*. We then propose a conceptual framework for when and where translocations may be both feasible and beneficial for amphibian species threatened by chytridiomycosis, by considering mechanisms that favor host persistence. Lastly, building on insights from the Australian review and the conceptual framework, we then develop a set of
| Source | Species (IUCN status) | Translocation type | Release strategy (years of release) | Monitoring | Results | Bd monitoring and impact | Outcome |
|--------|-----------------------|-------------------|-------------------------------------|------------|---------|-------------------------|---------|
| Klop-Toker et al. (2021) | *Litoria aurea* (VU) | Mitigation translocation, population augmentation, and other (experimental) | 10,000 tadpoles released into experimental sites, 40,000 tadpoles released into compensation wetlands (2015–2017) | Four years of capture-mark-recapture surveys. Frogs swabbed for Bd | Population persistence throughout 4-year study period. Breeding in several ponds. Population increase of 1,200% | Observed lower survival due to Bd, some potential success altering habitat (salinity) to lower Bd | Highly successful |
| Brannelly et al. (2016) | *Litoria variegata alpina* (VU) | Population augmentation | 1,241 subadults released in autumn at 4 sites (2013) | 1–3× weekly surveys in the following spring and again in the year after. Recaptured frogs swabbed for Bd | Breeding occurred in spring following release. No marked released or extant animals found the following season | Bd infection intensity and prevalence was high and increased throughout the breeding season | Partially successful |
| McFadden et al. (2016) | *Pseudophryne pengilleyi* (CR) | Reintroduction | 785 tadpoles and eggs, 160 subadults and 49 adults released at 2 sites (2010–2014) | Annual monitoring to detect mature males and egg clutches | Survivorship of a small proportion of released tadpoles to maturity at the two sites. 14 males detected in 2014, 20 males and eggs in 4 nests (12–15 clutches) in 2015 | Bd present at release sites | Partially successful |
| Koehler, Gilmore, and Newell (2015) | *Litoria raniformis* (EN) | Mitigation translocation | 1,900 tadpoles, 324 subadults, and 156 adults captured from to be developed dam and released at new wetlands (2010/2011) | 0.3–0.6× annually for 3 year. Released frogs and dead/sick (n = 3) frogs swabbed for Bd | Breeding may have occurred in first year but not in subsequent years and population gradually declined | Bd present, but impact may have been reduced due to environmental temperatures unfavorable for Bd | Failure |
| Hoskin and Puschendorf (2014) | *Litoria lorica* (CR) | Reintroduction | 20 males and 20 females (17 carrying eggs) released over 2 year, 4 km upstream from only known site of occurrence (2013/2014) | Reproduction occurred at new site | Bd present at release site | Highly successful |
| McFadden, Hunter, Harruff, Pietsch, and Scheele (2010) | *Litoria booroolongensis* (CR) | Reintroduction | Juveniles collected from site and bred in captivity, 610 juveniles released in summer (2008) | Survivorship of natural populations was lower than translocated population | Bd observed in first year but few released frogs found in the following season | Bd present at site and suspect contributed to relatively low survivorship of released frogs | Partially successful |
| Hunter et al. (2010) | *Pseudophryne corroboree* (CR) | Reintroduction | 2,000 tadpoles release into 20 artificial pools (2008–2010) | Tadpole counts prior to metamorphosis | Survivorship to metamorphosis increased compared to natural populations | One pool was infected with Bd | Partially successful |
| Hunter et al. (2010) | *Pseudophryne corroboree* (CR) | Reintroduction | 211 adults released across two sites (2006) | 6× per site for 4 year. Recaptured animals swabbed for Bd | Estimated survivorship 1–17% with some breeding observed | One recaptured frog Bd+ | Partially successful |
| Daly, Johnson, Malolakis, Hyatt, and Pietsch (2008) | *Litoria aurea* (VU) | Reintroduction | 6,000 tadpoles released over 3 year (2005–2007) | 32 total surveys over 2 year | 12 tadpoles, 2 metamorphlings, and 2 adults observed | Bd not detected at release site but present in frogs sampled near the release site | Failure |

(Continues)
| Source                          | Species (IUCN status) | Translocation type                      | Release strategy (years of release)                                                                 | Monitoring                                                                 | Results                                                                 | Bd monitoring and impact | Outcome |
|--------------------------------|-----------------------|-----------------------------------------|--------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------|------------------------------------------------------------------------|--------------------------|---------|
| Stockwell, Clulow, Clulow, and Mahony (2008) | *Litoria aurea* (VU)  | Reintroduction                          | 850 tadpoles released, 200 of which were in baskets (2005)                                       | Daily monitoring in baskets and 2-4×/ month in ponds for 1 year. 60 recaptured frogs swabbed for Bd | Gradual decline of juveniles over winter and none seen since March 2006 | Bd prevalence was 53%. Decline attributed to Bd infection | Failure |
| Pyke, Rowley, Shoulder, and White (2008) | *Litoria aurea* (VU)  | Reintroduction                          | 10,878 tadpoles released over 11 releasing events into excavated ponds (1998–2004)            | Weekly to monthly monitoring for 7 year                                    | No breeding, some calling males, low survivorship to adulthood          | No screening. No signs of Bd were observed | Failure |
| White and Pyke (2008)           | *Litoria aurea* (VU)  | Mitigation translocation and population augmentation | 3 adults from to be developed wetland and 200 captive-bred tadpoles released at extant site (2000/2001) | 8 year of regular surveys                                                | Breeding commenced and adult population estimated at 50 individuals in 2008 | No screening                  | Highly successful |
| White and Pyke (2008)           | *Litoria aurea* (VU)  | Reintroduction                          | Tadpoles and juveniles released at excavated ponds (1996–2000)                                | Opportunistic                                                             | Low survivorship to metamorphosis and no breeding                      | No screening                  | Failure |
| White and Pyke (2008)           | *Litoria aurea* (VU)  | Other (experimental)                    | Tadpoles released in artificial, fenced-off pond (1998–2000)                                  | Weekly to fortnightly monitoring                                          | Some breeding occurred until Bd invaded site                           | Dead frogs Bd+             | Partially successful |
| Hunter (2007)                   | *Pseudophryne corrobore* (CR) | Population augmentation                | Eggs collected from site and 2,761 released at late stage the following spring (1997)      | Fortnightly surveys for 2 year                                             | Survivorship to metamorphosis increased by 30% but had no discernible effect on adult numbers | Suspected tadpoles would have become infected with Bd and caused mortality after reaching metamorphosis | Partially successful |

Note: All species listed were primarily threatened by chytridiomycosis. Translocation type was determined according to Linhoff et al. (2020). Outcome was categorized by the authors as highly successful, partially successful, or failure, based on IUCN criteria (Soorae, 2010).
recommendations to guide practitioners and improve future translocation efforts for amphibians threatened by Bd. Although much general guidance is available for translocations (Armstrong & Seddon, 2008; IUCN/SSC, 2013; Linhoff et al., 2020; Taylor et al., 2017), specific advice on undertaking these conservation actions in the context of chytridiomycosis is lacking.

2 | REVIEW OF AUSTRALIAN FROG TRANSLOCATIONS

In this section, we provide some brief background on chytridiomycosis in Australia and review published translocations involving Australian frog species threatened by Bd. Chytridiomycosis was first described in Australia in 1997 and has been the focus of extensive research and management efforts (Berger et al., 2016; Skerratt et al., 2016). Retrospective sampling of museum specimens indicates that Bd has been present in Australia since at least 1978 and the first frog declines thought to be linked to Bd date from 1979 (Scheele, Skerratt, Grogan, et al., 2017). In total, 43 of Australia’s 238 frog species have declined or become extinct because of Bd, with declines concentrated along the temperate and tropical eastern ranges (Scheele, Skerratt, Grogan, et al., 2017). Of the species that declined but remain extant, population trajectories are highly variable; 6 species are experiencing ongoing declines, 8 species appear stable, and 11 species are recovering (Scheele, Skerratt, Grogan, et al., 2017). Australia represents a valuable case-study as the impacts of Bd are relatively well-understood and a range of translocations have been undertaken and documented for Bd-threatened amphibian species.

We searched the literature for reports of Australian frog translocations using Google Scholar and checked the reference lists of all translocation studies identified. We found reports of 15 translocations in the published literature for species threatened by Bd (Table 1). Eight studies (53%) reported reintroductions, four (27%) reported mitigation translocations, four (27%) featured population augmentations, and two (13%) included experimental translocations (Linhoff et al., 2020) (some studies reported multiple translocation types). Two (13%) translocations involved eggs, ten (67%) involved tadpoles, and seven (47%) involved postmetamorphic animals (four studies used a combination of life stages). Outcome success was scored based on the categories used by the IUCN Global Re-introduction Perspectives (Soorae, 2010) and were defined as: highly successful (evidence of reproduction occurred several years post-release), partially successful (animals were recovered for a short time period <1 year, one season of reproduction, and/or animals were present but monitoring continued for <1 year), or failure (very few animals were recovered and/or no reproduction was observed). Three translocations (20%) were considered highly successful, seven (47%) partially successful, and five (33%) failures (note, for simplicity, we did not include the “successful” category used by IUCN). Some factors associated with project success included population augmentation to extant sites, reintroductions to similar habitat in their native range from which frogs had been extirpated, the release of adults versus other life stages, and habitat management (e.g., fish removal). Translocations performed after the discovery of Bd often included prerelease Bd assessments of animals and release sites, and postrelease Bd monitoring. Given the susceptibility of all species involved to chytridiomycosis, and the ubiquitous presence of Bd in the environment, it is likely to have been an important determinant of translocation success (Table 1) (Stockwell et al., 2008). The only highly successful nonpopulation augmentation translocation involved the movement of adults to environmental refuges where Bd had less impact on frogs (Litoria lorica) (Hoskin & Puschendorf, 2014).

Our review indicates that in many cases, failure to specifically address Bd, and mechanisms by which susceptible amphibians may coexist with Bd, is likely to have contributed to translocation failures or only partially successful outcomes. Failure to explicitly address Bd may have been driven by the fact most studies we reviewed were over a decade old and were undertaken at a time when our understanding of mechanisms of coexistence between susceptible amphibian hosts and Bd was limited. Translocations of highly susceptible species occurred within the species’ former ranges and rarely involved habitat modifications to promote coexistence with Bd. Furthermore, virulence of local Bd strains and the degree of evolved resistance/tolerance of translocated hosts were not assessed. Therefore, there is a pressing need to consider the mechanisms that may allow threatened amphibians to persist with Bd and how this can be used to identify circumstances where translocations could be beneficial in the context of Bd.

3 | CONCEPTUAL FRAMEWORK FOR MECHANISMS OF PERSISTENCE AND THE ROLE OF TRANSLOCATIONS

Although our review revealed that many previous translocations had met with limited success, we argue that, with improved knowledge of Bd, increased success is possible under certain conditions. We present a conceptual framework identifying two main contexts in which host species that have suffered declines caused by Bd may persist longer-term (Figure 1). The first context for host persistence involves inducement of a fundamental change in
the underlying host–pathogen–environment interaction in favor of the host, which we call “systemic change.” The second context involves cases whereby population persistence may be possible in the absence of systemic change. Conservation translocations may be a beneficial management strategy in both these contexts under certain circumstances.

The classic declining-population paradigm posits that the agent of decline must be removed or neutralized for a population to persist (Caughley, 1994). The conventional wisdom has since been adapted to imply that conservation translocations will fail if the threat that led to a species’ decline is not first removed or sufficiently reduced.

**FIGURE 1** Conceptual model illustrating the different mechanisms by which susceptible amphibian species may be able to coexist with *Batrachochytrium dendrobatidis*, with examples of how conservation translocations might assist host persistence.
ties, translocation projects involving less likely to be a realistic outcome. Because of these difficulties or sufficiently reducing resistance to Bd (Rachowicz & Vredenburg, 2004) and can survive for weeks in the environment (Johnson & Speare, 2003). Thus, removing or sufficiently reducing Bd in the natural environment is unlikely to be a realistic outcome. Because of these difficulties, translocation projects involving Bd-threatened species are predicted to have low success (Tapley, Bradfield, Michaels, & Bungard, 2015), and translocation failures have been associated with chytridiomycosis (see Table 1) (Joseph & Knapp, 2018; Stockwell et al., 2008). However, we argue that removal of the pathogen is not the only way to ensure host persistence and that translocations can indeed play an important conservation role despite the continued presence of the pathogen.

The main goal of conservation translocations is to establish, re-establish, or to augment a population of the target species to enable it to persist long-term. Although the ideal scenario may involve the species attaining its former abundance and range, the widespread distribution of Bd means this is unlikely. Thus, we consider conservation translocations successful if they promote (a) long-term population persistence over multiple generations, while (b) maintaining appropriate genetic diversity of the target species.

3.1 Systemic change

The shift to coexistence of hosts and novel pathogens is often assumed to require some form of intergenerationally persistent systemic change in the balance of processes that caused the host population to decline initially (Figure 1a) (Brannelly et al., 2021; McKnight et al., 2017). Such processes can be grouped under changes in (a) the host species or host community composition (Figure 1Aa–c), (b) the pathogen (Figure 1AId), or (c) the environment (Figure 1AJe). In practice, systemic change implies that if the pathogen was locally eradicated, then reintroduced, the pattern of disease outbreaks and host declines would not be repeated, as one or more aspects of the system have fundamentally changed.

In the case of increased host resistance/tolerance to infection, there is immunogenetic evidence of positive selection on major histocompatibility complex (MHC) class IIB alleles corresponding with increased field and laboratory survival in some susceptible amphibian species (Savage & Zamudio, 2011, 2016) (Figure 1AIIa). As suggested by Menden-III et al. (2019), populations of hosts with increased resistance/tolerance may act as suitable source populations for conservation translocations with the aim of facilitating redistribution across species’ former range. Ongoing research is also evaluating whether assisted selection targeting MHC genes can be used in captive-breeding programs to improve resistance or tolerance to Bd infection in highly susceptible species, such as the southern corroboree frog (Pseudophryne corroboree) in southeastern Australia (Kosch et al., 2019). Reintroductions of resistant/tolerant animals may then be used to increase the frequency of such phenotypes in wild populations (Figure 1AIIb). It is not yet clear whether non-immunological adaptive changes in phenotype (e.g., earlier maturation; Scheele et al., 2017) are sufficiently heritable or beneficial to be used similarly (Figure 1AIIb).

Systemic changes in the amphibian community could shift Bd dynamics (Figure 1Aic). Within a community, both species composition and population densities can affect Bd dynamics and the environmental Bd zoospore burden (Brannelly et al., 2015; DiRenzo, Langhammer, Zamudio, & Lips, 2014). If initial chytridiomycosis outbreaks result in the extirpation of certain species and/or reductions of population density, then population re-establishment using translocations may be possible, with careful attention focused on community composition and density.

Virulence attenuation in Bd or the presence of hypovirulent Bd lineages could allow amphibian-Bd coexistence (Figure 1AId). Although a study from Panama found no evidence for Bd attenuation over a period of 11–13 years postepidemics (Voyles et al., 2018), Bd lineages do vary in virulence (O’Hanlon et al., 2018). Rapid reductions in virulence have been reported in the laboratory with repeated passage of Bd (Refsnider, Poorten, Langhammer, Burrows, & Rosenblum, 2015). Furthermore, recent research has reported variation in virulence within different isolates of the global pandemic lineage (BdGPL) and the presence of low virulence BdGPL in northern Europe may provide protection for susceptible species from high virulence isolates (Greener et al., 2020). Further work on potential virulence attenuation and hypovirulent lineages is needed to inform how these processes might be considered in translocations.

A systemic change in environmental conditions—such as habitat manipulation to reduce environmental abundance of Bd—may alter the outcome of Bd infection (Figure 1AJe). Given that much has been written about environmental manipulation as a management tool to
reduce \( Bd \) (reviewed in Woodhams et al., 2011; Scheele et al., 2014; Garner et al., 2016) and the conceptual overlap with environmental refugia, we expand on this concept in the following section.

### 3.2 No systemic change

While systemic, intergenerationally persistent changes may facilitate the coexistence of amphibian hosts and \( Bd \), coexistence following disease-associated declines is also possible in the absence of such shifts (Figure 1b). Indeed, host persistence in the face of infection is the classic endemic disease scenario involving density-dependent transmission and the within-generation development of a resistant state (Brauer, Castillo-Chavez, & Feng, 2019) (Figure 1Bla). Cases of disease causing population declines are usually limited to scenarios involving:

- (a) nondensity-dependent transmission (inhomogeneous mixing or vector-borne infections);
- (b) infection reservoirs (biotic or abiotic);
- (c) small population sizes (exacerbated by Allee effects, population bottlenecks and synergistic threatening processes); and
- (d) lags or delays (long demographic time scales of the host, chronic infections, long incubation periods and pathogens affecting fecundity rather than mortality) (de Castro & Bolker, 2005).

Even in these scenarios of decline, host persistence in the absence of systemic change may be possible through several mechanisms. These include (a) metapopulation dynamics and increasing population connectivity (Figure 1Bb); (b) spatiotemporal heterogeneities and persistence in or translocation to refuges (Figure 1Bc); and (c) demographic compensation and the active reduction of other nondisease threats (Figure 1Bd). Conservation translocations may assist the goal of host persistence in each of these scenarios especially by offsetting the risk of extinctions associated with small populations and stochastic dynamics (de Castro & Bolker, 2005).

Maintenance of population connectivity (Figure 1Bb) is crucial for the long-term persistence of many amphibian populations that are vulnerable to extinction resulting from environmental or demographic stochasticity. Indeed, many amphibian populations exist within connected population networks or metapopulations (Marsh & Trenham, 2001). Disease-associated mortalities can undermine population structure and decrease the number of potential emigrants, resulting in extirpation of individual populations and reduced overall network connectivity (Scheele, Foster, et al., 2019). Where metapopulation networks have broken down, connectivity can be artificially maintained through translocations. Although increasing population connectivity through translocations might be expected to increase risk of disease transmission (Hess, 1994), this risk is generally of lesser concern where the pathogen is already endemic throughout the landscape. The human-assisted movement of declined species may greatly increase the speed of recovery given the limited dispersal capacity of many amphibian species (Smith & Green, 2005) and dispersal barriers formed by anthropogenic habitat fragmentation (Cushman, 2006).

Biotic threats such as \( Bd \) can have highly variable impacts across environmental gradients (Figure 1Bb), thus opening the opportunity to identify areas with conditions conducive to species persistence/coexistence, which can then be evaluated as possible candidate translocation sites (Scheele, Foster, Banks, & Lindenmayer, 2017). Scheele, Foster, et al. (2019) outlined three key environment-based mechanisms that can lead to variable population impacts in \( Bd \)-threatened amphibians and are relevant in the context of translocations. First, species can persist in environmental refuges, where \( Bd \)-induced mortality is reduced because environmental conditions are either unfavorable for \( Bd \) growth or more favorable for amphibian immunocompetence. For example, the critically endangered armored mist frog (\( \text{Litoria lorica} \)) in northern Australia was thought to be restricted to rainforest streams but was found in an adjacent dry savannah stream where high insolation appeared to reduce mortality associated with chytridiomycosis (Puschendorf et al., 2011). Second, because amphibian species display high variability in innate susceptibility to \( Bd \), when multiple amphibian species co-occur, host community composition can affect \( Bd \) dynamics (Brannelly et al., 2018; Scheele, Hunter, Brannelly, Skerratt, & Driscoll, 2017). For example, all monitored populations of the critically endangered northern corroboree frog (\( \text{Pseudophryne pengilleyi} \)) in southeastern Australia that co-occur with the reservoir host species, the common eastern froglet (\( \text{Crinia signifera} \)) (Brannelly et al., 2018), have either been extirpated or experienced major declines (Scheele, Hunter, Brannelly, et al., 2017). However, the northern corroboree frog persists in habitats where other amphibian species are absent or at very low abundance, despite the presence of \( Bd \) (Scheele, Hunter, Brannelly, et al., 2017). Third, under certain environmental conditions, \( Bd \)-associated mortality can be offset by high recruitment (Muths, Scherer, & Pilliod, 2011; Scheele, Hunter, Skerratt, Brannelly, & Driscoll, 2015). For example, compensatory recruitment in boreal toads (\( \text{Bufo boreas} \)) in the western United States offsets elevated rates of adult mortality associated with \( Bd \), facilitating population persistence (Muths et al., 2011).

Declining amphibian species commonly face multiple threats (Grant et al., 2016). In such circumstances, the causes of amphibian mortality may be at least partly compensatory (Figure 1Bb) rather than additive (e.g., predation of sick frogs), promoting population persistence despite endemic disease (Anderson & Burnham, 1976). Alternatively, where the effects of these threats are additive,
addressing co-occurring threats may be a feasible approach to promote host persistence (Figure 1BIIIe) (Scheele et al., 2014; West, Todd, Gillespie, & McCarthy, 2020). An example is population modeling indicating that removal of invasive fish from streams with the critically endangered spotted tree frog (*Litoria spenceri*) in southeastern Australia could allow coexistence with *Bd* (West et al., 2020). Another example is the successful re-establishment of the mountain yellow-legged frog (*Rana sierrae*) (a species which has experienced severe declines associated with *Bd*) populations in the United States following control of invasive fish (Knapp et al., 2016). While mitigating other threats offers a potential path forward in some cases, caution is warranted as it is often difficult to determine the relative importance of the various causes of decline, and whether concomitant threats act synergistically.

### 4 Recommendations for Translocations Involving Bd-Threatened Species

Building on our review of published Australian studies and our conceptual framework (Figure 1), we provide recommendations for undertaking amphibian translocations for species threatened by chytridiomycosis (Figure 2). We assume that a decision to undertake a translocation has already been made on the basis of our conceptual framework above (Figure 1) and the guidance provided by other authors in this space, such as Converse and Grant (2019) and Linhoff et al. (2020). Crucially, funding availability for the foreseeable life of the project must be considered before deciding whether to commence a translocation (Linhoff et al., 2020).

#### 4.1 Translocation Objectives

Setting clear, measurable objectives is a core element of any translocation project. In most cases, it is useful to differentiate between fundamental (overall goal) objectives and means objectives (specific goals) (Gregory et al., 2012). The development of fundamental objectives requires engagement of all relevant stakeholders and should be specified in the initial decision-making process on whether to undertake a translocation. Means objectives need to be carefully specified and paired with associated indicators to assess whether the objective is achieved (Ewen, Soorae, & Canessa, 2014). For example, a fundamental objective for a translocation could be the establishment of a self-sustaining population at a release site. Associated means objectives could focus on (a) the rate of survival of released animals, (b) rate of reproduction, (c) offspring survival, and so forth. In each case, indicators can be specified for each means objective. For example, an objective relating to survival may be considered achieved if the survival of released animals exceeds 60% after 6 months. Indicators need to be context-specific and must reflect the life history and ecology of the study species.

While in many cases means objectives will understandably focus on amphibian survival and reproduction, we also encourage the inclusion of objectives that focus on elucidating the processes that facilitate amphibian coexistence with *Bd*. For example, a means objective could be to assess the target species’ capacity to persist at a novel environmental refuge with *Bd*. Specifying indicators associated with amphibian survival, *Bd* dynamics, and environmental conditions will provide valuable information that will improve understanding of why the translocation either
failed or succeeded. Likewise, for many species, important aspects of their ecology remain unknown, and translocation objectives can be included that focus on improving our understanding of species ecology.

Specifying a range of means objectives and associated indicators allows for ongoing assessment throughout the life of the project, which can facilitate adaptive management and iterative program improvement (Tear et al., 2005). More broadly, given the risk of failure for translocations involving Bd-threatened species, specifying clear objectives and associated indicators is crucial when it comes to learning from translocations and determining where improvements are needed.

### 4.2 Contextual model of the system

A key element of translocation planning is the development of a contextual model of the focal system (Scheele et al., 2018). A contextual model is useful for articulating abiotic and biotic processes that may influence site suitability for the target species and potential mechanisms of coexistence with Bd. For example, if Bd is present at the recipient site, what processes are hypothesized to underpin successful population establishment or persistence? What is the optimal life stage to release? Are environmental conditions hypothesized to mediate Bd prevalence and/or infection intensity? For example, Scheele et al. (2014, fig. 3) illustrated seasonal influences on both Bd and P. corroboree populations in Kosciuszko National Park, indicating how management approaches can benefit from an understanding of temporal context. Clearly articulating hypothesized relationships and processes is central in identifying important areas of uncertainty and outlining assumptions. Once key uncertainties are identified, a priori hypotheses can be stated and tested during the translocation (Armstrong & Seddon, 2008). Lastly, while appropriate caution is needed when dealing with high levels of uncertainty, it is important to ensure that management actions for threatened species do not stall (Scheele et al., 2018).

### 4.3 Candidate site identification

For a translocation to succeed, the candidate site must have habitat attributes conducive to the persistence of the species. Methods to assess general habitat suitability are outlined elsewhere (Armstrong & Seddon, 2008; Linhoff et al., 2020). Here, we focus on evaluating candidate sites in the context of whether the process(es) hypothesized/demonstrated to underpin coexistence with Bd in the target species (Figure 1) are likely to operate at those sites. The capacity for environmental conditions to promote coexistence of amphibians with Bd is a key consideration as translocations will generally occur at sites where Bd is now endemic.

Important elements to consider in evaluating whether a site may be conducive to coexistence with Bd include (a) environmental suitability for Bd; (b) amphibian community composition, with a focus on the presence/density of reservoir hosts; and (c) presence of other threatening processes, which may be mitigated by management (e.g., invasive predatory fish). It is also crucial to appraise a site’s vulnerability to stochastic events that may affect recruitment and survival (e.g., drought, flood, fire). This is particularly important as mortality associated with Bd can decrease the capacity of a population to withstand the effect of environmental stochasticity (Scheele et al., 2016). Likewise, it is important to consider how environmental conditions affect demographic factors such as juvenile development rates and age to maturity, which can influence a population’s capacity to persist despite mortality associated with Bd (West et al., 2020).

The broad range of factors that need to be considered when evaluating candidate sites is illustrated in the example of the critically endangered spotted tree frog (L. spenceri). Although the species is not known to occur in environmental refuges, it was hypothesized that spotted tree frogs may coexist with Bd where environmental conditions reduce disease prevalence and infection intensity (in the sense of the environmental refuge concept outlined by Puschendorf et al., 2011 for the critically endangered Australian treefrog L. loricata). Identifying candidate sites involved a two-step process (Scheele et al., 2014). First, broadscale screening of riverine habitat within and outside the species’ range was conducted, with criteria initially focused on habitat suitability. Second, at sites with appropriate habitat, the suitability of the site for Bd was evaluated, with the goal of identifying a site with characteristics that aligned with the environmental refuge concept. Once a site with suitable habitat and refuge conditions was identified, detailed temperature monitoring was undertaken, with baseline information also collected at a site where the species had recently been extirpated. Comprehensive stream surveys were also conducted to determine whether any other amphibian species, which may act as reservoir hosts, were present at the site, as well as to determine whether invasive, predatory fish were present (Scheele et al., 2014). Detailed evaluation indicated the site could be suitable and a translocation program commenced, which initially proved successful, but severe bushfire impacts in 2020 and associated sedimentation have since degraded the site.

### 4.4 Translocation tactics

Translocation tactics are defined as “techniques capable of influencing post-release individual performance or
population persistence” and can focus on either the animal or the environment (Batson, Gordon, Fletcher, & Manning, 2015, p. 1599). Animal-focused tactics important for amphibian translocations include the number of animals released, demography (life stage), and genetics. A positive relationship between the number of animals released and translocation success has been repeatedly demonstrated across translocation projects (Armstrong & Seddon, 2008), including specifically for amphibians (Germano & Bishop, 2009). If the fundamental objective is population establishment, the minimum number of animals needed to establish a viable population should be determined before commencing the translocation, taking into consideration risks associated with demographic and environmental stochasticity. Semlitsch (2002) suggested that the goal should be a minimum breeding population size of at least 100 individuals, although actual numbers will be context-specific and species-specific. In the context of Bd, it is important to consider the timing of releases to minimize infection risk (e.g., breeding vs. nonbreeding season, summer vs. autumn) and whether all animals are released together or releases are staggered.

The demographic composition of animals released requires careful consideration. Different life stages vary in their susceptibility to Bd infection (Bradley, Snyder, & Blaustein, 2019), and risk of exposure to Bd can also vary across life stages. Decisions about whether to release eggs, larvae, or adults (or a combination) should be informed by species-specific information on the processes underpinning amphibian coexistence with Bd. For example, if Bd-associated mortality is highest at metamorphosis (Sauer et al., 2020), translocations may focus on releasing adults. Additional factors to consider include the potential for increased dispersal away from the release site by adults in contrast to releases involving eggs, genetic diversity (e.g., eggs from the same clutch contain limited diversity), and the mortality/survival rates of different life stages (e.g., eggs may experience higher mortality than adults). The relative cost effectiveness of releasing different age animals should be evaluated, as should the potential impact of removing different age animals from wild source populations.

Animal translocations often seek to maximize genetic diversity (Armstrong & Seddon, 2008). Genetic considerations are highly dependent on the process underpinning species coexistence with Bd. Where resistance/tolerance is hypothesized or demonstrated there needs to be a specific focus on capturing a subset of genetic diversity (i.e., individuals from persistent/naturally recovering populations). In other contexts, such as translocations to environmental refuges, maximizing genetic diversity is likely to be desirable to increase fitness and adaptive capacity. Genetic considerations also need careful evaluation for population augmentations, where animal releases could result in undesirable genetic swamping if selection is occurring in the population.

Environment-focused tactics can be used to both increase amphibian survival and reduce environmental suitability for Bd. Habitat modification can be applied to decrease suitability for Bd such as through salt application or vegetation management (Clulow et al., 2018; Heard et al., 2018). Habitat modification can also be used to reduce other sources of mortality (other threats or stochastic), such as manipulating hydroperiod for lentic breeding species to improve recruitment (Shoo et al., 2011) or to minimize invasive fish impacts (Beranek, Maynard, McHenry, Clulow, & Mahony, 2021). For example, in a translocation program for the critically endangered southern corroboree frog (P. corroboree), eggs are released in large plastic tubs rather than natural pools to reduce tadpole mortality associated with premature pond drying (Hunter et al., 2010).

### 4.5 Monitoring

Monitoring is a crucial component of any translocation project, but is frequently neglected despite ongoing calls for improvement (Armstrong & Seddon, 2008; Berger-Tal et al., 2020). To ensure adequate monitoring is conducted, it needs to be clearly planned and budgeted for from the start; it cannot be considered an ad hoc activity to be undertaken only when resources are available. A monitoring plan needs to be prepared with a clear timetable and indicators linked to objectives, and include specific monitoring methods, with a realistic appraisal of likely detection probabilities. For example, when translocations involve egg releases or juveniles, it is important to recognize that individuals may have very low detectability until they reach breeding age. In many cases, monitoring will need to be conducted over multiple successive years.

As budget limitations will almost always be a concern, it is important to balance costs with the level of detail required to ensure that monitoring is fit-for-purpose. Defining fit-for-purpose monitoring is context specific and must relate to the project’s objectives (Legge et al., 2018). For example, in some cases, detailed information on vital rates will be collected throughout the life of the project, while in other cases counts will be appropriate. Importantly, irrespective of the level of monitoring detail, a key element in most cases will be explicit triggers for actions—either in terms of postrelease management actions or subsequent releases (Robinson et al., 2018). Lastly, the monitoring plan needs to cover data management and storage, as well as metadata collection.

In most translocations, monitoring is focused on the survival of the released individuals or subsequent offspring. However, for translocations involving Bd-
threatened amphibians, there is also often a need for parallel monitoring of Bd dynamics. Information on Bd dynamics will help distinguish mortality associated with Bd from other sources of mortality. Where possible, post-release monitoring should incorporate swabbing of captured individuals to determine Bd related mortality and infection dynamics, which may be estimated using capture-mark-recapture models or disease-structured N-mixture models for unmarked animals (DiRenzo, Castaldo, Saunders, Grant, & Zipkin, 2019). Practitioners should be aware that swabs often fail to detect low-level infections and that multiple swabs per individual may be warranted (Shin, Bataille, Kosch, & Waldman, 2014).

4.6 Communication of results

Clearly communicating the results from translocation projects is crucial to enable ongoing learning within and across projects. In the case of successful projects, it is important that the reasons for success are clearly articulated to ensure other translocation projects can identify key elements. Although word limits restrict the amount of detail that can be communicated in scientific articles, we encourage the development of accompanying appendices to communicate greater levels of detail about the actions undertaken, as well as providing context for why certain decisions were made. It is also valuable to communicate the results to the broader public, particularly for successful programs that can build support for, and highlight the benefits of, conservation actions. Clear communication also includes openly reporting failures to avoid repeating mistakes, as well as allowing realistic evaluations of failure risk during the planning and contextual model development phases (Scheele et al., 2018).

5 Conclusions

The conservation of amphibian species in the wild that are threatened by chytridiomycosis is dependent on the development of new and effective conservation strategies. While we found Bd has been a key factor limiting frog translocation success in Australia, improved knowledge has created new opportunities. We trust that application of our conceptual framework (Figure 1) to specifically articulate and test potential mechanisms of amphibian-Bd coexistence, alongside our recommendations (Figure 2), will help improve translocation outcomes and elucidate mechanisms contributing to translocation success or failure. With careful development and refinement, translocations may prove a useful tool to combat the unique conservation challenges posed by emerging diseases.

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Conflict of interest

The authors declare no potential conflict of interest.

Author Contributions

Ben C. Scheele and Laura F. Grogan led the conceptualization and writing of the article. Matthijs Hollanders and Emily P. Hoffmann led the Australian review component. All authors contributed to conceptual development, writing, and revisions.

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