Landsc Ecol (2024) 39:185
https://doi.org/10.1007/s10980-024-01978-x

RESEARCH ARTICLE

Combining graph theory and spatially-explicit, individual-based models to improve invasive species control strategies at a regional scale

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Received: 28 May 2024 / Accepted: 6 October 2024 / Published online: 25 October 2024

Abstract

Context Invasive species cause widespread species extinction and economic loss. There is an increasing need to identify ways to efficiently target control efforts from local to regional scales.

Objectives Our goal was to test whether prioritizing managed habitat using different treatments based on spatial measures of connectivity, including graph-theoretic measures, can improve management of invasive species and whether the level of control effort affects treatment performance. We also explored how uncertainty in biological variables, such as dispersal ability, affects measures performance.

Methods We used a spatially-explicit, individual-based model (sIBM) based on the American bullfrog (*Lithobates catesbeianus*), a globally pervasive invasive species. Simulations were informed by geographic data from part of the American bullfrog's non-native range in southeastern Arizona, USA where they are known to pose a threat to native species.

Results We found that total bullfrog populations and occupancy declined in response to all treatments regardless of effort level or patch prioritization methods. The most effective spatial prioritization was effort-dependent and varied depending on spatial context, but frequently a buffer strategy was most effective. Treatments were also sensitive to dispersal ability. Performance of treatments prioritizing habitat patches using betweenness centrality improved with increasing dispersal ability, while performance of eigenvalue centrality improved as dispersal ability decreased.

Conclusions With the careful application of connectivity measures to prioritize control efforts, similar reductions in invasive species population size and occupancy could be achieved with less than half the effort of sub-optimal connectivity measures at higher effort rates. More work is needed to determine if trait-based generalities may define appropriate connectivity measures for specific suites of dispersal abilities, demographic traits, and population dynamics.

Keywords Spatially structured populations · Colonization-extinction · Agent-based modelling · Dispersal · HexSim · Network theory

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-024-01978-x.

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Introduction

Invasive species are a key threat to biodiversity, causing extinction, cascading ecological effects, and economic loss around the world (Pyšek et al. 2020). Management of invasive species is often difficult and complex due to the labor and resources required to successfully eradicate or suppress alien species (Green and Grosholz 2021). Further, once an invasive species is established in a region, spatially structured population dynamics may render local management strategies ineffective (Sakai et al. 2001). Populations of invasives linked by dispersing individuals among a regional habitat network may undermine local control efforts by providing ample population sources to recolonize previously treated locations (Wilkerson 2013; Lurgi et al. 2016). Managing invasions locally, such as eradication in a protected area, can provide substantial conservation benefits (Jones et al. 2016), but action at a larger regional scale is likely necessary to mitigate the effects of biological invasions (Genovesi and Monaco 2013). A paucity of data for invasions at regional scales and uncertainty in biological parameters such as dispersal can undermine traditional analytical methods (Ashander et al. 2022) and can negatively affect the ability to select appropriate management strategies (Simberloff 2003; Trotter and Hull-Sanders 2015; Pepin et al. 2020). However, spatial prioritization of management that is informed by the landscape connectivity of a patch habitat network may be able to help alleviate these issues (Lurgi et al. 2016; Pepin et al. 2020; Ashander et al. 2022).

Quantifying landscape connectivity is critical to identifying locations at risk of invasion (With 2004). The spatial structure of habitat patches, a vital component of landscape connectivity, can influence the spread and establishment of invasive species (With 2002). The goal of describing patch contributions to connectivity has often been for managing habitat and wildlife of conservation concern (Galpern et al. 2011; Saura et al. 2014) but can also help identify patches that facilitate invasive species spread and persistence (e.g. Drake et al. 2017b; Kvistad 2019). At a regional scale, identifying patches most likely to facilitate spread of invasives is an important component of proactive exclusion, early detection, and rapid response to invasives before their establishment (Vander Zanden and Olden 2008; Kvistad 2019; Runghen et al. 2023). However, spatial prioritization of management efforts and resources for the control or eradication of invasive species may also be useful in later stages of the invasion process such as after they have established a regional presence.

Graph theory (also commonly referred to as network theory) has become an increasingly popular method to identify the contributions of patches to regional connectivity for conservation and ecology (Minor and Urban 2008; Correa Ayram et al. 2016), in part due to a perceived simplicity and limited data requirements. Calculating graph-theoretic measures need in their simplest form the connections (referred to as *edges*) among patches (referred to as *nodes*) to identify priority patches (Estrada and Bodin 2008). This can be done in landscapes with clearly delineated patches such as pond networks and also can be applied to less well delineated habitat gradients (Dilts et al. 2016). Graph-theoretic measures can also be better predictors of movement than distance-only measures (Lookingbill et al. 2010). However, assuming movement along graph edges may bias results as these metrics may not accurately represent dispersal behavior, landscape connectivity, or population dynamics that results from their interaction (Bishop-Taylor et al. 2018; Ovaskainen and Hanski 2004). The performance of connectivity measures for spatial prioritization may also depend on the amount of effort conducted (Lustig et al. 2019), where a minimum amount of effort may be required to observe benefits from the inclusion of graph-theoretic information (Perry et al. 2017). Graph measures of a patch's contribution to connectivity can be meaningfully distinct to reflect nuance in the dispersal process or other ecological mechanism behind the successful control of invasive species (Laita et al. 2011).

Despite this flexibility, graph theory-based methods have been more slowly applied to questions involving the management of invasive species (Ashander et al. 2022), potentially due to limited guidance historically for network-based management at small spatial scales (Chadès et al. 2011). However, studies have used graph measures to describe real-world spatial networks for invasives management, often identify hypothetically important patches in networks (McIntyre et al. 2016; Drake et al. 2017a) or through population-level simulations which constrain dispersal along graph edges (Perry et al. 2017; Kvistad 2019). This approach may undermine our ability to appropriately prioritize management in response to

individual variation in dispersal behavior which can affect the invasion process (Galib et al. 2022; Jessop et al. 2024). Also, managers often must consider how to protect a focal area within a regional invasion context (Morgan et al. 2006; Genovesi and Monaco 2013; Gallardo et al. 2017), where even the rare individuals with long distance dispersal can disrupt management strategies based on exclusionary barriers, buffers, targeting population clusters, and connectivity (Morgan et al. 2006; Perry et al. 2017; Pietrek et al. 2017; Morel-Journel et al. 2019).

The question then remains, how do we effectively prioritize where to focus control efforts for invasive populations at a regional scale? This study begins to address this gap through the combination of spatial connectivity measures and spatially-explicit, individual-based models (sIBMs) to explore if and where differing measures of spatial prioritization may impart efficiencies to invasive species management. sIBMs provide a flexible, dynamic model framework to ask "what if" questions related to prioritization of control efforts for invasive species (Messager and Olden 2018), yet few studies have compared or integrated sIBMs with graph-theoretic approaches (but see Minor and Urban 2007; Lookingbill et al. 2010) or other connectivity measures in general. The combination of both methods presents an underutilized opportunity to test spatial prioritization of control *in-silico* where not possible "on-the-ground" (Peck 2004). sIBMs are also useful when key biological parameters such as dispersal ability are uncertain, allowing a range of values to be tested to understand model sensitivity in drivers of population dynamics relevant for conservation and management (Barros et al. 2016). Thus, we use our modelling framework to ask:

(1) How do spatial measures of connectivity, including graph-theoretic and distance-based measures, compare as methods to improve spatial prioritization of control efforts?
(2) Does the level of control effort affect performance of spatial measures of connectivity?
(3) Does uncertainty in dispersal ability affect the relative performance of prioritization methods?

To address these questions, we introduce a novel sIBM based on the American bullfrog (*Lithobates catesbeanus*) using the HexSim platform (Schumaker and Brookes 2018). The American bullfrog is a global invader that has caused over 95% of the $6.3 Billion USD in economic harm attributed to invasive amphibians worldwide (Soto et al. 2022). In the western United States, this invasive species is considered one of the largest threats to native aquatic taxa due to predation, competition, and being a prominent vector of diseases such as chytridiomycosis (Rosen and Schwalbe 1995; Yap et al. 2018; Mims et al. 2020). They are an effective disperser, traveling long distances, but with an unknown upper limit of their dispersal ability (Kahrs 2006; Suhre 2010; Cooper 2017). This makes bullfrog management especially difficult as differences in dispersal behavior could influence the efficacy of management treatments (Trotter and Hull-Sanders 2015).

Since their introduction, bullfrogs have become well established in many areas outside of their native range of eastern North America, including portions of southern Arizona (Fig. 1). Historically introduced for sport and food in the western United States (Tellman 2002), bullfrog establishment was facilitated by the augmentation of local wetland habitats to be increasingly permanent and construction of artificial catchments that allowed bullfrogs to breed and disperse to new areas (Rosen and Schwalbe 1994; Maret et al. 2006). Some control efforts have been locally successful (Clarkson and deVos 1986; Suhre 2010; Jarchow et al. 2016), but these have often involved intensive removal and control efforts at specific prioritized areas of conservation concern (Rosen et al. 2013). These control efforts often require many years of physical labor and consistent surveillance of focal areas and surrounding habitat. Understanding if any efficiencies can be identified when prioritizing the scale and distribution of control efforts is crucial where resources are continually stretched to meet increasing conservation needs (Lustig et al. 2019).

We hypothesize that targeting spatial prioritization of control efforts using treatments based on graph-theoretic measures should outperform our other spatial prioritization methods because of the included topological context, i.e. relative spatial arrangement, inherent to graph-theoretic connectivity measures (Minor and Urban 2007; Perry et al. 2017). As well, we hypothesize that as effort increases, the relative difference in performance among spatial connectivity measures will also increase. Lastly, we hypothesize that increasing dispersal will erode the ability of

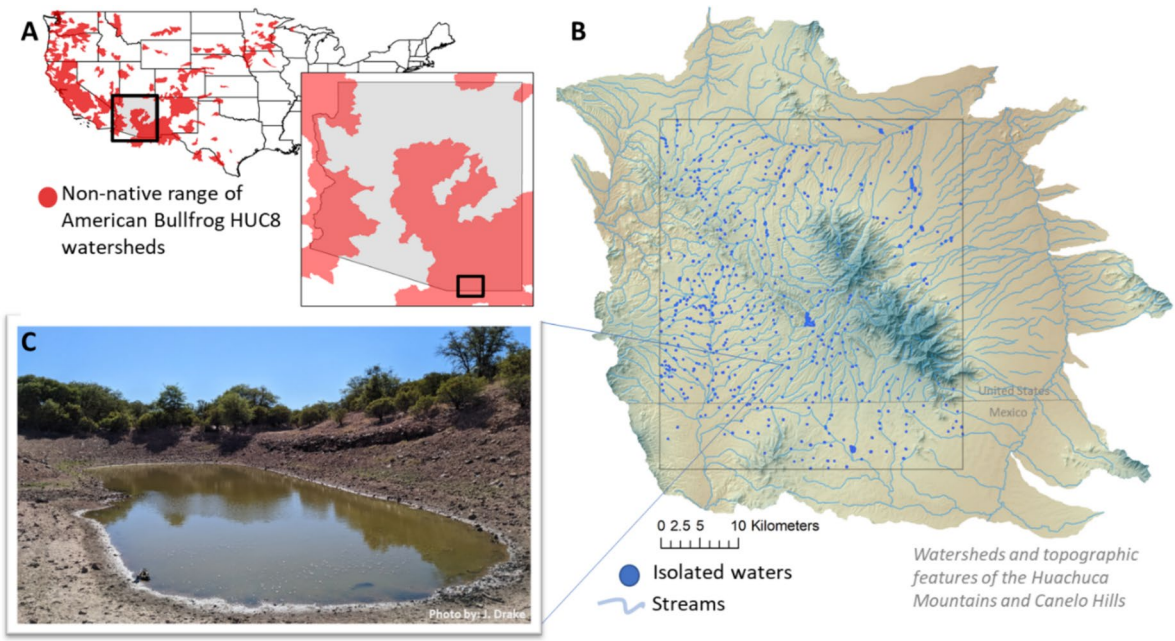


Fig. 1 Study system upon which simulations were based. **A** The American bullfrog (*Lithobates catesbeianus*) is a pervasive global invasive species. It has a wide distribution in the western United States where it affects many local species. We were interested in a portion of southeastern Arizona where the control of bullfrogs is an ongoing management priority. **B** The Huachuca Mountains and Canelo Hills are home to many permanent and intermittent isolated waters. We used geospatial data and satellite imagery to determine the amount of available habitat for bullfrogs to help parameterize the landscapes generated for the simulation. **C** A typical habitat patch (e.g., pond), often built for stock animals but used by many other organisms including the invasive bullfrog. Invasive range data developed from (U.S. Geological Survey 2018, 2023)

connectivity measures to benefit spatial prioritization for invasives control.

Methods

We simulated the response of the American bullfrog to different treatments of spatial prioritization for removal based on spatial connectivity measures, to increasing levels of control effort, and to a range of dispersal ability (Fig. 2). To do this, we constructed a spatially-explicit, individual-based simulation and population model using the HexSim software (Version 4.0.20.0; Schumaker et al. 2022). Our model uses the ecology of the American bullfrog to inform management in simulated landscapes generated from empirical spatial data from a portion of the bullfrog's invasive range in southeastern Arizona, USA and northern Sonora, Mexico (Fig. 1). This allows more realistic translation of results to on-the-ground management and mitigation of invasive species while simultaneously reducing the bias from an idiosyncratic representation of a real landscape. This should help address regional needs while simultaneously producing generalizable results, increasing the transferability of insights to other species and systems. We present methods germane to general readership, and further details can be found in a TRACE document (Schmolke et al. 2010; Augusiak et al. 2014; Grimm et al. 2014) provided in Appendix S1. Data on model parameterization can be found in Appendix S2. HexSim environments and code for spatial data generation and analysis is available via a public GitHub Repository https://github.com/MimsLabVT/LICA_HexSim_Drake_etal (Appendix S3).

Spatially explicit individual-based model

We created an event sequence that models an annual cycle for American bullfrogs in a simulated landscape informed by empirical spatial data. Each event in the event sequence pertains to a different aspects

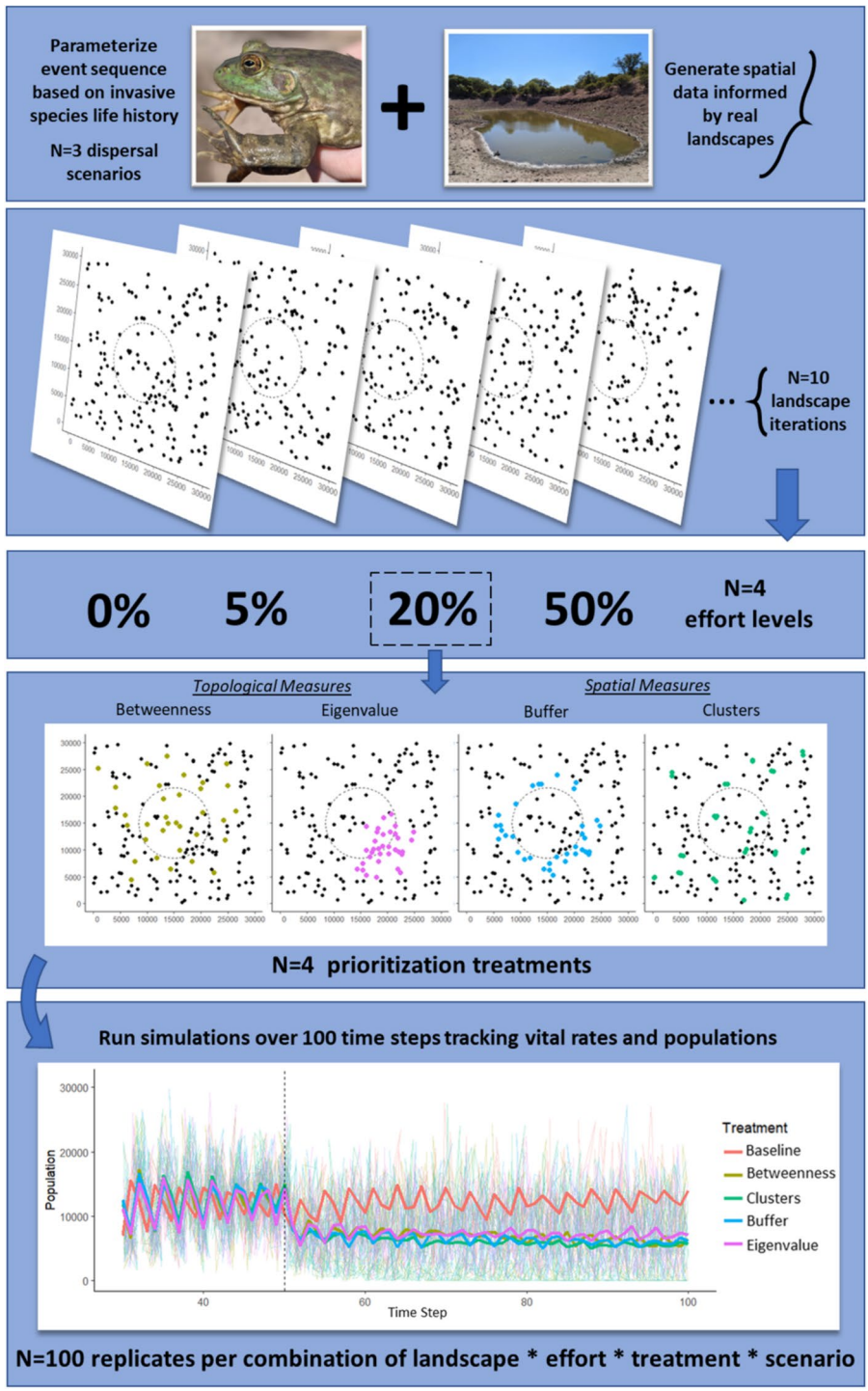


Fig. 2 Conceptual diagram of our modelling framework using spatially-explicit, individual-based models to explore if efficiencies can be gained for invasive species management using spatial prioritization of control efforts. Using the American bullfrog (*Lithobates catesbeianus*), we parameterize an event sequence with life-history data testing 3 different dispersal abilities. Selecting an area of interest that is invaded by the invasive species, we generate spatial data informed by real-world context and simulate landscape iterations with the same underlying statistical distributions. Within the simulated landscapes, we define a core area of 15% of the landscape as a protected area (shown within the dotted line). Exploring a range of control efforts, we prioritize which locations will be targeted for treatment based on competing measures of connectivity that highlight different ecologically relevant processes (Table 1). Then simulations are run for many replicates across pertinent combinations of experimental design levels. Populations are tracked across the full landscape and within the protected area to determine management treatment efficacy

of life history or simulation parameterization. Here, we briefly summarize the model, and further details and event sequence diagram are available in Appendices S1 & S2. The event sequence is subjected to 10 different iterations of patch networks (example network Figure S2, Appendix 1) to increase stochastic variation in population responses to management and reduce bias that could emerge from an

idiosyncratic landscape as patch network arrangement may affect ecological response to management actions (Wilson et al. 2023). The event sequence is set to run for 100 annual cycles (i.e. time-steps or generations). The model is female-only and is initiated with an adult individual at each habitat patch in the landscape. The model orients individuals towards randomly selected habitat patches (e.g. ponds) within a 5 km radius of the individual to reflect random dispersion among a likely neighborhood of available habitat. Then the model initiates a dispersal movement toward habitat patches where individuals stop at the first available habitat. Individual home ranges are established within habitat patches if breeding habitat is not completely occupied. If individuals have found acceptable breeding habitat, reproduction occurs with censuses before and after the event allowing the tracking of population dynamics. A single control event occurs once at time-step 50 in a defined area. Concurrently in management treatments, starting at time step 50, a control event occurs every time step until the simulation ends for habitat patches identified for management by the treatment's respective prioritization method. Censuses occur before and after control to track numbers of individuals removed from specific locations on the landscape. In all versions of the model, an overwintering mortality event occurs with stage-based survival rates. A final census occurs, individual age is incremented, and the event cycle starts over.

The event sequence is parameterized to model the population response of the bullfrog to five different competing management treatments. These represent either no continuing treatment (*baseline*) or a connectivity-based spatial prioritization for control efforts including both graph-theoretic and distance-only measures Graph-theoretic-based treatments prioritize patches for control based on either a patches betweenness centrality (Freeman 1977) or eigenvalue centrality (Bonacich 1972). Centrality measures hypothetically can be used for the prioritization of patches for control efforts, with the hope of increasing efficacy or reducing costs (Banks et al. 2015), because such measures can be better predictors of movement than distance only measures. Distance-based spatial prioritization focuses on either identifying clusters of patches closest to each other or in identifying patches in proximity to a focal area which form a buffer. Hereafter, we refer to each prioritization method by their measure: *betweenness*, *eigenvalue*, *cluster*, or *buffer* (Table 1).

The different methods represent a spectrum of spatial prioritization for eradication that spans a landscape to a local perspective. For example, a potential conceptual ranking of management treatment from landscape to local focus of connectivity metrics may be as follows: betweenness is concerned with movement through the entire network; eigenvalue is concerned with those patches connected to many other patches; clusters are those close to each other with no regard for the wider network; and buffers are dependent on the effort to determine the spatial extent of eradication in proximity to a protected area after an initial local control effort. Generally, we hypothesized that this should be the order in which the management treatments should perform in controlling the invasive bullfrog in our simulations at both landscape and local scales across all control effort levels.

Each management treatment is assessed under three different levels of effort, which identifies the top 5%, 20% or 50% of patches to prioritize for control efforts, in addition to a baseline 0% control effort to compare increasing control efforts against. Each combination of management treatment (n = 5), level of control effort (n = 4), and patch network iteration (n = 10) is run for 100 replicates (each replicate being 100 time steps long). This set of combinations is run for a range of dispersal scenarios (n = 3). We compare output of population size and patch occupancy within a focal protected area and across the entire simulated landscape. Although White et al. (2014) discourages the use of inferential statistics to analyze simulation output, graphical or correlative analyses are useful tools for identifying trends from simulation output (Perry et al. 2017). To this end, we used nested analysis of variance (ANOVA) tests followed by Tukey's HSD post hoc test to test for significant differences among management treatments. We used R Version 4.3.1 (R Core Team 2023) for all statistical analyses.

Spatial data and simulated landscape

We built our simulated landscape with empirical data from a region of interest: the Huachuca Mountains and surrounding Canelo Hills in southeastern Arizona, USA (hereafter referred to as HMCH; Fig. 1). This region represents a small portion of the invasive

Table 1 Spatial patch prioritization methods for a spatially-explicit individual-based model informed by spatial and biological data for the invasive American bullfrog in the Huachuca Mountains and Canelo Hills in southeastern Arizona, USA. The measures for prioritization which define each treatment are either graph-theoretic (*Betweenness and Eigenvalue*) or spatial (*Buffer and Cluster*). Graph-theoretic measures are hypothesized to increase efficacy of control efforts because they incorporate information from the entire patch network to define the relative importance of each patch to the movement of individuals across the network. Distance-only measures, in contrast, are informed by the Euclidean position of patches in the landscape without the network context

Treatment	Application	Definition	Ecological Context	Study Context
Baseline	Once at time-step fifty; included in all other treatments	Patches within defined circular protected area encompassing 15% of the landscape	Represents a single mass eradication event to protect a focal location, e.g. a home range of a species of conservation concern	Bullfrog eradication may improve resiliency to other compounding threats in species' home range including reduced habitat availability from climate change[a]
Betweenness	Annually; Starts at time-step fifty	Betweenness centrality[b] measures the influence of a patch to channel information through a network, described as having the most-shortest paths to connect patches	Hypothesized to act as stepping-stones across the "backbone" of a newtork[c,d], facilitating the quick spread across large distances[e]	Bullfrogs may be able to disperse long distances to colonize new waters, thus prioritizing eradication at patches with high betweenness should help reduce spread and (re)colonization[f]
Cluster	Annually; Starts at time-step fifty	These patches represent clusters of nearest neighbors on a landscape	Patches in these clusters would likely be able to facilitate local persistence, potentially through a mechanism such as rescue effects[g]. Targeting population sources is an established and simple method for optimizing control[h]	Bullfrogs can disperse long distances, but close clusters of patches are more likely to be colonized and be potential source populations. Consistent eradication at these patches should help prevent invasions in the surrounds patches by eliminating source populations[i]
Buffer	Annually; Starts at time-step fifty	These patches are selected based on their proximity to the protected area	This spatial "cordon" area around the protected area should reduce connectivity among patches within and outside its extent to prevent/reduce (re)invasion[f,j]	Dispersing bullfrogs are hypothetically prevented from colonizing patches near the protected area, reducing connectivity to the protected area by spatial proximity[k]
Eigenvalue	Annually; Starts at time-step fifty	Patches in networks with high eigenvalue centrality are connected to other highly connected patches, which are also connected to other highly connected patches, etc[l]	Densely connected networks should facilitate fast spread. Simulations suggest eigenvalue centrality could be useful for identifying locations for invasives spread[m] and control[n]	Bullfrogs should (re)colonize quickly through densely connected patch networks and eradication at these locations should disrupt their ability to colonize patches with many potential connections

[a]Mims et al. 2023, [b]Freeman 1977, [c]Estrada and Bodin 2008, [d]Urban et al. 2009, [e]Perry et al. 2017, [f]Drake et al. 2017a, [g]Eriksson et al. 2014, [h]Hastings et al. 2006, [i]Baker 2017, [j]La Fuente et al. 2018, [k]Pietrek et al. 2017, [l]Bonacich 1972, [m]Upadhyay et al. 2019, [n]Kvistad 2019

range of the American bullfrog in Western North America (U.S. Geological Survey 2023). The area informing our simulations is approximately 2000 km^2 and includes portions of Arizona, USA and Sonora, Mexico (Fig. 1). In part, the interest in this region stems from active efforts to suppress bullfrogs and their potential overlap and interactions with species of conservation concern such as the Arizona treefrog (Mims et al. 2016, 2023) and federally listed species such as the Chiricahua leopard frog (USFWS 2012) and Mexican gartersnake (USFWS 2014). To increase computational efficiency of the sIBM, we reduced the simulated study extent to be 30 km^2, which is 45% of the full extent of the area from which we are drawing spatial information. The underlying matrix among habitat patches represents a uniform dispersal habitat such that variation in dispersal behavior is solely attributable to the movement of the individual and distance among patches in the network. Managers are often tasked to remove invasive species from and/or prevent them from successfully invading some core area, which we represent here with a protected area. We define the *protected area* to be in the center of our simulated landscape represented by a circle with a radius of 6.56 km encompassing a 15% subset of the total landscape (Fig. 2). We tracked populations inside this protected area to represent a "focal" scale for management treatments, and across the entire simulated landscape for a "landscape" scale for management treatments and to evaluate the effects of management within the focal area at an extent beyond their application.

To determine the number of habitat patches to simulate for our landscape extent, we used a database of locally available water sources and their hydroperiods (Parsley et al. 2020). In our real-world area of interest in the HMCH region, we have approximately 600 known water locations with hydroperiods that range from permanent to never filling based on the images available across 2+ decades of satellite imagery. We calculated an annual hydroperiod index, where the index value was the percent of available images with water present compared to all total images for that location. As bullfrogs in this area are thought to require permanent waters to effectively breed and metamorphose (Willis et al. 1956), we selected ponds from the study area with a hydroperiod index greater than 0.6, meaning that they were more likely to be wetted than not in a given year. Given the proportional size of our simulation and the number of waters with a hydroperiod index greater than 0.6, we include 170 habitat patches in our simulation. We maintained patches at the same size to maintain equal carrying capacities in patches. Patches are 1 grid cell in the HexSim landscape grid, which reduces potential bias to the emergent connectivity from increased availability of dispersers in larger breeding patches. The patch locations were generated using random draws from uniform distributions within the bounds of our landscape extent. We generated 10 different realizations of the patch networks with the same macroscopic statistical structure (sensu Perry et al. 2017). Patch locations were used to generate network topologies, defining connections to be maintained between patches within 5 km as this related to demographic settings (see below). We used R libraries spatstat (Baddeley et al. 2015), matrixStats (Bengtsson 2023), and igraph (Csardi and Nepusz 2006) for graph and point pattern analyses. We used R Version 4.3.1 (R Core Team 2023) and packages terra (Hijmans 2023), sf (Pebesma 2018), and ggplot2 (Wickham 2016), for generation, manipulation, analyses, and visualization of spatial data (Appendix S3).

Spatial prioritization of control efforts

Management treatments are defined by prioritization method and focus on different approaches to controlling invasives (Table 1). We describe the collective spatial footprint of selected patches based on any of these prioritization measures as *removal areas* in our event sequence (Appendix S1). Our baseline treatment represents our informed null model. In our baseline treatment, we eliminate all individuals a single time at the 50th time step inside of the protected area. This is reflective of an intensive eradication plan in one year such as volunteer driven "Invasive Blitz" programs (e.g. Wood and Gupta 2016) and then no follow-up management to maintain exclusion of invasives from our protected area or reducing populations to a functional eradication or suppression (With 2002; Simberloff 2009; Green and Grosholz 2021). All other management treatments (i.e. *betweenness*, *eigenvalue*, *cluster*, or *buffer*) include this single eradication event coupled with one of the four different approaches to prioritizing which habitat patches receive additional, ongoing invasive species control (Table 1). Eradication in the removal areas under

each treatment also begins at the 50th timestep, concurrently with the single eradication event that occurs in the protected area. The removal event then occurs every time step until the simulation ends. We use the mean and SD percent differences of each prioritization method compared against baseline mean population and occupancy for time steps 81–100 as metrics to gauge relative performance (Mims et al. 2023).

Demographic parameters

We searched known literature for bullfrog demographic parameters and life-history data. When such data could not be found for the bullfrog specifically, we referenced closely related congeners or similar species; failing that, we used expert opinion. Little data are available regarding demographic rates and life-history information of bullfrogs in their invasive distribution. For that reason, most parameter estimates refer to the bullfrog in its native habitat. Summary description of parameters used in HexSim models by category and event sequence can be found in Appendices S1 and S2. Sensitivity analyses for key parameters such as fecundity and survival were conducted to ensure that models responded predictably to these changes.

Traits were assigned to each individual for age, group status, and event dependent locations. Age class is accumulated once per time step, beginning with class 0 (larvae) and finishing at 4+ (adult). Group status, which describes whether or not an agent is part of a group of individuals associated with a habitat patch, was dependent on available breeding habitat, wherein groups formed within home ranges in habitat patches. Being part of a group in a habitat patch dictated whether the individual would have a breeding attempt later in the event sequence. The home range area was set to a single hex cell, the size of our simulated habitat patches, which are also realistic representation of many of the available water sites in the study area. Max group size was set to 20 individuals to improve computational efficiency (Appendices S1 & S2). We examined the model for sensitivity to max group size and doubled the value to 40 individuals per habitat patch (30 m hexagon cell). Traits for location tracked whether or not the individual was in either a protected area or removal area and which habitat patch it was located in.

Only those individuals that joined or formed groups in home ranges were allowed to reproduce. Fecundity a function of snout-to-vent lengths based on relationships for the Ranidae family (Wells 2007). Reproduction is also stage based, wherein larval (stage 0), and juvenile (stages 1–2) do not contribute to reproduction in the model. This reflects the average age to reproductive maturity for bullfrog females (Moore et al. 2021). Once adults (stages 3–4+), reproductive contributions are made and fecundity is adjusted for larval mortality (Cecil and Just 1979; Appendix S2). We tested model sensitivity to fecundity, running a scenario with fecundity higher by 50%.

Mortality occurred in two ways: (1) simulated removal within the protected area and removal areas, and (2) overwintering death, including those unsuccessful dispersers left in the matrix. Mortality induced during management treatments were assumed 100% effective within target location, and all stages were targeted equally. In contrast, our overwintering mortality was stage-based and a function of group membership and age. Post-metamorphs and juveniles have higher probability of mortality than adults (Raney 1940; Govindarajulu et al. 2005; Howell et al. 2020). We assume larvae have 100% survival as we adjusted for larval mortality in the reproduction event. Individuals that do not establish or join a home range group are assumed to not survive the overwintering survival event (Appendix S1; Appendix S2). Bullfrogs require aquatic habitat for both overwintering adults and larvae. We tested model sensitivity using a scenario exploring a 50% increase of all adult stage's survival.

Dispersal from natal habitat occurs after an initial exploration, where the agent is limited to movement within 50 hex cells around the habitat patch to identify whether any habitat is available locally before dispersing. Dispersal is carried out by non-larvae stages, and the youngest individuals (stages 1–2) would be most likely not to belong to an existing home range and need to search for new habitat (Willis et al. 1956). Then in the event sequence, a spatial affinity event is used to "attract" individuals during dispersal towards a habitat patch drawn randomly from those available in a 5 km radius surrounding their starting location. The dispersal is set to a minimum of 1 hexagon and a maximum of 234 hexagons (7020 m) as our "standard dispersal scenario" (Currie

and Bellis 1969; Kahrs 2006; Suhre 2010; Cooper 2017). This maximum distance is at the upper end of expected bullfrog movements and allows individuals the opportunity to reach habitat within the 5 km spatial affinity event bounds. However, to account for the variability in and unknown upper extent of bullfrog dispersal in their invasive range, we also tested a "high dispersal scenario" with changes in maximum dispersal with an increase to 300 hexagons (9000 m) and a "low dispersal scenario" with a decrease to 167 hexagons (5010 m) for maximum dispersal distance. The dispersal distance is drawn from a uniform distribution. The setting which determines the randomness of paths, autocorrelation, was set to 60%. Both path distribution and autocorrelation allow for increased opportunistic arrival in patches not selected during the spatial affinity event, while also allowing realistic movement paths through the uniform matrix (Suhre 2010; Cooper 2017; Joly 2019). Once any habitat patch is encountered, dispersal terminates and a second exploration event of 50 hexagons initiates to start new or join existing home range groups that are not full. Dispersal distances are generally shorter than the maximum as individuals discover habitat and end their dispersal phase. However, some individuals do not find a habitat patch before their movement finishes, cannot join a group in acceptable breeding habitat, and subsequently die in the matrix as transients. This type of mortality occurs commonly in overland dispersal, particularly in arid landscapes for pond-obligate amphibians.

Results

We found that total bullfrog populations and occupancy declined in response to all treatments regardless of effort level or patch prioritization methods. However, the most effective spatial prioritization was effort-dependent and varied depending on spatial context (Table 2; Figs. 3a and 4a). Results reported throughout are mean occupancy and population size for time steps 81–100 under the standard dispersal scenario unless otherwise noted.

For the full landscape, baseline mean bullfrog population size was 12,673 (SD = 4038). Within treatments, mean percent difference values decreased when level of effort was higher (Table 2). Population sizes were significantly different among effort levels ($F = 42{,}295$, $df_1 = 3$, $df_2 = 9$, $p = < 0.001$), and within each effort level there were significant differences of mean population sizes among treatments ($F = 780$, $df_1 = 9$, $df_2 = 12{,}987$, $p = < 0.001$). The Tukey HSD post-hoc test revealed that all prioritization methods were significantly different from baseline population numbers. Among the 78 potential pairwise combinations of treatments and control effort, all but 6 were significantly different from each other (Appendix S4). Among treatments, the non-significant comparisons occurred at 5% level of control effort (Appendix S4). The percent differences in the magnitude of standard deviations among treatments also show a similar trend: the magnitude of difference was reduced when control effort was higher. All combinations showed a reduction from the baseline treatment ranging from − 3 to − 161% with the exception of the 5% level of control effort for buffers, which increased SD differences to baseline by 5%.

Within the protected area, mean percent differences among treatments increased when effort was lower, but optimal treatment also varied by effort level (Fig. 3b). Baseline mean bullfrog population size within the protected area was 2178 (SD = 1382). Mean populations in the protected area were significantly different among effort levels ($F = 27{,}999$, $df_1 = 3$, $df_2 = 9$, $p = < 0.001$) and among treatments within each effort level ($F = 1106$, $df_1 = 9$, $df_2 = 12{,}987$ $p = < 0.001$). A Tukey HSD post-hoc test showed that 70 of 78 combinations were significantly different (Appendix S4). Most combinations among the 5 and 20% control effort levels were significantly different from each other in the Tukey HSD test; those combinations showing a statistical insignificance are generally those at the 50% effort level (Appendix S4). For example, betweenness and clusters prioritization methods showed very low population sizes with mean differences of − 200 and − 197%, respectively. Buffer treatment at 50% control effort resulted in eradication of bullfrogs from the protected area by time step 81 with exclusion maintained through the remainder of the simulation (Table 2; Figs. 3b and 4b), outperforming both betweenness and cluster treatments. Betweenness and buffer treatments performed as well at 20% control as betweenness, buffers, clusters, and eigenvalue. For example, 20% effort betweenness treatment was not different from the 50% control effort level for eigenvalue treatments. The 20% control effort buffer treatment also did not show

Table 2 American bullfrog simulation mean outputs for response metrics for the last 20 time steps. *Mean % difference* are the differences between the mean of baseline simulations where there was no sustained eradication and those where varying levels of control efforts are based on spatial prioritization using either network (betweenness and eigenvalue) or spatial (clusters and buffer) methods. *SD % differences* represent the magnitude of differences in standard deviation between baseline population and spatial prioritization of eradication efforts

	Effort	Prioritization Method	Mean	Mean % Difference	SD	SD % Difference
Population—Landscape	0%	Baseline	12,673	–	4038	–
	5%	Betweenness	11,055	− 14	3938	− 3
	5%	Clusters	11,014	− 14	3755	− 7
	5%	Buffer	11,033	− 14	4235	5
	5%	Eigenvalue	10,855	− 15	3932	− 3
	20%	Betweenness	6633	− 63	2971	− 30
	20%	Clusters	4946	− 88	2722	− 39
	20%	Buffer	5580	− 78	2802	− 36
	20%	Eigenvalue	8006	− 45	3316	− 20
	50%	Betweenness	1004	− 171	1213	− 108
	50%	Clusters	133	− 196	442	− 161
	50%	Buffer	1403	− 160	1404	− 97
	50%	Eigenvalue	3614	− 111	2339	− 53
Population—Protected Area	0%	Baseline	2179	–	1383	–
	5%	Betweenness	1398	− 44	1133	− 20
	5%	Clusters	2004	− 8	1376	0
	5%	Buffer	1729	− 23	1314	− 5
	5%	Eigenvalue	1624	− 29	1223	− 12
	20%	Betweenness	195	− 167	482	− 97
	20%	Clusters	945	− 79	1020	− 30
	20%	Buffer	29	− 195	223	− 145
	20%	Eigenvalue	927	− 81	1021	− 30
	50%	Betweenness	0	− 200	0	− 200
	50%	Clusters	16	− 197	124	− 167
	50%	Buffer*	0	− 200	0	− 200
	50%	Eigenvalue	157	− 173	394	− 111
Patch Occupancy Rate—Landscape	0%	Baseline	81	–	8	–
	5%	Betweenness	76	− 7	13	53
	5%	Clusters	76	− 7	9	22
	5%	Buffer	76	− 7	15	62
	5%	Eigenvalue	75	− 8	13	56
	20%	Betweenness	53	− 43	12	42
	20%	Clusters	44	− 59	15	66
	20%	Buffer	44	− 59	12	47
	20%	Eigenvalue	57	− 35	11	38
	50%	Betweenness	10	− 156	8	5
	50%	Clusters	2	− 193	4	− 62
	50%	Buffer	12	− 148	7	− 3
	50%	Eigenvalue	28	− 99	10	25
Patch Occupancy Rate—Protected Area	0%	Baseline	79	–	22	–
	5%	Betweenness	71	− 10	25	12
	5%	Clusters	77	− 2	23	3

Table 2 (continued)

	Effort	Prioritization Method	Mean	Mean % Difference	SD	SD % Difference
	5%	Buffer	72	− 9	27	18
	5%	Eigenvalue	73	− 7	25	11
	20%	Betweenness	50	− 45	35	43
	20%	Clusters	65	− 20	29	24
	20%	Buffer	40	− 65	41	59
	20%	Eigenvalue	61	− 26	30	29
	50%	Betweenness	39	− 67	42	60
	50%	Clusters	42	− 61	40	57
	50%	Buffer	39	− 68	42	61
	50%	Eigenvalue	44	− 56	39	53

*Buffers at 50% treatment effort had no effective mean standard deviation percent difference as there were no individuals recorded within habitat patches within the protected area to calculate means and standard deviations with

significant difference from the 50% control effort for clusters. As well, 20% effort buffer treatment was not significantly different from 50% effort buffer treatment, suggesting that with carefully selected connectivity measures, the same results (eradication or control) can be achieved with less than half the effort of sub-optimal connectivity measures at higher effort rates.

Patch occupancy shared the same general trend with other metrics wherein the mean percent difference values decreased when levels of control effort within treatments where higher (Table 2; Fig. 3c). Mean patch occupancy of 138 (SD = 13) was significantly different for each level of effort ($F = 44{,}425$, $df_1 = 3$, $df_2 = 9$, $p = < 0.001$) and among all treatments in each level of effort ($F = 779$, $df_1 = 9$, $df_2 = 12{,}987$ $p = < 0.001$). However, a Tukey HSD post-hoc test shows that 7 of the 78 combinations did not significantly differ (Appendix S4). Of these, six of the combinations were those comparing 5% levels of control effort and the same identified when considering population size and the seventh was not identified in other response variables (20% Effort—Buffers vs. 20% Effort—Clusters). Mean percent differences ranged from − 77% (5% Effort—Clusters) to − 193% (50% Effort—Clusters). Percent differences of standard deviations was more complicated than in other response metrics. In contrast to population size, standard deviation of patch occupancy was higher than baseline for most treatments. Percent differences of standard deviations range from 66% (20% Effort—Clusters) to − 62 (50% Effort—Clusters). Within the protected area, patch occupancy followed similar trends as population size in response to treatments wherein buffers and betweenness reduced occupancy better (Fig. 3, Table 2, Appendix S4).

Mean baseline population and occupancy increased with high dispersal and decreased with low dispersal scenarios. High dispersal simulation results showed significant differences among treatment types and among effort levels (Appendix S4), yet post hoc Tukey HSD tests reveal fewer pairwise combinations lacked significance compared to scenarios using lower dispersal abilities. In low dispersal scenarios, clusters were the most effective spatial prioritization method for landscape population and occupancy at all effort levels, while prioritization in the protected area with buffers was most effective across all levels of effort (Appendix S4).

Treatment efficacy appeared to be dispersal ability dependent (Appendix S4). In high dispersal scenarios, betweenness improved performance relative to analyses with standard dispersal ability across all response variables. In particular, in the protected area betweenness was the most effective prioritization method at both 5% and 20% efforts (mean % difference = − 132%). At the 50% effort level, betweenness was not statistically different from buffers (200% for both). At the 20% level, betweenness more than doubled the mean percent difference compared to the next best method with the same effort level (Eigenvalue centrality: − 59%).

Sensitivity analyses suggest that our model is robust. Simulation results for sensitivity analyses

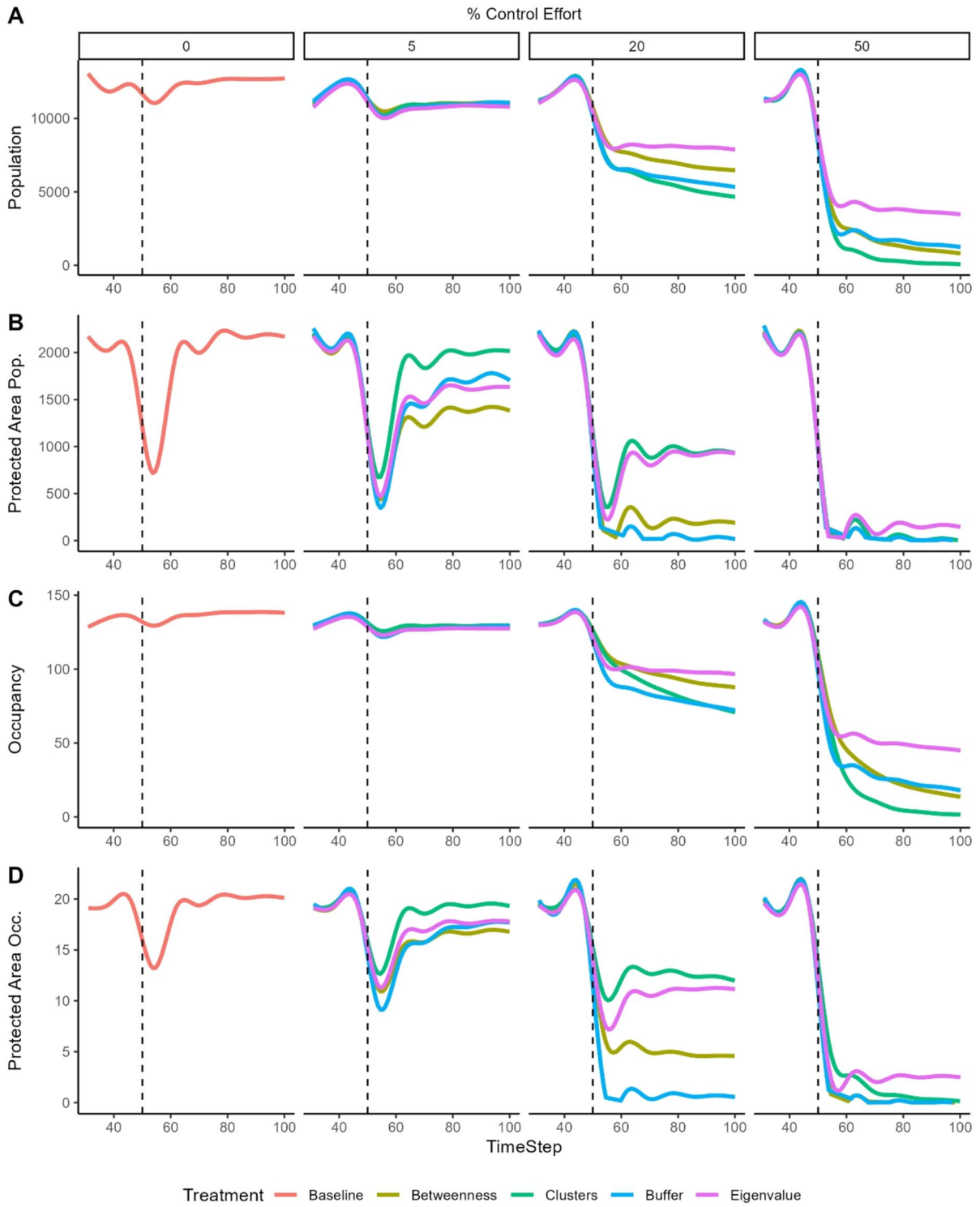
show proportional responses to changed parameters. When reproduction rates increase or decrease by 50% for each stage class, population levels increase and decrease proportionately (Appendix S2 & S4). Increasing stage-based overwintering and foraging survival by 50% increased population sizes as well (Appendix S2 & S4). This more than doubles the mean population size, and this is likely due to the ability of older individuals surviving to produce more offspring as well as the higher in-habitat survival rates compensating for the individuals that could not reach or find available habitat each time step and subsequently died.

Discussion

We used spatially-explicit, individual-based models to simulate invasive bullfrog population dynamics in a patch network informed by real data. In contrast to our first general hypothesis, we found that graph-theoretic patch prioritization for control efforts can, but do not always, outperform non-topological methods. Results show the most effective treatment was effort and spatial context dependent; as well, the difference in efficacy of treatments was not consistent across effort or spatial context. However, at the regional landscape scale, the magnitude of difference in performance of the worst to best treatment did increase when effort was higher, suggesting a conditionally supported secondary hypothesis. Treatment efficacy was also sensitive to the simulated dispersal ability of bullfrogs, but not as expected by our last hypothesis. Results from the standard dispersal parameterization combined with results from the other dispersal scenarios suggest there may be a threshold at which the best choice in prioritizing habitat for control efforts may be dependent on the interaction between the spatial arrangement of habitat and dispersal ability of the target species. Dispersal ability did influence the performance and variability of population responses to different prioritization methods. The relative performance of betweenness increased when dispersal ability was higher across the landscape and within the protected area. Demographic stochasticity, landscape structure, and individual variation in behavior may all contribute to such inconsistencies (Baguette et al. 2013; Ferrari et al. 2014; Wilson et al. 2023). For example, while we maintained consistent carrying capacities among all patches in this study, the performance of graph-theoretic metrics may change if the assumed area-abundance relationship is disrupted (Drake et al. 2022a, b). The use of sIBMs like ours can help uncover which assumptions and factors may affect the efficacy of invasive species control efforts.

The interaction between dispersal biology and landscape structure, which ultimately represents the potential or functional connectivity of a system (Kool et al. 2013; Drake et al. 2022a), indicates that the appropriate measure for site prioritization is likely to be both taxon- and objective-specific (Perry et al. 2017). Because each connectivity measure captures different aspects of the landscape (Kindlmann and Burel 2008), the effectiveness for site prioritization is likely to be dependent on both structure and function. Graph-theoretic measures of connectivity have been proposed to be a useful tool for site prioritization based in part due to their representation of the flow of information (i.e. organisms) through spatial networks (Banks et al. 2015). For example, locations with high betweenness centrality are assumed to facilitate spread. Within a real world network, locations with high betweenness centrality have been found to be facilitators of disease spread (Ortiz-Pelaez et al. 2006) and correlated with the presence of invasive species in lake networks (Kao et al. 2021).

Patch prioritization using betweenness centrality performed better under a high dispersal scenario than a low dispersal scenario in our simulation. This finding differs from Perry et al. (2017) and Minor & Gardner (2011), where higher dispersal confounded the effectiveness of betweenness centrality site prioritization. However, both studies modelled species with relatively local dispersal, whereas bullfrogs can be highly vagile. The bullfrog's ability to move through hostile matrix and for relatively long distances may make high betweenness stepping-stone patches that much more important for facilitating invasive spread. The probability of encountering a high betweenness patch should increase as dispersal ability increases. The ability to model the dispersal process in a spatially-explicit manner may also help explain the difference in performance among studies. Our study did not assume movement along graph edges amongst patches; our model allowed bullfrogs to disperse using a correlated random walk where they may stop at non-target patches or die if they do not encounter habitat. Assumptions in connectivity



modelling process, such as restricting movement along graph edges, can bias results as they may not accurately represent individuals' dispersal behavior (Lookingbill et al. 2010), the realized connectivity among habitat patches on the landscape (Bishop-Taylor et al. 2018), or the emergent population dynamics

◂**Fig. 3** Bullfrog population and patch occupancy response to management treatments from a spatially-explicit, individual-based model using HexSim. Time series starts after 30-year burn-in time, and dashed vertical lines represent a single eradication of all individuals within a protected area at time step 50. Response variables represent the mean of all replicates iterated over 10 simulated habitat networks. Columns represent changing levels of control effort ranging from no treatment to 50% treatment of habitat patches using different spatial prioritization strategies. These prioritizations include graph-theoretic-based measures (eigenvalue and betweenness centralities) and distance-only spatial measures (clusters of highly connected habitat and buffers of patches surrounding the protected area). **A** Bullfrog populations are suppressed across the landscape in relation to the control effort conducted, while **B** Populations in the protected area are eliminated under certain treatments. **C** Occupancy of habitat patches follow similar trends as populations levels and **D** occupancy in the protected area is shows similar trends as populations in protected area. Measures are smoothed with a running mean, such that the magnitude of eradication at time step 50 can be under-represented or over-represented graphically, particularly for time series of measures within the protected area

(Ovaskainen and Hanski 2004; Drake et al. 2022a, 2022b). Such assumptions are often necessary due to modeling decisions or data constraints such as static network representations, dispersal distances, or limiting connections arbitrarily (Moilanen 2011; Ferrari et al. 2014). While our model relaxes many of these assumptions, exploration of the sensitivity of a connectivity measure to the modelling of the dispersal process should be a continued topic for future research.

Other connectivity measures may also perform unexpectedly under spatially realistic conditions. Eigenvalue centrality may be a useful tool to identify priority locations for invasive species control because it identifies the parts of a network that can rapidly saturate the network with dispersers (Kvistad 2019). For example, eigenvalue measures have been used in simulations to identify which ports to prioritize for management of invasives in ballast water (Kvistad 2019) and has been used to identify locations pertinent to the potential spread of an invasive plant (Upadhyay et al. 2019). However, our results suggest there are conditions that may reduce effectiveness relative to other measures of connectivity. Eigenvalue centrality was a consistently poor performer for site prioritization of control efforts for bullfrogs. This may be in part due to the dispersal characteristics of the bullfrog compared to the invasives modelled by Kvistad (2019) or Upadhyay et al. (2019). The ability of bullfrogs to bypass close patches due to high relative vagility may also undermine the measure's ability to identify important patches. Eigenvalue centrality may thus be best suited for management scenarios in which dispersal is limited to a few neighboring patches and where saturation across a network may require many relatively constrained dispersal steps via short dispersal distances or limited pathways in a constrained graph. This may also be true in other graph-theoretic measures that focus on neighbor adjacency. For example, degree centrality, or the number of nodes connected to a specific node, was not a reliable measure for the spread of simulated 'generic' invasives across a habitat network (Ferrari and Lookingbill 2009). The relative importance of specific dispersal traits and their effect on connectivity measure effectiveness should be further explored across taxa to confirm whether this is a widespread phenomenon (Minor and Gardner 2011).

Contrary to our expectations based on the vagility of the bullfrog, buffer zones provided a consistently high performing prioritization method. The underlying mechanism could be that buffers reduce the structural connectivity among habitat, preventing colonization. This management method has been proposed to reduce the spread of invasive species, including the American bullfrog (Drake et al. 2017a, 2017b). Our results provide *in-silico* evidence that this method may be a reasonable approach depending on the shape of the network (Wilson et al. 2023) and dispersal behavior of the organism. The outward edges of the buffer may also benefit the surrounding unmanaged landscape by providing a sink habitat which may impact nearby colonization-extinction dynamics (Gundersen et al. 2001; Heinrichs et al. 2018). As well, this may produce a "halo effect", where the negative impacts of invasive species on local species populations are reduced beyond the bounds of the management area (Glen et al. 2013) such as through the subsequent coextirpation of the invasive bullfrog and the pathogens they harbor (Hossack et al. 2023).

The targeted disruption of metapopulation dynamics may further Allee effects, the phenomena of low population density dependences, contributing to a wider population decline through local extinction events (Taylor and Hastings 2005; Tobin et al. 2011). This type of effect was also seen in an sIBM study that explored spatial prioritization of management for the common brushtail possum

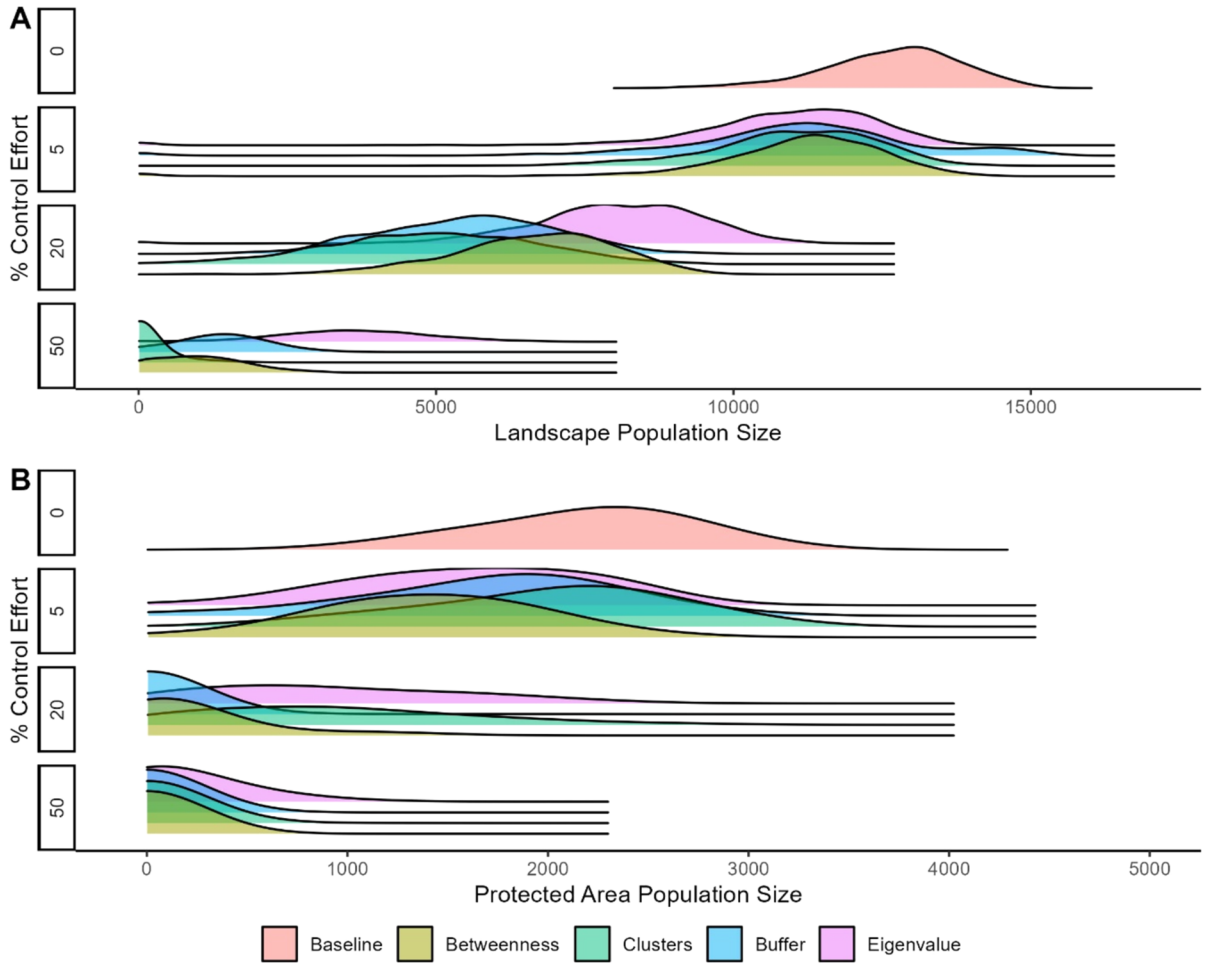


Fig. 4 Density distribution of mean **A** landscape population and **B** protected area population sizes across time steps 81–100 under varying levels of control effort and spatial prioritization treatments for bullfrog eradication. Note the x-axis scales are different between panels **A** and **B**. There are increasingly noticeable differences in population sizes among treatments as effort level at the landscape scale. However, for populations in the protected area, betweenness and buffers outperform other methods at 20% and are not different at or from 50% effort, suggesting that with carefully selected connectivity measures, similar control results can be achieved with less than half the effort of sub-optimal connectivity measures at higher effort rates

(*Trichosurus vulpecula*) where immigration was most likely to initiate recovery (Lustig et al. 2019). Combining as large a buffer as possible while taking advantage of natural barriers could improve buffer treatment efficacy, reducing dispersal success of invaders which may eventually bypass any defined buffer zone (Baker and Bode 2016; Pietrek et al. 2017). Our simulation assumed perfect eradication of species within prioritized habitat patches, yet complete removal relies on perfect detection of invasives, which is unlikely to occur (Rout et al. 2014). Missed individuals may be able to (re)colonize the exclusion area, undermining efforts. A simulation study by Pietrek et al. (2017) that examined buffer-based exclusion of beavers in Patagonia showed that the performance of buffers was resilient to changes in levels of control effort. However, this study assumed the invaders were novel and not recently eradicated from the study area before further culling. Future research should test how sensitive spatial prioritization treatments are to imperfect removal.

In the semiarid western United States, bullfrog populations can be spatially structured because they require aquatic habitats which can be limited in many areas. Habitat is often isolated or only connected through transient windows of connectivity when monsoon rains temporarily wet dry creek beds (Zeigler and Fagan 2014). Access to these remote water sites is often logistically constrained because of poor road conditions, making monitoring and management difficult. Management of such locations is complicated by the use of isolated waters for agricultural interests, recreation, and species of conservation concern such as the Sonoran tiger salamander (*Ambystoma tigrinum stebbinsi*) and Sonora mud turtle (*Kinosternon sonoriense sonoriense*). Some management techniques for invasive species, such as the temporary draining of habitat which ensures complete removal of all life stages of bullfrogs, may not be an option in the presence of protected aquatic species. Other habitats, such as those for which size or habitat complexity pose a significant challenge to complete eradication, can further complicate regional management of invasive species. For example, near the center of our study area, bullfrogs are also found in a large reservoir, which is a likely source of dispersers. These factors complicate bullfrog management and removal in the region.

Our results, however, suggest that the right combination of spatial prioritization, particularly using buffers and betweenness centrality, and modest effort levels may be sufficient to protect focal areas of concern (e.g. Arizona treefrog breeding habitat: Mims et al. 2023). While we do not have an independent dataset available to validate our model (Augusiak et al. 2014), there are several pieces of evidence that allow us to assert confidence in our bullfrog model. For example, a connectivity-focused management approach has worked in a nearby system as well. Within a wetland network at San Bernadino Wildlife Refuge (< 100 miles away), initial ad-hoc eradication attempts were unsuccessful, and populations rebounded within 3–4 months (Rosen and Schwalbe 1995). Populations were ultimately controlled using a widespread and increased control regime that also accounted for riparian connectivity (Jarchow et al. 2016). Just north of the Canelo Hills region is the Las Cienegas National Conservation Area (LCNCA), where bullfrog removal was conducted to support reintroductions of the Chiricahua leopard frog. Bullfrogs were removed from an exclusionary buffer zone that was established between LCNCA and nearby known bullfrog populations. Monitoring was conducted such that only singleton dispersals were found on occasion and removed from the buffer area before populations could establish (Hall 2020; Bauder and Prewitt 2024). Further, removals combined with buffer treatments have been successfully preventing recolonization of important aquatic habitat for sensitive species of conservation concern on the Coronado National Forest for several years (J. Kraft pers. obs.). Finally, our bullfrog model can be compared to similar models of other taxa. A HexSim model for Arizona treefrogs was able to be validated using an independent dataset (Mims et al. 2023). Simulated (meta) population dynamics and dispersal behavior reflected observed population structure and response to landscape features that were derived from genetic analysis of populations of treefrogs in the HMCH area (Mims et al. 2016; Parsley et al. 2020).

Conclusion

Eradication of invasive species is possible, even after establishment (Jarchow et al. 2016; La Haye et al. 2023), but long-term suppression may become the norm for many established invasive species (With 2002; Green and Grosholz 2021). Here we provide a modeling framework that uses a sIBM to explore how different spatial prioritizations of control efforts may provide improved management results. Our results suggest that graph-theoretic measures of connectivity can help prioritize areas for effective management against the invasive bullfrog. However, we also demonstrated that graph-theoretic measures of connectivity are not always the best method of spatial prioritization across all levels of effort, or dispersal ability explored. A common thread between the highest performing measures was a sufficient disruption of connectivity among patches across the entire habitat network. Reduced bullfrog dispersal among increasingly isolated subpopulations often led to localized extinctions, potentially due to Allee effects. A potential boon to simplifying management prioritization schema was the relatively high performance of a simple buffer surrounding a protected area. When sufficiently wide enough around a protected area, buffers prevented recolonization (Glen et al. 2013; Pietrek

et al. 2017). Our work suggests that under spatially realistic conditions, with carefully selected connectivity measures, the same management results can be achieved with much less effort compared to suboptimal connectivity measures conducted at much higher effort rates. Given our results, we believe there is potential this model could be used to identify relatively superior management strategies for controlling bullfrog populations in specific cases and locations. Our results also provide some evidence that appropriate selection of connectivity measures may require a taxa-specific approach (Perry et al. 2017), but this is an area that remains an important avenue for future research. More work is needed to determine whether organism's traits help define which connectivity measures are most appropriate for specific suites of dispersal behavior, demographic traits, and population dynamics. Such work could lead to trait-based generalities that could be useful for parameterizing models for species with limited available data.

Acknowledgements We thank the following individuals and institutions for their support: Justin Stover and Dr. Matthew Grabau for contributions to study ideas and management scenarios tested; Dr. Nathan Schumaker for support in model development; Dr. Daryl Trumbo, Sam Silknetter, Erin Crone, and Dr. Ben Padilla for feedback on early versions of the manuscript; the 2023 SMARTSIM Bullfrog Management Workshop Participants Dr. Javan Bauder, Karlee Jewell, Joseph Barron, Ian Latella, Chris Prewitt, David Hall, and Solena Daniels for perspectives on invasive bullfrog ecology and management that helped inform the scope of simulations; and Audubon Society's Appleton-Whittell Research Ranch for logistical support for the 2023 SMARTSIM Bullfrog Management Workshop.

Author contributions All authors contributed to manuscript conception, design, and development. J.D. developed the simulation model, wrote the main text, conducted analyses, interpreted results, and prepared all figures and tables. M.M. and G.O. helped with interpretation of results, development of figures/tables, and provided extensive feedback on revisions. All authors reviewed the manuscript.

Funding This work was supported by U.S. Fish and Wildlife Grant No. F20AC11469-00, U.S. Forest Service Agreement No. 21-PA-11030500-131, and the Virginia Tech Fralin Life Sciences Institute through the Virginia Tech Invasive Species Collaborative.

Data availability We provide germane methods in the main manuscript and a TRACE document (Schmolke et al. 2010; Augusiak et al. 2014; Grimm et al. 2014) is provided in Appendix S1. Data on model parameterization can be found in Appendix S2. HexSim environments and code for spatial data generation and analysis is available via a public GitHub Repository https://github.com/MimsLabVT/LICA_HexSim_Drake_etal (Appendix S3). Appendix S4 contains expanded results tables.

Declarations

Competing interests The authors declare no competing interests.

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