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Successful eradication of invasive American bullfrogs leads to coextirpation of emerging pathogens

Blake R. Hossack[1] ⓘ | David Hall[2] | Catherine L. Crawford[3] | Caren S. Goldberg[4] |
Erin Muths[5] | Brent H. Sigafus[6] | Thierry Chambert[7]

[1]U.S. Geological Survey, Northern Rocky Mountain Science Center, Wildlife Biology Program, W. A. Franke College of Forestry & Conservation, University of Montana, Missoula, Montana, USA

[2]School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona, USA

[3]U.S. Fish and Wildlife Service, Pacific Region, Portland, Oregon, USA

[4]Washington State University, Pullman, Washington, USA

[5]U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado, USA

[6]U.S. Geological Survey, Cooperative Research Unit, Tucson, Arizona, USA

[7]CEFE, University of Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France

Correspondence
Blake Hossack, U.S. Geological Survey, Northern Rocky Mountain Science Center, Wildlife Biology Program, W. A. Franke College of Forestry & Conservation, University of Montana, Missoula, MT 59812, USA.
blake_hossack@usgs.gov

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Abstract

Interventions of the host–pathogen dynamics provide strong tests of relationships, yet they are still rarely applied across multiple populations. After American bullfrogs (*Rana catesbeiana*) invaded a wildlife refuge where federally threatened Chiricahua leopard frogs (*R. chiricahuensis*) were reintroduced 12 years prior, managers launched a landscape-scale eradication effort to help ensure continued recovery of the native species. We used a before-after-control-impact design and environmental DNA sampling of 19 eradication sites and 18 control sites between fall 2016 and winter 2020–2021 to measure community-level responses to bullfrog eradication, including for two pathogens. Dynamic occupancy models revealed successful eradication from 94% of treatment sites. Native amphibians did not respond to bullfrog eradication, but the pathogens amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) and ranaviruses were coextirpated with bullfrogs. Our spatially replicated experimental approach provides strong evidence that management of invasive species can simultaneously reduce predation and disease risk for imperiled species.

KEYWORDS
amphibian, chytrid fungus, chytridiomycosis, disease, endangered, extinction, intervention, non-native, ranavirus, reintroduction

1 | INTRODUCTION

Ecological and economic costs of invasive species and infectious diseases continue to increase globally (Crowl et al., 2008; Marbuah et al., 2014). Threats from invasive species are diverse but often include predation and acting as reservoirs or vectors of pathogens (Chalkowski et al., 2018; A. M. Dunn & Hatcher, 2015). These threats can be additive or interactive, potentially compounding risk posed to native species and ecosystems (A. M. Dunn & Hatcher, 2015; Rosa et al., 2022).

Native to eastern North America, the American bullfrog (*Rana* [*Lithobates*] *catesbeiana*; hereafter, bullfrog) is one of the world's most problematic invasive species (Lowe et al., 2000). The bullfrog is a strong predator that can reduce abundance or exclude native species and has been linked with the spread of amphibian chytrid fungus (*Batrachochytrium dendrobatidis*; hereafter Bd) and ranaviruses, pathogens of global conservation concern (Adams & Pearl, 2007; Daszak et al., 2004; Garner et al., 2006). Transmitted by aquatic zoospores released from infected amphibians, Bd attacks keratin in the skin of infected hosts and has contributed to population declines and extirpations globally (Berger et al., 1998; Russell et al., 2019). Ranaviruses are a group of lethal, multihost iridoviruses that are transmitted directly and indirectly to amphibians, reptiles, and fishes (Gray & Chinchar, 2015). Bullfrogs are susceptible to infection by Bd and ranaviruses, but they have high resistance to disease and death (Brunner et al., 2019; Daszak et al., 2004).

The negative effects of invasive aquatic predators may be particularly strong in arid regions, where limited aquatic habitats and frequent drought increase crowding and risk of predation or disease transmission (Greer & Collins, 2008; Hossack et al., 2017). Negative effects of bullfrogs and other invasive predators, along with habitat loss and disease, contributed to listing the native Chiricahua leopard frog (*R. chiricahuensis*) as federally threatened in the USA (USFWS, 2007). In the early 2000s, local eradication of bullfrogs from several ponds aided the successful 2003 reintroduction of the Chiricahua leopard frog on a national wildlife refuge in southern Arizona, USA (Chandler et al., 2015). Over the next 12 years, native leopard frogs increased in abundance and colonized several ponds on and adjacent to the refuge, forming the strongest known metapopulation for the species (Chandler et al., 2015; Howell et al., 2020). After bullfrogs recolonized the refuge in 2015, quick actions removed them and reduced the threat in the near term, but the invasion highlighted the tenuous nature of recovery gains for native species.

The threat of reinvasion of bullfrogs and their potential impacts on native species motivated funding for a multiyear, landscape-scale eradication program starting in 2016. To measure the outcome of eradication efforts, we used a spatially replicated before-after-control-impact (BACI) framework and environmental DNA (eDNA) sampling to estimate changes in the pond-level presence of several taxa in treatment sites. We used dynamic occupancy models to estimate changes in the occurrence of bullfrogs, Chiricahua leopard frogs, western tiger salamanders (*Ambystoma mavortium*), Bd, and ranaviruses in eradication and control sites between fall-winter 2016 and winter 2020−2021. The replicated experimental approach allowed for strong tests of whether management of invasive predators that are also vectors of multihost pathogens can simultaneously reduce predation and disease risk for imperiled species.

2 | METHODS

Our study occurred near the Arizona–Sonora border in the arid, southwestern USA (Figure 1). Our study included 19 sites where bullfrog eradication occurred and 18 control sites (eight with bullfrogs, 10 without) during 2016 and 2020−2021 (Table 1 and Figure 1). Eradication methods included removing egg masses, seining larvae, and removing adults via hand capture, spearing, and shooting (Hall & Koprowski, 2018). Most eradications were completed by summer 2019. Details of the eradication methods and results are reported elsewhere (Hall & Koprowski, 2018). One of the eradication sites (Agua Caliente; northernmost site in Figure 1) was originally a control site in 2016, but unbeknownst to us, the county drained it in 2019 specifically to eradicate bullfrogs and other invasive species (https://tinyurl.com/5n6jb9zf). We, therefore, treated it as an eradication site for analyses.

Eradication and control sites were isolated livestock ponds and small lakes with simple habitat (Table 1). We selected sites that we expected were permanent, but extreme drought caused four eradication sites and four control sites to dry during winter 2020−2021. We replaced the four dry control sites with ones that had similar occurrence status for bullfrogs and Chiricahua leopard frogs in 2016, based on prior surveys (e.g., Hossack et al., 2017; Howell et al., 2020). For the dry eradication sites, we substituted four similar eradication sites in the same area. We had not previously sampled any of the replacement sites with eDNA methods. Counting the replacement sites, we sampled a total of 45 distinct waterbodies, with 29 of those sites sampled during both 2016 and 2020−2021.

Sites within the main eradication area and to the west were the primary areas where Chiricahua leopard frogs were known to occur in 2016 (Figure 1). Similarly, bullfrogs were not present on the refuge after eradication efforts in the early 2000s except at the Arivaca Cienega (Chandler et al., 2015). Sites to the east of the core eradication area
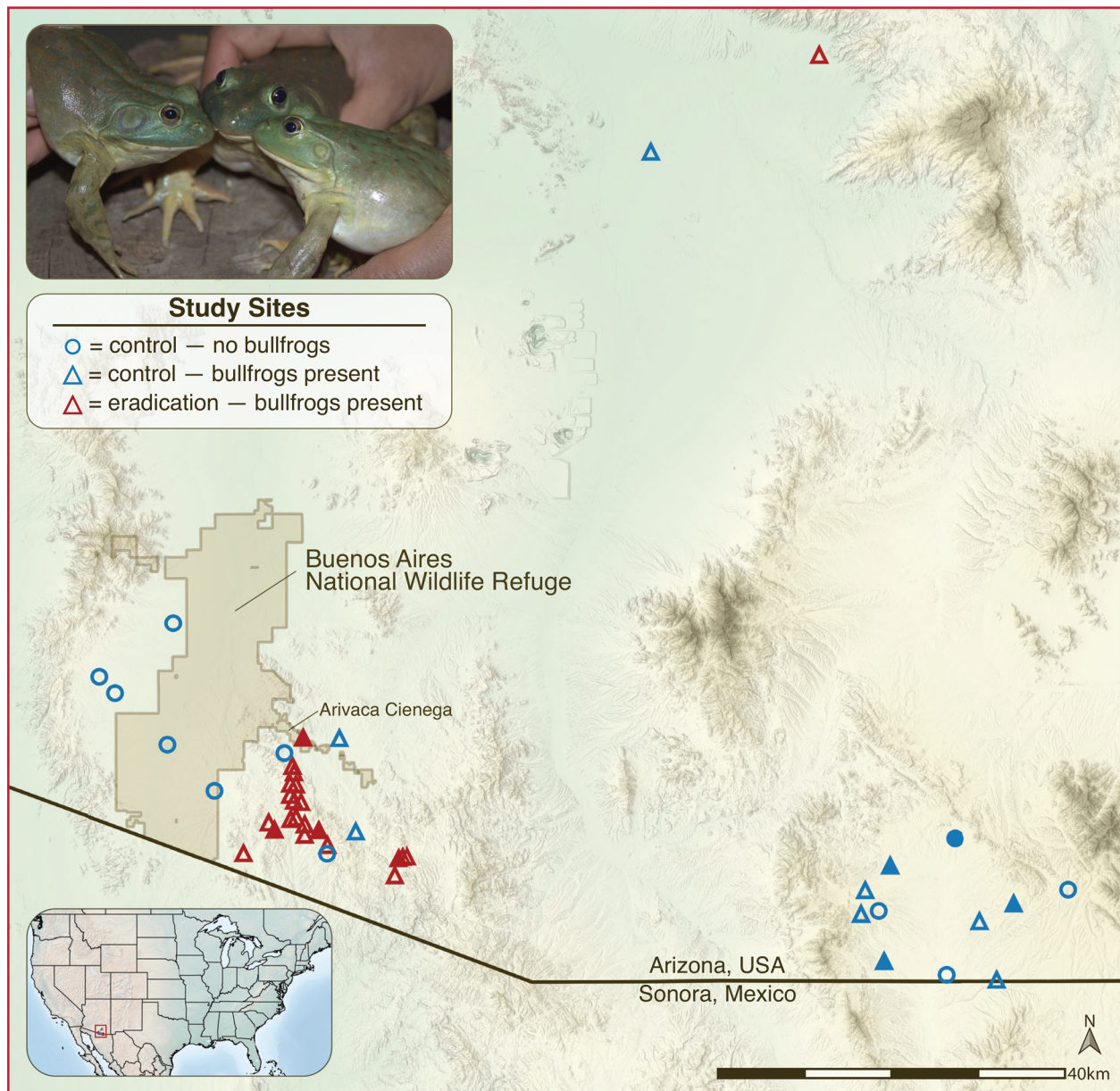
FIGURE 1 Study area in southern Arizona (USA), where we used a BACI framework to measure responses of amphibians, amphibian chytrid fungus (Bd), and ranaviruses to eradication of invasive American bullfrogs. Bullfrog eradications were initiated to support recovery of federally threatened Chiricahua leopard frogs on Buenos Aires National Wildlife Refuge and neighboring areas. The hollow symbols indicate the original sites sampled during fall 2016 and the solid symbols indicate the eight sites added during posteradication sampling (winter 2020−2021) to replace dry sites. The inset photo (*B. sigafus*, U.S. Geological Survey) shows the three American bullfrogs that invaded the wildlife refuge, where prior bullfrog eradication in the early 2000s set the stage for the reintroduction of federally threatened Chiricahua leopard frogs.

served as controls for bullfrogs (i.e., bullfrogs present but no eradication efforts applied) and tiger salamanders but not for Chiricahua leopard frogs, which were extirpated several decades ago (USFWS, 2007). Selection of control sites east and north of the main eradication zone was weighted toward sites with bullfrogs, so across all control sites combined, we had an approximately even mix of sites with and without bullfrogs presence (Hossack et al., 2017; Howell et al., 2020).

2.1 | Field methods

We collected two to three eDNA filter samples per site, per sampling session (e.g., December 2020; Table 1) using previously validated methods for the study area. (See Supplemental 1 for details on field and laboratory eDNA methods.) Planned sampling of eradication sites and some control sites was delayed until late February 2021, after most control sites were sampled in early December 2020.

TABLE 1 Summary (mean [*SD*; range]) of waterbody characteristics, sampling effort and timing, and naïve detections of targeted taxa based on environmental DNA (eDNA) from a BACI eradication of American bullfrogs in southern Arizona (USA). We sampled 18 control sites and 19 treatment (eradication) sites before (fall 2016) and after (winter 2020−2021) eradication efforts. Four control sites and four treatment sites dried between 2016 and 2020−2021; dry sites were replaced with sites that had similar bullfrog status as the original sites, resulting in a total of 45 distinct waterbodies sampled. Detections based on laboratory results for eDNA filters are summarized at the site-level for American bullfrogs, Chiricahua leopard frogs, Western tiger salamanders, amphibian chytrid fungus (Bd), and ranaviruses.

	Control Sites		Eradication Sites	
	Pre-eradication	Post-eradication	Pre-eradication	Post-eradication
Waterbody size (m²)	3464 (2617; 1178−7658)	1288 (1304; 177−5736)	3978 (3815; 544−14,137)	3728 (4747; 199−21,748)
Number of filters collected	3 (0; 3−3)	4.7 (1.45; 3−6)	2.9 (0.23; 2−3)	3 (0; 3−3)
Volume filtered (mL)	203 (62; 10−250)	111 (100; 3−500)	228 (46; 75−250)	129 (84; 20−250)
Sample dates	October 3–November 7, 2016	December 1—3, 2020; February 18–March 5, 2021	September 14–October 29, 2016	February 17–February 24, 2021
Number of sites American bullfrogs detected	8	8	18	1
Number of sites Chiricahua leopard frogs detected	4	5	1	1
Number of sites western tiger salamanders detected	7	11	2	0
Number of sites Bd detected	5	3	3	0
Number of sites ranaviruses detected	4	2	6	0

To help adjust for any temporal effects on detection due to the delay, we resampled 11 control sites during February 18–March 5, 2021, that had already been sampled in early December 2020.

2.2 | Statistical analysis

We used dynamic occupancy models to estimate changes in the presence of taxa relative to site type (eradication, control), before (2016) and after (2020−2021) eradication efforts (MacKenzie et al., 2017). We represented taxa with a single categorical term that included the three amphibian species and two pathogens; this coding shares information and allows joint estimation from a single model (MacKenzie et al., 2017). We classified sites according to whether they hosted bullfrogs and whether sites were treatment (eradication) or control sites (Supplemental Table 1). We also included a covariate for waterbody size (Table 1) because we expected taxa to be more likely to occur in larger sites. We allowed extinction to differ between eradication and control sites and based on waterbody size. We held colonization constant because models that included covariates systematically failed to converge, likely because observed colonization events were extremely rare. For detection, we included the volume of water filtered, filter type (5 vs. 0.45 μm), and a term to account for variation in timing of sampling (Table 1).

We used a step-down approach to evaluate and simplify fitted models, starting with the most parameterized model and sequentially removing covariates to assess support, based on the Akaike Information Criterion (AIC). We applied this procedure to detection first, then initial occupancy, and then extinction. Models were fit in R version 4.1.0 using the package *unmarked* (Fiske & Chandler, 2011). To evaluate the sensitivity of our conclusions to substituting four eradication and four control sites that dried, we refit the top-ranked model using only the 29 sites that were sampled before (2016) and after (2020−2021) eradication efforts.

3 | RESULTS

The best supported model indicated initial occupancy of taxa depended on whether a site hosted bullfrogs and extinction rates for most taxa were higher in eradication sites than in control sites (Figure 2 and
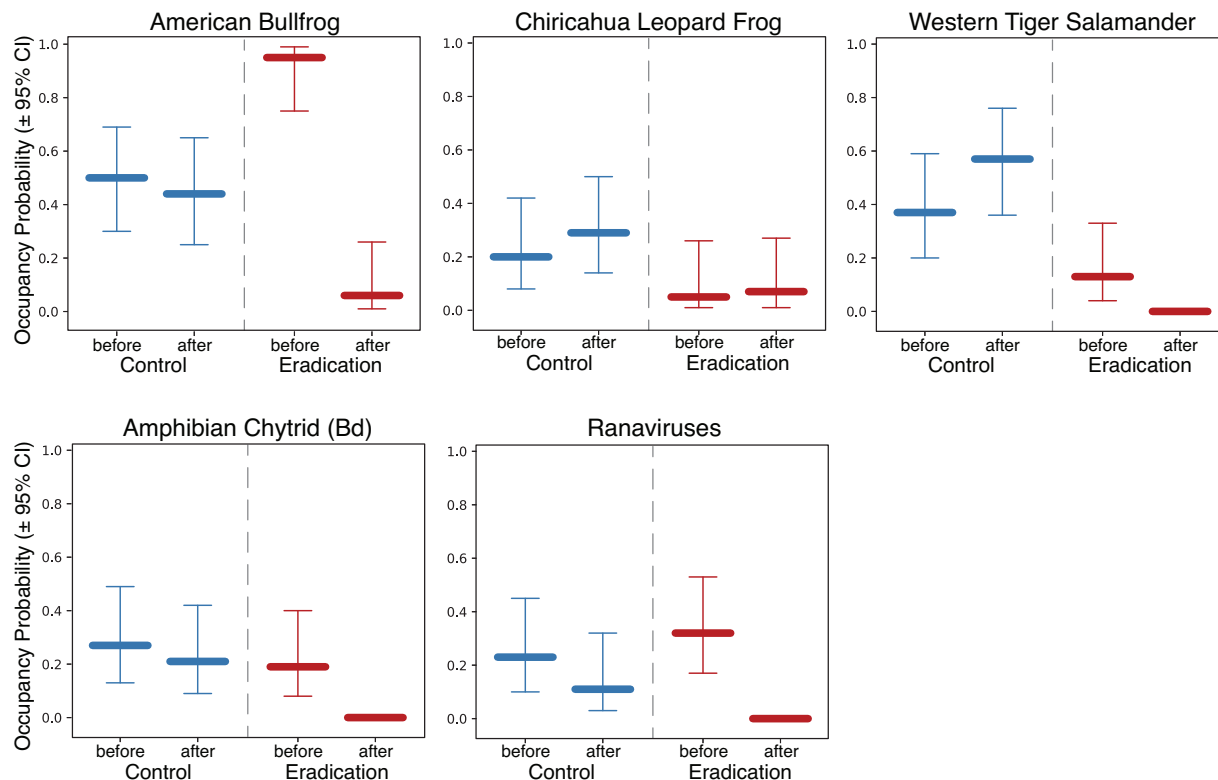
FIGURE 2 Occupancy probabilities (mean, 95% confidence interval [CI]) derived from the posterior of the top-ranked dynamic, multispecies model used to estimate changes in the presence of amphibians and pathogens relative to site type (control, eradication) before (fall 2016) and after (winter 2020−2021) bullfrog eradication efforts in southern Arizona, USA. The changes in occupancy in 19 eradication sites relative to 18 control sites show effective eradication of invasive bullfrogs and coextirpation amphibian chytrid fungus (Bd) and ranaviruses. Changes in salamander occupancy were driven partly by having to replace sites that dried from drought (see Discussion and Supplemental Table 4). Some 95% CI for estimates of occupancy posteradication were inestimable because of point estimates of 0.

Supplemental Tables 1 and 2). Detection of taxa varied during October–November 2016 (mean per-filter detection [± 95% CI]: 0.90 [0.70−0.97]), December 2020 (0.84 [0.66, 0.93]), and February–March 2021 (0.47 [0.19−0.78]; Supplemental Table 1). There was only weak evidence detection varied with filter type or volume filtered (Supplemental Table 1).

At eradication sites, bullfrog presence fell from an estimated 0.95 (0.78−0.96) of sites in 2016 to 0.06 (0.04−0.22) of sites during 2020−2021 (Figure 2 and Supplemental Table 3). In 2016, bullfrogs were detected via eDNA at 18 of 19 eradication sites; we failed to detect them at one site where they seemed uncommon based on traditional survey methods (Hall & Koprowski, 2018). At control sites, bullfrog presence was steady between 2016 (0.50 [0.36−0.50]) and 2020−2021 (0.44 [0.36−0.45]). The contrasting trends in treatment and control sites provide evidence of effective eradication.

Bd and ranaviruses were estimated to be present at 0.19 (0.08−0.40) and 0.32 (0.17−0.53) of bullfrog sites in 2016, respectively, but were not estimated to be present at eradication sites during 2020−2021 (Figure 2 and Supplemental Table 2a). Estimated presence of Bd and ranaviruses also declined at control sites, but much less than in eradication sites (Table 2 and Figure 2). The presence of tiger salamanders increased moderately in control sites relative to eradication sites between 2016 and 2020−2021, whereas the presence of Chiricahua leopard frogs remained stable (Table 2 and Figure 2). The sensitivity analysis based only on the 15 eradication sites and 14 control sites surveyed during both fall 2016 and winter 2020−2021 showed our results were not strongly influenced by having to replace eight sites that dried (Supplemental Table 4).

4 | DISCUSSION

Our spatially replicated BACI study of community responses to eradication of nonnative American bullfrogs provides evidence for successful local eradication of an invasive species and coextirpation of Bd and ranaviruses. Eradication of invasive species is an increasingly important component of recovery for many imperiled species, especially when all life stages of invasive species are fully

aquatic, such as fishes (e.g., Knapp et al., 2007; Rytwinski et al., 2019). Empirical estimates of the relative success or failure of these efforts for invasive species that occupy both terrestrial and aquatic environments are still rare (e.g., Kamoroff et al., 2020; Lafferty et al., 2018), especially across a network of sites. Further, we are unaware of prior evidence linking eradication of invasive amphibians to coextirpation of pathogens.

Like many invasive species, bullfrogs have many life-history characteristics that challenge successful control, including high fecundity, strong dispersal and colonization capabilities, and sometimes extraordinary local abundances (Adams & Pearl, 2007; Holycross et al., 2021; Kamoroff et al., 2020). In our study system, estimated presence of bullfrogs fell from 18 sites in 2016, prior to eradication efforts, to one site during 2020−2021, after most eradication efforts were completed. The one site where we detected bullfrogs (on only one of three filters) at the end of the study was the last site to have a small number of bullfrog larvae that proved difficult to eradicate.

Amphibian chytridiomycosis has been described as the most destructive wild disease recorded (Scheele et al., 2019). One reason Bd has caused severe declines or even extinction of some species stems from its ability to infect several species in a community, allowing the fungus to maintain high levels of pathogen pressure even as some species become rare (Becker et al., 2014; DiRenzo et al., 2018). Ranaviruses infect an even wider variety of hosts than Bd, and, for both pathogens, hosts in the terrestrial environment act as reservoirs that re-inoculate waterbodies (Brunner et al., 2004; Gray & Chinchar, 2015). Despite these characteristics that foster high persistence, Bd and ranaviruses were both estimated to have been coextirpated from all bullfrog eradication sites. Bd and ranaviruses were present at an estimated 19% and 32%, respectively, of bullfrog sites in 2016, but neither pathogen was detected at any eradication sites during 2020−2021. At control sites, estimated presence of Bd and ranaviruses decreased by 23% and 52% between 2016 and 2020−2021, respectively, while bullfrog presence remained steady. This temporal variation for pathogens in control sites is similar to that from 233 sites sampled in the region during 2016−2018 (including the 2016 samples in the current paper) and suggests large among-year variation in pathogen occurrence, especially for ranaviruses (Hossack et al., 2023), but the experimental BACI framework allowed us to control for most variation and identify changes associated with bullfrog eradication.

Susceptibility of pathogens to extirpation is generally linked with abundance and diversity of potential hosts (Moir et al., 2010; Wobeser, 2002). Culling is commonly used to control disease in multihost systems, sometimes greatly reducing pathogen prevalence or eliminating disease even absent complete eradication of primary hosts

(Chalkowski et al., 2018; Viana et al., 2014). Yet, the only other case we know of that demonstrated coextirpation of invasive hosts and disease vectors occurred on a small island, where eradication of nonnative rats led to extinction of nonnative Asian tiger mosquitoes (*Aedes albopictus*) that relied on mammalian hosts (Lafferty et al., 2018). Although our results follow an intentional removal of a nonnative species in a single study area, they also highlight the broader concern over hidden loss of parasite and pathogen biodiversity via extirpations of native hosts (R. R. Dunn et al., 2009; Koh et al., 2004).

The ability of Bd and ranaviruses to infect multiple host species in the aquatic and terrestrial environment makes the apparent coextirpation of Bd and ranaviruses at bullfrog eradication sites moderately surprising. However, sites with invasive bullfrogs often have simplified amphibian communities (Atobe et al., 2014; Miller et al., 2012; Rowe et al., 2019). In a prior survey in the region, Bd and ranaviruses were 2.5- and 10-times more likely, respectively, to be present at sites with bullfrogs than without bullfrogs, providing support for bullfrogs as the primary driver of pathogen dynamics in our study system (Hossack et al., 2023). Reduced presence of other amphibian hosts in sites with bullfrogs likely aided the apparent extirpation of Bd and ranaviruses. It is also possible the pathogens were still present in waterbodies, but their abundance was reduced below detectable limits, given our sampling methods.

The primary motivation for the landscape-scale bullfrog eradication effort was to support recovery of the federally endangered Chiricahua leopard frog, which we did not observe. Also, our demonstration of successful eradication and associated community changes are short-term and were hindered by exceptional drought that caused many normally permanent waterbodies to dry. While drying waterbodies can "reset" the local community, reducing predation pressure and fostering coexistence of native amphibians with bullfrogs and other aquatic invasive species (Hossack et al., 2017; Miller et al., 2012), drought might have also limited opportunities for native species to colonize sites. Still, reducing abundance of pathogens could reduce risk for other native species and can recover, including reintroduction efforts of imperiled species susceptible to Bd and ranaviruses (e.g., Hossack et al., 2022; Kamoroff et al., 2020).

Effects of the exceptional drought were evident in causing four eradication sites and four control sites that normally hold water year-round to dry after they were sampled in 2016, but before posteradication sampling occurred. Replacing these sites added variation to the response data and uncertainty to evidence for apparent extirpation of amphibians and pathogens, but our sensitivity analysis showed substituting sites did not strongly

influence conclusions (Supplemental Table 4). This variation was especially evident for salamanders, which decreased in occupancy in eradication sites and increased in occupancy in control sites between 2016 and 2020−2021. However, salamanders were detected at only two of 19 bullfrog eradication sites before interventions started. One of these sites dried after 2016 and its replacement site did not have salamanders; this replacement site may have inflated apparent extirpation, compared to the original site if it had not dried. In the other site where salamanders apparently went extinct locally, we suspect they were rare in even 2016 when we detected their DNA from only one of three filters. Further, all four control sites that we had to replace during 2020−2021 had salamanders, whereas we did not detect salamanders in any of the 2016 control sites that were replaced. These substitutions likely caused the large increase in mean occupancy for salamanders in control sites during 2020−2021, whereas changes in sites sampled during both 2016 and 2020−2021 were much smaller (Supplemental Table 4).

Our study adds to a small set of well-documented cases where removal of invasive amphibians has been successful (e.g., Kamoroff et al., 2020; Rice et al., 2011). While having to substitute some sites that dried and not sampling animals for pathogens directly leaves uncertainty in our results, integrating eDNA sampling into monitoring of management actions provided an effective framework to measure community-level responses and provided strong support for interventions to eradicate or limit abundance of nonnative bullfrogs. The efficacy of targeting specific species to reduce disease risk also depends on several factors, including abundance and interaction strength of hosts and how pathogens are transmitted (Miguel et al., 2020). Although these factors must be considered, our results based on the experimental BACI approach indicate that eradicating bullfrogs locally may simultaneously reduce the distribution and abundance of an invasive predator and pathogens of global conservation concern.

AUTHOR CONTRIBUTIONS

B.R.H, D.H., C.L.C., E.M., and B.H.S. designed the research; B.R.H., D.H., C.L.C., C.S.G., E.M., B.H.S. and T.C. performed the research; B.R.H. and T.C. analyzed the data; B.R.H., D.H., C.L.C., C.S.G., E.M., B.H.S., and T.C. wrote the paper.

DATA AVAILABILITY STATEMENT

All data and metadata are available at https://doi.org/10.6084/m9.figshare.23579832

ORCID

Blake R. Hossack https://orcid.org/0000-0001-7456-9564

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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