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Brielle Kwarta Thompson

Quantitative modeling tools for invasive species management decisions

Brielle Kwarta Thompson

A dissertation
submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington
2024

Reading Committee:
Sarah J. Converse, Co-chair
Julian D. Olden, Co-chair
Andrew M. Berdahl

Program Authorized to Offer Degree:
Quantitative Ecology and Resource Management

University of Washington

Abstract

Quantitative modeling tools for invasive species management decisions

Brielle Kwarta Thompson

Chairs of the Supervisory Committee:
Sarah J. Converse
USGS Washington Cooperative Fish and Wildlife Research Unit
School of Aquatic and Fishery Sciences & School of Environmental and Forestry Sciences

Julian D. Olden
School of Aquatic and Fishery Sciences

Invasive species threaten biodiversity and cause harm to the environment, economies, and human health. Natural resource managers tasked with determining management plans for controlling or eradicating invasive species often grapple with challenges such as ecosystem complexity, uncertainty about the effectiveness of management actions, limited budgets, and conflict with the public regarding management practices. Quantitative population models applied to invasive species management provide a cost-effective tool for evaluating management outcomes in a

virtual environment before management is implemented. In particular, simulation models provide insight into the performance of alternatives under varying ecological states and management assumptions prior to substantial time investment or expensive on-the-ground experiments.

Here, I demonstrate how quantitative models can be harnessed to effectively inform invasive species management decisions. First, I provide an extensive review of mechanistic models that are used for invasive species management to address the gap between those who build models and those who are tasked with actual management implementation (Chapter 2). Second, I provide a simulation study to assess different spatial strategies for invasive rusty crayfish (*Faxonius rusticus*) removal in the complex riverine environment of the John Day River, USA (Chapter 3). The model indicated that to minimize overall population abundance, crayfish should be removed in locations where their abundance is highest, and removal at the most downstream extent of their invasion is key for preventing invasion to new areas, i.e., the Columbia River, USA. Third, I provide an adaptive management framework for invasive flowering rush (*Butomus umbellatus*) management in the Columbia River to support decisions regarding allocation of resources towards monitoring and control under two invasion conditions (Chapter 4). The model revealed that for an established invasion, it was beneficial to conduct monitoring and removal at spatially fixed areas, whereas for an emerging invasion, effort can be more effectively allocated in highly invaded areas. The model also indicated that for an emerging invasion, managers may benefit by integrating community science data into their monitoring to help track the emerging invasion. Finally, I examined how to identify optimal invasive species management actions involving multiple decision makers, each with their own management objectives (Chapter 5). To do so, I compared multiple-criteria decision analysis (MCDA), used for decisions involving multiple objectives, and game theory, used in circumstances with multiple decision makers. I showed that MCDA sometimes failed to reveal invasive species harvest actions that were identified in game-theoretic analyses as providing improved outcomes, but MCDA provided better insight into the preferred actions of each individual decision maker. Overall, my research demonstrates ways in which quantitative models can be used to help decision makers identify promising solutions to invasive species management. Broadly, my research demonstrates ways in which quantitative modeling tools can be used to help inform decision making in natural resource management.

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ACKNOWLEDGEMENTS

My PhD student era was not all “rainbows and sunshine” – I made it through many dark and dreary Seattle winters after all. Graduate school was tough, but it was made a lot easier by all the professors, friends, and family who supported me. I would like to thank all of those who have helped me academically and personally.

I would like to thank the various funding sources that supported throughout my PhD including the Quantitative Ecology and Resource Management program, the School of Aquatic and Fishery Sciences, the Washington Cooperative Fish and Wildlife Research Unit, the U.S. Geological Survey Invasive Species Program, the U.S. Geological Survey Science Support Program in collaboration with the U.S. Fish and Wildlife Service’s Pacific Region, and the ARCS foundation Seattle Chapter.

One of the greatest aspects of my graduate school experience was being in two labs, making my academic support family twice as large. I would like to thank all the members of the Converse Lab including Abby Bratt, Amelia DuVall, Amanda Warlick, Eve Hallock, Hannah Sipe, Lisanne Petracca, Liam Pendleton, Mark Sorel, Matt Farr, Nate Redon, Tim Chen, and Staci Amburgey. Also, I would like to thank Olden Lab members including Bekah Stiling, Claire Vaage, Emily Jameson, Gio Jacuzzi, Jess Diallo, and Rachel Fricke. Thank you for all your advice, help, and venting sessions. I would also like to thank the QERM program and my cohort including John Henry, Kelly Mistry, and Logan Arnold, who helped me get through the first year classes.

I would like to thank my academic committee including Andrew Berdahl and Jennifer Ruesink. I would like to thank Chris Anderson for his game theory guidance on Chapter 5 of my dissertation. I would like to thank my two advisers Sarah Converse and Julian Olden. Sarah,

thank you for teaching me so much about Bayesian population modeling and giving me opportunities to help teach decision analysis workshops with you. Julian, thank you for teaching me about invasive species ecology and for helping me communicate my research better. Thank you both for being my advisors.

I would like to thank my friends and family who have supported me from thousands of miles away across the country. Special thanks to my family: my mom, dad, Bethany, Bradley, Kayla, and Spencer, and the Thompson family: Lisa, Mike, Lydia, and Blake. Thanks for not being too mad that I decided to go to graduate school quite far away, and I apologize for all of the holidays, birthdays, and celebrations that I missed. Thank you to the Kwarta family and the larger MacKecknie clan for all the summers we spent at our family cabin in Skaneateles Lake, NY scraping invasive zebra mussels off rocks at the bottom of the lake. All the moments spent in the water inspired my PhD research. I would like to thank my closest friends, Anita, Elise, Emmalie, Katy, Katelyn, and Torri. I am grateful for all the brief moments together these past few years. Special thanks to the Seattle Green Lake Running Group for all the fun miles we ran together.

Most importantly, I would like to thank my husband, Alex. It cannot be easy being married to a PhD student. Thank you for single handedly “holding down the fort” these past five years. I am so incredibly thankful for all your support, love, and patience. You and our pup Bandy have brought me so much joy and laughter on days that I needed it the most. Thank you and I love you.

CHAPTER 1. INTRODUCTION

1.1. BACKGROUND

Invasive species are a primary threat to global biodiversity, economies, and human health (Pyšek and Richardson 2010; Early et al. 2016). They disrupt ecosystems by altering habitats, introducing diseases, and competing with or depredating native species, which can reduce or cause extinctions of native populations (Gurevitch and Padilla 2004). Invasive species can be a socio-economic burden; they can decimate cultivated species, damage infrastructure, and contribute to recreation loss. As a result, various management efforts have focused on eradicating, containing, and suppressing invasive populations. Quantitative population models can aid invasive species management decisions by forecasting the spread of invasive species and guiding optimal allocation of resources for prevention, control, and eradication (Hastings et al., 2005; Addison et al., 2013; García-Díaz et al. 2019).

Population models can be used to evaluate management actions by estimating key vital rates (e.g., spread and survival rates), simulating the potential effects of invasive species, and exploring implications of various control or eradication strategies (Baker & Bode, 2021). Compared to the scales at which empirical data are typically available, population models can be used to simulate system dynamics at larger spatial and temporal scales, thus better supporting management decisions (Schmolke et al., 2010). In addition, when linked with economic analysis, these models can be used to explore the economic costs of management and identify strategies that strike optimal tradeoffs between management objectives and costs (Converse 2020).

Despite their potential to inform decision making, there are some notable challenges to using population models. First, there exists a significant disconnect between those who build models and those who are tasked with their real-world application to invasive species management. This disconnect is triggered by differences in training, skill sets, outlook, and commonly a lack of direct collaboration during model development and application. For example, model consumers often consider models to be faultless predictive tools when they are often imperfect representation of reality. There has been much discussion about the challenges associated with integrating research and management of ecological systems (Schmolke et al. 2010) and various solutions, including the explicit use of decision-analytic approaches (Runge et al. 2020), have been proposed. One of the benefits of direct collaboration between managers and modelers in collaborative decision-analytic processes is the development of a shared understanding of modeling tools so that their strengths and weaknesses are understood by all involved (Garrard et al. 2018). However, currently there is a lack of approachable resources for managers that describe the available modeling tools.

A second challenge in using models is that many ecological systems are characterized by complex spatial heterogeneity, and ignoring this complexity can impede identification of optimal spatially explicit management strategies. Spatially explicit population models are complex and difficult to construct, which may reduce their use in conservation (Corrales et al. 2020; Caradima et al. 2021). Specifically, population models are rarely developed in riverine contexts due to challenges of collecting movement data and a lack of software in aquatic contexts to simulate populations compared to terrestrial settings (Ogburn et al., 2017; Quaglietta and Porto 2019).

A third challenge associated with using population models is that models require information, often from monitoring data, to inform accurate estimates of key population vital rates. However, monitoring is often costly and time intensive, and therefore can reduce the resources allocated towards removal of invasive species (Rout et al., 2014; Koch et al., 2020). A variety of studies have examined how to balance monitoring and removal efforts within the context of one decision making body that is both collecting data and conducting management (Hauser and McCarthy 2009; Regan et al. 2011; Rout et al. 2017). However, in invasive species management, a variety of external monitoring data streams may also be collected, including data from community science campaigns (Crall et al., 2010; Larson et al., 2020). This additional data source, combined with data integration methods that can produce improved estimates of parameters (Fletcher et al., 2019), can be used to help guide decisions for natural resource managers . Data integration techniques have been used more infrequently in invasive species settings compared to other conservation applications, such as endangered species management (Baker and Bode 2021).

Fourth, selecting the right decision tool to inform multiple objective and multiple decision-maker problems in invasive species management may be difficult. In general, invasive species management in any given area is often conducted by a “mosaic” of organizations, including public agencies, private landowners, and tribal communities, all of whom may have different or even conflicting objectives regarding management (Epanchin-Niell et al., 2010; Crowley et al., 2017). Mutli-criteria decision analysis (MCDA) is a common decision analysis tool used to inform decisions involving tradeoffs among objectives, such as cost and management outcomes (Keeney and Raffia 1993; Converse 2020). However, game theory is an economic tool designed for multiple-decision maker settings (Luce and Raiffa 1957; Madani and Lund 2011). Identifying when MCDA or game theory techniques are most useful could improve guidance on invasive species management decisions for all decision makers.

1.2. RESEARCH OBJECTIVES

In my dissertation I aim to improve how models are used for invasive species management by addressing the four challenges described above. I first provide a review of mechanistic modeling approaches that can be used in invasive species management decision processes (Thompson et al., 2021, Chapter 2). Second, I describe a modeling designed to simulate population growth, dispersal, and management of invasive rusty crayfish (*Faxonius rusticus*) in the John Day River, USA (Chapter 3). I compared different spatially explicit management strategies in their ability to suppress the crayfish population, contain the spatial extent of invasion in the John Day River, and prevent spread into a larger river system, the Columbia River. Third, I examine optimal allocation of resources towards monitoring and management, using invasive flowering rush (*Butomus umbellatus*) in the Columbia River, USA as a case study (Chapter 4). I used a management strategy evaluation framework to simulate adaptive management of flowering rush under monitoring and management protocols that were iteratively updated through time. I additionally evaluated a subset of alternatives with the addition of community science data, which could help a management agency identify locations for removal effort and potentially improve management outcomes. Finally, I compared outcomes of MCDA and game theory in their ability to guide invasive species harvest decisions involving a natural resource manager and a neighboring landowner (Chapter 5). I considered three potential types of neighboring landowners: an environmentalist, who like the manager is concerned with minimizing cost and the invasive species population, a hobbyist who enjoys harvesting the invasive species, and a profiteer who receives profit from invasive species harvest. I compared management outcomes using MCDA and game-theoretic methods.

1.3. BROADER IMPACTS

Collectively, the following four chapters suggest ways in which quantitative models can be improved to inform decisions regarding invasive species management. In my second chapter, my review on mechanistic models for invasive species management will ideally encourage a shared understanding of the tools available to facilitate more effective collaboration between conservation scientists and practitioners who are tasked with combating invasive species. In my third chapter, I provide a modeling framework that could be adapted to a variety of riverine aquatic invasive species to help assess spatial management strategies. In my fourth chapter, I explore the tradeoffs between data collection and management effectiveness, which is a common concern in invasive species management. In this chapter I also demonstrated the value of adaptive management and integration of community science data when an invasion is just starting to unfold. Currently, data integration and adaptive management are seldom used in invasive species management. In my fifth chapter, I found that occasionally MCDA failed to reveal harvest actions, which were identified by game theory, with a better potential performance in a multi-decision maker environment. However, MCDA provides better insight into individual decision making preferences compared to game theory. Hence, game theory and MCDA can be used together to help inform decisions involving multiple decision makers. Overall, the insights provided by these four chapters can be used in future invasive species management decision contexts to help obtain favorable conservation outcomes.

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CHAPTER 2. MECHANISTIC INVASIVE SPECIES MANAGEMENT MODELS AND THEIR APPLICATION IN CONSERVATION

Publication history: This study was co-authored with Julian D. Olden and Sarah J. Converse and was published in *Conservation Science and Practice* in 2021.

Citation:
Thompson, B. K., Olden, J. D., & Converse, S. J. (2021). Mechanistic invasive species management models and their application in conservation. Conservation Science and Practice, 3(11), e533. https://doi.org/10.1111/csp2.533.

2.1 ABSTRACT

Management strategies to address the challenges associated with invasive species are critical for effective conservation. An increasing variety of mathematical models offer insight into invasive populations, and can help managers identify cost effective prevention, control, and eradication actions. Despite this, as model complexity grows, so does the inaccessibility of these tools to conservation practitioners making decisions about management. Here, we seek to narrow the science-practice gap by reviewing invasive species management models (ISMMs). We define ISMMs as mechanistic models used to explore invasive species management strategies, and include reaction-advection-diffusion models, integrodifference equations, gravity models, particle transport models, non-spatial and spatial discrete-time population growth models, cellular automata, and individual-based models. For each approach, we describe the model framework and its implementation, discuss strengths and weaknesses, and give examples of conservation applications. We conclude by discussing how ISMMs can be used in concert with adaptive management to address scientific uncertainties impeding action and with multiple objective decision processes to evaluate tradeoffs among management objectives. We undertook this review to support more effective decision-making involving invasive species by providing

conservation practitioners with the information they need to identify tools most useful for their applications.

2.2 INTRODUCTION

Invasive species are pervasive drivers of global change (Pyšek & Richardson, 2010; Early et al., 2016). They disrupt ecosystems, leading to loss of biodiversity and ecosystem function (Doherty et al., 2016), introduce diseases threatening human health (Mazza et al. 2014), compromise social well-being (Pejchar & Mooney, 2009), and impose a massive economic burden to society (Diagne et al., 2020). Recent decades have witnessed alarming rates of human-mediated movement of species beyond their native ranges (Seebens et al., 2017) as well as considerable advances in our understanding of invasive species ecology (Richardson & Pyšek, 2008). However, many conservation scientists and practitioners lament the persistent and widening disparity between growth in scientific knowledge and the management capacity to effectively respond (Papeş et al., 2011). One barrier to effective management is the capacity to assess alternative outcomes or the efficacy of proposed approaches. To this end, mathematical models play an important role in supporting effective responses by forecasting invasive species spread (Hastings et al., 2005) and guiding optimal allocation of resources for prevention, control, or eradication (Büyüktahtakın and Haight, 2018).

Models represent indispensable tools for invasive species management. They allow scientists to estimate key vital rates such as spread rate, simulate the potential effects of invasive species, and explore implications of various control or eradication strategies (Baker & Bode, 2020). We characterize models fulfilling this last function as invasive species management models (ISMMs). These models couple the temporal and/or spatial dynamics of invasive populations with the ability to simulate and evaluate management actions in terms of specified outcomes. ISMMs capture system dynamics at larger spatiotemporal scales compared to those at which empirical data are typically available and field experimentation is possible, thus better supporting management decisions (Schmolke et al., 2010). Also, when linked with economic analyses, ISMMs can explore the costs of management and identify strategies that strike an optimal tradeoff between management objectives such as suppression and cost (Epanchin-Niell, 2017; Converse, 2020; Pepin et al., 2020). ISMMs have been used in numerous invasive species contexts, in both terrestrial and aquatic ecosystems, including plants, insects, mammals, fish, and mussels, among others (Büyüktahtakın & Haight, 2018). The wide variety of species and systems modeled is matched by the diversity of model forms represented by ISMMs.

ISMMs are used in conservation to understand the effects of human actions on the invasion process in terms of specific management objectives. They formalize the link between what practitioners can do and what they seek to achieve, thus helping inform which set of candidate strategies will be most effective (Holden & Ellner, 2016). Management effects can be incorporated into models in at least two ways. First, models can represent modifications to the state of the system by reducing population abundance via direct removals, i.e., by subtracting individuals from population abundance projections (Hastings et al., 2006, Link et al. 2018). Second, models can express adjustments to invasive species vital rates from management. For instance, dispersal rate can be reduced in a model to represent the effect of intentional barrier construction (e.g., Sharov et al., 1998), or fecundity rates could be reduced if management actions alter reproductive capability, such as neutering mammals (e.g., Lohr et al., 2013) or destroying fish spawning sites (e.g., Loppnow et al. 2013). Management-based adjustments to vital rates can be informed by empirical studies (e.g., Hyder et al., 2008) or expert judgement (e.g., Holmes et al., 2019).

Despite their potential to inform decision making, a disconnect exists between those who build models and those who are tasked with their application (Grimm et al., 2014). This gap is triggered by differences in training, skill sets, outlook, and commonly a lack of direct engagement with decision makers and stakeholders during model development (Schmolke et al., 2010). Because modelers are often not trained nor incentivized to translate models into terms non-modelers can understand, mathematical models are typically viewed as too complex or considered a “black box” (Lorscheid et al., 2012). Thus, there is a need to clearly articulate the modeling process to promote collaboration between modelers and practitioners (Cartwright et al., 2016). One of the benefits of direct collaboration is developing a shared understanding of modeling tools, so their strengths and weaknesses are understood by all involved (Garrard et al., 2018). This can lead to better integration of scientific information into management decisions via decision-analytic processes (Runge et al., 2020).

Here we seek to narrow the gap between increasingly sophisticated modeling tools and the capacity to effectively apply these models to invasive species management challenges. The array of ISMM frameworks available provides a menu from which the most appropriate tools for a given application can be selected. To facilitate the selection process, we describe the canonical mathematical form of each model, provide example applications, and explore strengths and weaknesses of each model. We review models that describe biological processes, hence mechanistic models, and omit discussion of statistical models (e.g., species distribution models, regression models, etc.) that also play an important role in invasive species management (e.g., for estimating parameters; Hauser & McCarthy 2009; Baker et al., 2018) but have received extensive treatment elsewhere in the literature (e.g., Elith & Leathwick, 2009; Jiménez-Valverde et al., 2011). The model types we cover include reaction-advection-diffusion models, integrodifference equations, gravity models, particle transport models, non-spatial and spatial discrete-time population growth models, cellular automata, and individual(agent)-based models. We conclude by discussing two common impediments to invasive species management: uncertainty and challenging tradeoffs amongst management objectives. We describe adaptive management and multi-objective decision processes, and the application of ISMMs within these decision-support frameworks. Our review compliments existing literature that describes the use of models for invasive species management and conservation (Addison et al., 2013; García-Díaz et al. 2019; Baker & Bode 2020). Our goal is to provide a shared understanding of the tools available to facilitate more effective collaboration between conservation scientists and practitioners who are tasked with combating invasive species.

2.3 INVASIVE SPECIES MANAGEMENT MODELS (ISMMs)

Our review explores several types of ISMMs, including reaction-advection-diffusion models, integrodifference equations, gravity models, particle transport models, non-spatial and spatial discrete-time population growth models, cellular automata, and individual(agent)-based models. These modeling approaches are characterized by different functional forms of two invasion processes: population growth and population spread, where ISMMs incorporate either one or both processes. In subsequent sections, we provide a background to the methodology, describe model implementation, provide example applications from literature, and discuss strengths and weaknesses. Although some applications we describe are not management modeling efforts per se (i.e., management actions are not explicitly evaluated), the examples suggest the capacity for models to evaluate invasive species management.

2.3.1 REACTION-ADVECTION-DIFFUSION MODELS

Reaction-advection-diffusion models (RADMs) provide a spatially explicit, continuous-time approach to predict invasive species population growth and spread (Figure 2.1,Table 2.1). RADMs estimate continuous dispersal in space and time and portray spread from areas of high to low concentration (density) of species, via diffusion, and directionally based movement (e.g., wind) via advection. Versions of RADMs incorporate jump dispersal (see Baker, 2017), but typically RADMs predict continuous long or short dispersal events, biased towards nearby locations. Dispersal processes described with RADMs will generally be passive dispersal through physical (e.g., wind, water), human, and animal vectors. However, RADMs can be written to represent directed movement, such as movement that varies with resource availability (Murray, 2002; 2003).

RADMs predict spatiotemporal population density through both dispersal and growth rate terms. A generalized RADM is expressed as:

$$\frac{\partial N}{\partial t} = \nabla D \nabla N - \nabla \boldsymbol{v} N + f(N) \tag{1}$$

where *N* is the density of organisms at spatial coordinates *x*, *y*, and time *t* (Holmes et al., 1994; Baker 2017). The first term on the right-hand side represents diffusion, where *D* is a diffusion coefficient (in units of distance^2 time^{-1}) and ∇ represents change in 3-dimensions (*x*, *y*, and time *t*). The second term represents advection, with advection coefficient $\boldsymbol{v}$, which can vary in space or time. The third term, function *f*(*N*), describes population growth, which can take a variety of forms to represent exponential growth, positive or negative density-dependent growth, or other types of continuous time growth (Higgins & Richardson, 1996; Wang et al., 2001; Tobin et al., 2011). In the model, parameter *D* can be a function, and *f(N)* and *D* can be functions of time, space, and population abundance to represent heterogeneous and dynamic environments. More realistic spatial dynamics include embedding RADMs within a reaction-diffusion network where space is represented by discrete patches (Rosen, 1981). RADMs can be written in a variety of forms, with or without advection or diffusion. However, omitting the spatial aspect would reflect exclusively continuous growth of an invasive population (commonly called ordinary differential equations) described by $f(N)$ (see Baker et al., 2019).

RADMs have been used to understand and predict movement of invasive species with the goal of identifying optimal management strategies. RADMs can accommodate invasive species removals by adding a negative abundance term to equation 1. For example, Baker and Bode (2016) used a RADM to evaluate reduction in feral cat (*Felis catus*) abundance from baiting and removal in Australia. They used optimal control theory (Lenhart & Workman, 2007) to identify effective management strategies. They showed that long term management is often the optimal strategy and short intensive removal programs are best conducted only when population growth rates are high. The study also evaluated the efficacy of buffer zones assuming various rates of population growth and dispersal. RADMs have also been developed to understand the effect of uncertainty around vital rates. For example, Bonneau et al. (2017) modeled Argentine giant black and white tegus (*Salvator merianae*) spread in Florida, U.S., and incorporated uncertainty by evaluating various combinations of population parameters to represent different invasion dynamics. Using linear programming, they identified optimal management solutions that minimized invasive population under a fixed budget and compared solutions for decision-makers with different risk tolerances. The optimal solution, for risk-averse and risk-neutral decision makers, was to control near the point of introduction to contain the population. For a risk-seeking decision maker, distributing trapping effort over a large area with the goal of eradication was predicted to be optimal. In summary, RADMs have been used in a variety of invasive species management applications ranging from evaluating the effectiveness of poison baiting (e.g., Baker & Bode, 2013) to comparing prevention versus containment strategies (e.g., Carrasco et al., 2010; Epanchin-Niell & Liebhold, 2015).

Although RADMs have provided insight into invasive species dynamics in heterogeneous environments, limitations of this model exist. A notable drawback of RADMs is that the model produces expected, or averaged, dispersal and population growth. Although examples exist (see Baker, 2017), RADMs typically do not simulate specific long-distance dispersal events or model stochastic processes. Also, like many mathematical models, the complexity of RADMs could challenge some users (Cartwright et al., 2016). However, more user-friendly options exist such as the Spatial Population Abundance Dynamics Engine (SPADE), a software tool requiring minimal coding experience that codes RADMs and allows for comparing management strategies (Beeton et al., 2015).

2.3.2 INTEGRODIFFERENCE EQUATIONS

Integrodifference equations (IDEs) model invasive species spread and population growth across continuous space, but unlike RADMs, IDEs treat time in a discrete manner (Figure 2.1, Table 2.1). IDEs can incorporate a broad range of dispersal mechanisms, to allow leptokurtic (fatter-tailed) dispersal probabilities, integrating nonlinear and long-distance dispersal, which is commonly observed in nature (Neubert et al., 2000).

IDEs use population growth and dispersal terms to estimate local abundance of invasive species. The general IDE represents abundance of an invasive population, $N_t(x)$, at time *t* as:

$$N_{t+1}(x) = \int K(x-y) f\big(N_t(y)\big) dy \qquad (2)$$

where f represents population growth and $K(x - y)$ is the dispersal kernel, a probability density function that describes movement probability from source location y at time t to location x at t+1 (Wang et al., 2002). The kernel can describe broad or species-specific movement by allowing for accelerating movement rates and jump dispersal (Hudgins et al. 2020). Examples of dispersal kernels include the normal and Cauchy distributions (Wang et al., 2002). Function f can describe a variety of population growth forms and be modified to include positive and negative density-dependence (Higgins & Richardson 1996; Jongejans et al., 2011).

Conservation scientists have used IDEs to predict invasive species spread and population control efforts. In one example, Caplat et al. (2012) evaluated key demographic and dispersal parameters affecting spread of invasive Corsican pine (*Pinus nigra*) in New Zealand by integrating a mechanical wind dispersal mechanism into an IDE. They found that spread rate was most influenced by seed velocity, followed by juvenile survival and establishment, and fecundity. Gharouni et al. (2015) built a stage-structured IDE for European green crab (*Carcinus maenas*) on the North Atlantic coast of North America to model an invasive population. The authors evaluated demographic and spread parameters and reported that green crab spread was highly sensitive to larval dispersal, moderately sensitive to recruitment rate, and minimally sensitive to adult survival. Although not directly integrated with management strategies, these examples highlight how environmental and biological parameters can influence invasive species spread. For explicit evaluation of management strategies, IDEs could incorporate changes to invasive species dynamics from management by altering vital rate parameters in function f or modifying the dispersal kernel in equation 2. Removals could also be incorporated in equation 2. One way to do this is to introduce a parameter, h_t, to represent per capita removal rates (Joshi et al., 2006).

Despite being considered an intuitive approach to modeling population dynamics of invasive species, IDEs have several acknowledged weaknesses. First, in their basic form, IDEs typically consider population spread to be continuous and often radial (i.e., non-directional). This is an unrealistic assumption for many animal species, but more reasonable for plant species, where IDEs have seen greater application (e.g., Neubert & Caswell 2000; Neubert & Parker 2004; Caplat et al., 2012). Second, in basic form, IDEs treat the landscape as homogeneous, and thus the role of habitat heterogeneity in shaping species movement cannot be captured. These limitations may limit the accuracy of IDEs for predicting invasive species spread (Gilbert et al., 2014). However, IDEs can be expanded to incorporate various types of dispersal, dynamic environments, and environmental heterogeneity (Rodríguez, 2015).

2.3.3 GRAVITY MODELS

Gravity models (GMs) extend the dispersal mechanisms in RADMs and IDEs by integrating local and stochastic long-distance jump dispersal in patchy or heterogeneous environments. GMs are spatially explicit, yet they are one of two ISMMs we review that do not include a mechanism for population growth (particle transport models are the other; Figure 2.1, Table 2.1). Spread by jump dispersal can describe human-mediated extra-range dispersal of invasive species beyond the natural range of spread (Wilson et al., 2009). Jump dispersal can be caused by mechanisms such as vessel or aircraft traffic and estimated by the flow of people, boats, planes, etc., based on the distance to and suitability of destination points (Suarez et al., 2001). Therefore, GMs can evaluate spread patterns and locate areas to impose interventions and quarantine measures. As such, these models are not typically used to represent removal or eradication efforts.

GMs relate the force of attraction between an invaded site and a non-invaded site as a function of the distance between them weighted by the suitability for species establishment. They express the number of individuals N_{ij} moving from location *i* to *j* as:

$$N_{ij} = \frac{A_i O_i W_j}{{d_{ij}}^{\alpha}} \tag{3}$$

where A_i is a scalar that can be used if the modeler wants to require that all individuals at *i* reach some destination point, O_i is the number of individuals at *i*, W_j is the suitability of *j*, d_{ij} is the distance from *i* to *j*, and α is a coefficient on distance (Bossenbroek et al., 2001).

Existing applications of GMs were developed to forecast and understand factors influencing spread, though there is substantial potential to use GMs to evaluate strategies for reducing spread, e.g., by considering how management could modify parameters W_j or α. In perhaps the first application of GMs to invasive species, Bossenbroek et al. (2001) forecasted zebra mussels (*Dreissena polymorpha*) spread in the upper midwestern U.S. based on recreational boater activity among lakes and records of mussel occurrence. A variety of subsequent studies used similar model structures to estimate aquatic invasive spread (e.g., MacIsaac et al., 2004; Muirhead & MacIsaac, 2005; Leung & Mandrak, 2007). For example, Fischer et al. (2020) coupled a GM with a route choice component (Prato, 2009) to predict potential invasions of zebra mussels and quagga mussels (*Dreissena rostriformis bugensis*) in British Columbia, Canada, via specific transportation routes. They compared their hybrid gravity/route choice model to a basic GM and found that the hybrid model provided more insight by facilitating early detections and identifying traffic routes that minimized invasion probabilities. Prasad et al. (2010) used a GM to calculate the number of humans that traveled to campgrounds and spread emerald ash borers (*Agrilus planipennis*) in Ohio, U.S. The GM was coupled with a short-distance spread model, representing both anthropogenic and natural dispersal. They showed that current locations of infestation, roads with heavy traffic (i.e., major interstates), and metropolitan regions with high human population density are areas of significant infestation risk.

GMs are well-suited for incorporating local dispersal and long-distance jump dispersal; however, it is important to recognize some limitations. Although GMs are spatially dynamic, neither time nor population growth are explicitly included in its canonical form (Equation 3). Consequently, GMs must be linked with other models to include dynamics of growth and spread over time.

2.3.4 PARTICLE TRANSPORT MODELS

Particle transport models (PTMs), commonly applied to fluid dynamics, can predict the spread of invasive species whose dispersal depends on passive drift through air or water (Figure 2.1, Table 2.1). PTMs calculate the change in invasive species abundance and dispersal in continuous time and space according to movement velocity and dispersal in three dimensions, where the *x* and *y* dimensions refer to location and the *z* dimension refers to depth or elevation. PTMs seek to estimate realistic spread by incorporating environmental determinants of dispersal such as specific wind and water current parameters.

PTMs specify changes in local population abundance and movement velocity. These models describe the concentration of a population as the change in abundance resulting from individuals immigrating into and emigrating out of the system in three dimensions. The model is expressed as:

$$\frac{\partial c}{\partial t} = \nabla K \nabla c - \nabla \boldsymbol{v} c + Q \tag{4}$$

where $\frac{\partial c}{\partial t}$ represents the change in population concentration, *c*, through time, *t*. The movement of individuals into the system is $\nabla K \nabla c$ where *K* represents diffusion and movement functions (incorporating wind, water, weather, or related data). Individuals leaving the system is $-\nabla \boldsymbol{v}c$, where $\boldsymbol{v}$ represents velocity. The sources and sinks, Q, of the population are incorporated as an additive term for population concentration. The symbol ∇ represents changes in 3-dimensions, where $\boldsymbol{v}$, K, and c are all represented (Dimou, 1992).

PTMs have demonstrated utility in forecasting passive spread of invasive species by means of wind or water currents. For instance, Beletsky et al. (2017) used a PTM to predict larval transport during spawning seasons of ruffe fish (*Gymnocephalus cernua*) and golden mussel (*Limnoperna fortunei*) off the Pacific coast of North America. By including hydrological data, the authors identified locations where ballast water releases of invasive propagules result in high infestation risk and secondary coastal spread. Tilburg et al. (2011) used a PTM to examine the environmental and biological factors contributing to retention and transport of invasive Chinese mitten crabs (*Eriocheir sinensis*) on the mid-Atlantic coast of the U.S. Results indicated that during spawning seasons, estuarine and coastal circulation helped concentrate individuals in inland bays, leading to greater population sizes. Despite not directly integrating management strategies, these applications indicated the environmental factors contributing to invasive species spread. Management-focused PTMs could accommodate containment and prevention strategies, such as the construction of artificial barriers, by altering movement parameters K or $\boldsymbol{v}$. Direct removals could also be represented in equation 4. One way to include this is to subtract the right-hand side of equation 4 by hc, where h is the per capita removal rate.

Several studies have used PTMs to predict passive spread of invasive species by incorporating wind, water current, and weather data within the dispersal component of the model (e.g., Byers & Pringle, 2006; Michalak et al., 2013). Before implementing a PTM, there are several important considerations. First, PTMs do not explicitly include population growth terms, they must be linked with additional models to account for such dynamics. Second, PTMs are less suitable for invasive species that do not passively disperse through terrestrial or aquatic environments. Third, although the success of all models depends on robust population data, PTMs require precise environmental data, e.g., wind or water current data, to inform dispersal; aerial and aquatic monitoring stations providing such data are typically sparse with limited spatial coverage (Isard et al., 2005).

2.3.5 NONSPATIAL DISCRETE-TIME POPULATION GROWTH MODELS

Non-spatial discrete-time population growth models (PGMs) project changes in invasive species abundance in equal, regular time steps, where future populations depend on current abundance and where space is not explicitly represented (Figure 2.1, Table 2.1). PGMs are a broad and flexible class of models that describe the growth of (possibly) demographically structured populations in discrete time via birth and survival. PGMs are perhaps easiest to develop for seasonally breeding populations, in which reproduction occurs over a relatively short time interval. PGMs can be used in a variety of conservation contexts because environmental and biological data are typically available in discrete-time steps, for instance annual birth counts (Caswell, 2001).

In its simplest form, a PGM can be written as:

$$N_{t+1} = rN_t \tag{5}$$

where N_t describes population density at time *t*, and *r* refers to the population's intrinsic growth rate. In this example, an unstructured population increases exponentially for $r > 1$ and declines to extinction for $r < 1$. However, more frequently, a PGM is structured to calculate growth of various subsets of the population, such as ages or stages. Moreover, a recent innovation allows population structure to be continuous rather than discrete (integral projection models; Easterling et al., 2000).

In an age- or stage-structured PGM, the overall population growth rate, *r* (Equation 5) can be replaced with a matrix containing demographic rates controlling growth of each subset of the population. For age-structured populations, this is known as a Leslie matrix and for stage-structured populations, a Lefkovitch matrix. An age- or stage-structured model can be expressed as:

$$\boldsymbol{N}_{t+1} = \boldsymbol{L}\boldsymbol{N}_t \tag{6}$$

where $\boldsymbol{L}$ is a matrix defining vital rates of each subset of the population, and the dimension of $\boldsymbol{L}$ is defined by the number of ages or stages. Consider an invasive population consisting of newborns, 1-yr-olds, and adults (2-yrs old and older) and let n_1, n_2, and n_3 be the abundance of females in each class at time *t*, respectively. Given demographic rates of s_1= annual survival of individuals from birth to 1-yr old, s_2= survival from 1-yr old to 2-yrs old, s_3= survival of individuals 2-yrs old and older, and *f* = fecundity of individuals (number of female offspring per female) 2-yrs old and older, the population abundance vector at time *t* +1 is calculated as:

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & s_3 f \\ s_1 & 0 & 0 \\ 0 & s_2 & s_3 \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_t \tag{7}$$

The matrix can be time-varying to represent temporal stochasticity or other forms of temporal variation, and demographic stochasticity can be integrated by modeling demographic outcomes as, e.g., binomial- or Poisson-distributed stochastic outcomes.

Density-independent PGMs, such as the model described above, are appropriate for modeling early stages of biological invasions (e.g., Hastings et al., 2006). However, later in the invasion process, population growth frequently depends on conspecific density, and PGMs can be modified to incorporate density-dependent dynamics (Caswell, 2001). Both negative and positive (i.e., Allee effects) density-dependence can play important roles in invasive species establishment and spread.

PGMs have been used to describe invasive species growth in discrete-time, with density-dependence and age or stage structure. For instance, Hastings et al. (2006) applied a stage-structured density-dependent PGM to estimate optimal plant removal strategies for *Spartina alterniflora* on the coast of Washington State, U.S., by including a harvest term to represent age class specific population removal at each time step. They showed that focusing removal efforts of different age classes over time achieved better management outcomes as compared to controlling a single age class. Similarly, Govindarajulu et al. (2005) used a stage-structured density-dependent PGM to examine effects of seasonal and age selective control strategies on invasive American bullfrogs (*Rana catesbeiana*) in British Columbia, Canada. The model mimicked effects of removal by altering growth and survival rates. This study suggested that control strategy effectiveness was heavily dependent on the season and life-history stage of bullfrogs targeted for management. There are many additional examples where the strengths of PGMs have been leveraged to predict dynamics of aquatic (e.g., Taylor & Hastings, 2004), semi-aquatic (e.g., Melero et al., 2015), and terrestrial (e.g., Shyu et al., 2013) invasive species.

PGMs encompass a wide range of models describing population growth in discrete-time steps. Despite their broad utility in conservation practice, PGMs have at least two recognized limitations. First, they tend to perform best for species where reproduction is punctuated and occurs seasonally (though continuous time analogs exist; see Wangersky 1978; Higgins & Richardson, 1996). Second, and perhaps most critically, PGMs have no mechanism to represent invasive species spread; a drawback that can be remedied by incorporating dispersal dynamics through the inclusion of spatial units.

2.3.6 SPATIAL DISCRETE-TIME POPULATION GROWTH MODELS

Spatial discrete-time population growth models (SPGMs) extend PGMs by representing population distribution as well as demographic processes (Figure 2.1, Table 2.1). SPGMs can be formulated to describe population structure (i.e., age or stage structure) in each of a set of spatial units (Hunter & Caswell, 2005). The dispersal process in SPGMs is often described by a generalized dispersal function in a spatial patch- or grid-based environment stemming from empirical (e.g., Gamma or Lognormal models) or mechanistic models (e.g., behavior model of animal vectors; Jongejans et al., 2008).

Although demonstrating similarities in general form with IDEs, SPGMs model population growth and spread in discrete-time and space whereas IDEs represent population growth in discrete-time but spread in continuous space. In SPGMs, future abundance is a function of dispersal, births, deaths, and possibly other stage transitions. A simple SPGMs can be expressed as:

$$\boldsymbol{N}_{t+1,s} = \boldsymbol{L}_s \boldsymbol{N}_{t,s} \qquad (8)$$

where $\boldsymbol{N}_{t,s}$ is a matrix describing population density at time t for each of the s spatial cells. $\boldsymbol{L}_s$ is a transition matrix of size s x s that defines the demographic and dispersal processes that may vary across cells and stages. The matrix can be written as $\boldsymbol{L}_{t,s}$ if the transition matrix is spatially and temporally dependent (Hunter & Caswell, 2005). Similar to PGMs, SPGMs can incorporate age or stage structure and density-dependence or independence. Spatial forms of integral projection models have also been developed (Ellner & Rees, 2006).

SPGMs have been used to predict realistic discrete-time invasive species dynamics because of their ability to account for spatial structure. For instance, Blackwood et al. (2010) modeled spread and control of *S. alterniflora* on the coast of Washington State, U.S., and assumed adults were sedentary and cells were connected by offspring dispersal. They incorporated cell-specific nonlinear population removal and represented management cost rates by implementing a quadratic dependence on population size; in this case, removal costs were high with low populations. They used dynamic programming to show that habitat connectivity promoted plant spread over time which contributed to costly invasive control. In another example, Link et al. (2018) developed a statistical implementation of a SPGM based on removal data to understand growth, movement, and the effectiveness of removal effort on invasive veiled chameleons (*Chamaeleo calyptratus*) on the island of Maui, U.S. To illustrate eradication, the model reduced estimated population abundance and calculated removal rate as a function of management effort. Several additional studies have used SPGMs to compare and inform management efforts for terrestrial (e.g., Jongejans et al., 2011) and aquatic invasive species (Erickson et al., 2018).

The flexibility of SPGMs offers broad applicability to invasive species management and decision making. Despite this, SPGMs may be less appropriate for species whose movement or demography cannot be realistically modeled in regular, discrete time steps (e.g., McClintock et al., 2014). In addition, the explicit modeling of movement, births, and deaths within a SPGM can make these models data hungry.

2.3.7 CELLULAR AUTOMATA

Cellular automata models (CAs) simulate local, complex species interactions by incorporating stochasticity, random events, habitat heterogeneity, and multispecies interactions in discrete-time and space in one to three dimensions (Figure 2.1, Table 2.1). CAs represent the environment as discrete, equally sized cells, each of which is in one of a discrete set of states (e.g., occupied, unoccupied). At each time step, the state of each cell is updated through a set of local rules based on the current state of the cell and neighboring cells (Wolfram, 1984). These rules can be either uniformly applied to each cell regardless of its geographic condition, or stochastic and heterogeneous to represent ecological variability (Cole & Albrecht, 1999). CAs are related to patch-occupancy models, which are spatially averaged CAs where cell states follow global rather than local rules (Caswell & Etter, 1993).

CAs and individual-based models (IBMs; see 2.3.8 *Individual-based models*) are distinct from the models previously described. Instead of being based on a “top-down” modeling approach that describes population level dynamics, CAs and IBMs are founded on “bottom-up” dynamics where higher-order system characteristics, such as vital rates, emerge from interactions of model entities with each other and the environment (Zhang & DeAngelis, 2020). CAs differ from IBMs because the rules governing IBMs can be applied to both individuals and spatial locations, and CAs rules are bound solely to spatial cells. In addition, IBMs are more flexible than CAs and can be simulated in both discrete and continuous time and space, although CAs are computationally faster (Tonini et al., 2014).

CAs can be described as:

$$X_{s,t+1} = f\left(X_{s,t}, S\right) \tag{9}$$

where $X_{s,t}$ is a finite set that represents the state of cell *s* at timestep *t*. The cell’s state in the next time step, $X_{s,t+1}$, is described by a transition rule, *f*, a function of the current state of focal and neighboring cells, *S* (Huang et al., 2007). The transition rule *f* can describe events such as population growth, movement, and management, where management can be represented by a function that decreases population abundance or adjusts vital rates.

CAs have been used to simulate invasive species dynamics and evaluate management strategies. Crespo-Pérez et al. (2011) used a CA to describe natural and human-mediated spread of invasive potato tuber moths (*Tecia solanivora*) in Ecuador. The model showed that crop storage units that modify local temperatures promoted successful invasive spread in agricultural environments. In another example, Kovacs et al. (2014) used a CA to simulate an emerald ash borer population in Minnesota, U.S., and predicted optimal management solutions where a strict budget existed and spatial opportunities to manage host trees infested by emerald ash borer varied between public and private land ownership. They showed that increasing accessibility of privately owned trees by public managers can slow invasive species spread. Additional literature examples demonstrate that CAs can explore complex ecological phenomena such as competition between invasive and native species (e.g., Marco et al., 2002; Arii & Parrot, 2006).

Although CAs allow for greater ecological complexity, these models pose several potential challenges. First, CAs delineate the landscape to spatial units, and thus are unlikely to be appropriate in fragmented landscapes or other environments where movement probability is not uniform because of directional wind, water, or other currents. Second, while CAs show utility for modeling species dynamics using bottom-up rules, the rules are limited, and do not allow for differences in individual movement behaviors. For more complex individual-based rules, IBMs are likely more appropriate.

2.3.8 INDIVIDUAL-BASED MODELS

Individual- or agent-based models reproduce ecological events by simulating individuals that follow distinct rules (Figure 2.1, Table 2.1). Unlike CAs, these models simulate individuals that follow more complex decision rules in dynamic environments, and account for time and space in either a discrete or continuous manner. Both individual and agent-based models simulate decision-making individuals; however, agent-based models consider individuals or “agents” to be adaptive and autonomous (Grimm et al., 2005). Therefore, individual-based models have been used to simulate nonautonomous invasive species (Tonini et al., 2014), while agent-based models can represent self-governing organisms (Lustig et al., 2019) or human behaviors involved in species spread or removal (Rebaudo & Dangles, 2013). Here we refer to both individual and agent-based models as IBMs because they have similar mathematical foundations.

IBMs divide a population into discrete interacting individuals (i.e., plants, animals, humans) that are assigned different states, $x_{i,t}$, based on characteristics such as age, sex, spatial location, etc. at each time *t* (for *i* = 1 to *n* individuals). Individuals transition to new states, by selecting one updater function $f_{i,t}$ from probability space $P_{i,t}$, that describes events such as population growth, reproduction, dispersal, mortality, and management/control. For each $x_{i,t}$ the updater function can be written as:

$$f_{i,t}: S_t \longrightarrow x_{i,t+1} \tag{10}$$

where $f_{i,t}$ uses neighboring and current states denoted as S_t, to determine the new state, $x_{i,t+1}$ (Hinkelmann et al., 2011). In a simple case, updater functions can be based on probabilistic or deterministic rules with an “if-then” structure. In complex cases, IBMs use machine learning approaches, such as genetic algorithms and artificial neural networks, to generate individuals that make adaptive decisions (DeAngelis & Diaz, 2019). As in CAs, the updater function can describe a variety of events including population growth, movement, and management. Management is often represented by a function that aims to decrease population abundance or alter vital rates.

IBMs have been used to simulate invasive species spread and compare the effectiveness of management strategies. Carrasco et al. (2012) developed an IBM to simulate management of invasive western corn rootworm (*Diabrotica virgifera virgifera*) in the U.K. The model integrated social learning of farmers and found that negative public opinions on invasive species control communicated by media outlets contributed to control program failure. Lustig et al. (2019) built an IBM to test the success of management strategies for invasive brushtail possums (*Trichosurus vulpecula*) in New Zealand and incorporated sophisticated species-habitat interactions and spatially explicit carrying capacities. They showed that the optimal spatial control strategy depended on management effort. For instance, in a low-effort scenario, invasive habitats should be targeted for control, whereas in a high-effort scenario, control should be evenly distributed throughout the nonnative range. Numerous other studies have used IBMs to quantify population dynamics of aquatic (Messager & Olden, 2018) and terrestrial (Tonini et al., 2014) invasive species and evaluate the efficiency of management actions.

While IBMs have numerous advantages, they also come with several important caveats to recognize. First, added complexity results in IBMs being computationally demanding. Second, IBMs require autecological data to model invasive species dynamics at the individual-level and spatiotemporal environmental data at the site-level (DeAngelis & Diaz, 2019). Third, IBMs cannot be represented concisely within a mathematical framework (Hinkelmann et al., 2011) and effective communication to stakeholders requires the time-consuming activity of developing extensive documentation of the developed IBM. Consequently, published IBMs are often not reproducible (Grimm et al., 2006).

2.4 APPLYING MODELS TO INVASIVE SPECIES MANAGEMENT

ISMMs have substantial utility for predicting the effects of prevention, control, and eradication strategies to manage invasive species. In previous sections we highlighted a suite of ISMMs available to conservation practitioners, and for each we defined their mathematical underpinnings, provided literature examples, and explored strengths and weaknesses (Figure 2.1).

Several considerations should inform the appropriate selection of an ISMM framework. First, as articulated earlier, the management context, along with the spatial, temporal, and demographic attributes of a given invasive species management problem, should direct the user toward the ISMMs most likely to meet their needs (Table 2.1). For instance, if the user aims to model detailed dynamics of an invasive species, CA or an IBM are both good choices. Alternatively, if the user seeks to understand dispersal processes, they could choose a GM or PTM if estimates of population growth are not needed or a RADM, IDE, or SPGM if such estimates are desired. Further, consulting the strengths, weaknesses, and literature sources referenced in the previous sections should guide the user towards the most appropriate choice.

Second, the technical resources available may shape the selection of a modeling framework. Various platforms exist to implement ISMMs, ranging from general programming languages requiring varying degrees of expertise such as R (R Core Team, 2015) and Python (Python Software Foundation, 2008) to specific software such as NetLogo (Wilensky, 1999) and HexSim (Schumaker & Brookes, 2018), which are used for IBMs. A full detailing of these platforms is beyond the scope of this study, but the user’s programming experience is likely to influence model choice. In addition, the user’s available computing resources will be relevant. Generally, stochastic simulation will be the most computationally costly option, especially as model complexity increases. For example, CAs and IBMs will, as a rule, require substantial computational resources. By contrast, analytical evaluation of models, such as those associated with RADMs for calculating dispersal rates and eigenanalysis of PGMs for calculating population growth rates, is much less demanding in terms of computational resource requirements.

Third, the type of population or environmental data available is also likely to influence ISMM selection. For instance, fine-resolution individual-level and environmental data may be needed to build IBMs (DeAngelis & Diaz, 2019) while population-scale time series data can be used to parameterize RADMs, PGMs, or SPGMs. In addition, RADMs or PTMs benefit from precise environmental data, e.g., wind or water current data, to inform dispersal processes (Isard et al., 2005).

These considerations aside, the most important factor governing ISMM selection is the decision context in which it will be used (Dana et al., 2014). Decision analysis provides a powerful framework for understanding the decision context, so that the ISMM can be leveraged to inform management by linking management alternatives to objectives and predicting which alternatives will perform best in terms of desired outcomes. For instance, if a management objective is to minimize invasive species abundance in an ecologically sensitive area, an ISMM could predict abundance under alternative spatiotemporal removal schemes (e.g., Bair et al., 2018). ISMM results might be coupled with removal cost projections from an economic model to inform tradeoffs between cost and population outcomes. Thus, prior to model selection, management objectives and alternatives should be developed collaboratively with decision makers and stakeholders (Gregory et al., 2012).

Decision analysis reveals the key impediments to a decision, i.e., the factors hindering management selection, and identifies methods to deal with those impediments (Runge et al., 2020). Two common challenges associated with invasive species management are uncertainty and the navigation of trade-offs between management objectives. Thus, two critical decision analysis tools are adaptive management to grapple with scientific uncertainty, and multi-objective decision processes to deal with trade-offs. Here we review these tools and provide examples of how ISMMs have been used alongside them to inform management.

2.4.1 ADAPTIVE MANAGEMENT

Adaptive management is applicable in situations where decisions are recurrent (e.g., an annual allocation of control effort) and where structural uncertainty impedes decision making (Williams & Brown, 2014). Aspects of uncertainty include questions about the ecological dynamics of invasive populations (e.g., baseline rates of population growth and spread), environmental conditions, and the effects of management on these ecological dynamics. Monitoring is used to reduce critical uncertainties over time and select management actions iteratively, based on updated knowledge (McCarthy & Possingham, 2007). Hence, adaptive management processes are designed for "learning by doing," where management is revised based on new information, such as updated estimates of vital rates in the face of control activities (Walters, 1986; Westgate et al., 2013).

In adaptive management, alternative representations of the system, by means of different parameterized ISMMs, are developed to capture uncertainty, and management actions (e.g., removal or monitoring) are chosen based on management objectives, alternatives, and models of the system (Walters & Hilborn, 1978). In addition to requiring an ISMM, adaptive management requires an approach for learning from monitoring data over time (e.g., Bayesian updating), and for identifying the optimal action given the state of knowledge (e.g., Markov Decision Processes; Chadès et al., 2017). Bayesian updating involves updating parameter estimates based on prior distributions and monitoring data. Updated parameter values become subsequent prior distributions, in an iterative loop of monitoring, learning, and managing.

Adaptive management processes have been coupled with ISMMs to approach invasive species management under uncertainty. Parkes et al. (2006) developed a suite of SPGMs with density dependence and age structure to describe the effects of management on the population abundance of brushtail possums (*T. vulpecula*) and red foxes (*Vulpes vulpes*) in New Zealand and Australia, respectively. The authors focused on establishing the adaptive management process, and ways to improve control over time. Regan et al. (2011) used a SPGM for invasive branched broomrape (*Orobanche ramosa*) in Australia, wherein each spatial unit was assigned one of three population states: not occupied, occupied by seeds, or occupied by seeds and adult plants, and management influenced state transitions. The authors used stochastic dynamic programming to determine optimal actions, accounting for uncertainty in the form of imperfect observation. In a final example, Day et al. (2018) built an IBM to describe the spread and population growth of eastern brook trout (*Salvelinus fontinalis*) in the Pacific Northwest, U.S., in support of adaptive management. They evaluated different eradication and suppression strategies and found, while suppression was possible, eradication was unlikely.

Despite being frequently cited as a critical approach for management under uncertainty (Keith et al., 2011), adaptive management has been used relatively infrequently to guide on-the-ground invasive species management (see Hooten & Wikle, 2008; Dietterich et al., 2013). Adaptive management is criticized for being a long-term investment requiring stakeholder readiness, an elaborate decision-making framework, and campaigns to collect monitoring data (Williams & Brown, 2014). Because monitoring data are costly to collect, adaptive management should be applied only when the value of learning is greater than monitoring costs (Runge et al., 2011). However, there is opportunity to apply adaptive management in invasive species applications as practitioners continue to grapple with uncertainty (Allen et al., 2011; Runge, 2011; Williams & Brown, 2016).

2.4.2 MULTIPLE-OBJECTIVE DECISION MAKING

The key to any good decision is a clear articulation of management objectives, i.e., what the conservation practitioner hopes to accomplish. Like most resource management decisions (Converse, 2020), invasive species management is characterized by multiple objectives among which trade-offs must be made. Perhaps the most common trade-off involves achieving the conservation objective (e.g., securing native populations negatively impacted by an invasive population) versus minimizing management costs. Trade-offs also arise around objectives such as avoiding impacts of management on non-target species or reducing animal suffering. Especially in high-profile invasive species management programs, diverse stakeholder views must be considered when assessing trade-offs (e.g., feral cat management on islands; Lohr et al., 2013). Multiple-objective decision processes are designed to provide rational and transparent approaches to identifying compromises between conflicting management objectives. A variety of approaches are used to solve multi-objective problems (Converse, 2020), which require a value judgment by the decision-maker regarding the relative importance of conflicting objectives.

Many studies have linked ISMMs with a multi-objective decision making process to identify optimal management when facing competing objectives. For instance, Grechi et al. (2014) integrated a multi-objective decision framework with a SPGM to predict dynamics and optimal management of buffelgrass (*Pennisetum ciliare*), a commercially valuable invasive species, in Australia. They found that achieving an acceptable tradeoff between buffelgrass production and biodiversity conservation targets required up to a 50% reduction in buffelgrass production. In another example, a SPGM for invasive buffelgrass spread in Arizona, U.S., deployed a multi-objective approach with budget and labor constraints to identify strategies that minimized damage to native cactus, local buildings, and vegetation (Büyüktahtakın et al., 2014). They evaluated different objectives (i.e., protect native cactus vs. protect buildings) and reported that managers with opposing agendas must cooperate to minimize spread. In Bair et al. (2018), a SPGM described dynamics and downstream dispersal of invasive rainbow trout *(Oncorhynchus mykiss)* along the Colorado River into the Grand Canyon National Park, U.S. Implementing a multi-objective approach, they determined the best management strategy to minimize control cost while ensuring benefits to a population of endangered humpback chub (*Gila cypha*) was to apply high monthly removal of rainbow trout. Although additional examples exist where multi-objective decision making has been used to evaluate invasive species management approaches (e.g., Bogich et al., 2008; Liu et al., 2011; Lampert et al., 2014), the ability to use these explicit approaches to negotiate trade-offs has yet to be fully realized. Applying multi-objective decision making approaches more widely would allow conservation practitioners to make more efficient use of limited resources.

2.5 CONCLUSION

The spread of invasive species is a substantial threat to biodiversity and contributes to considerable environmental and economic impacts. A multitude of ISMMs can help users understand invasive species dynamics and evaluate management actions, and here we aimed to provide a comprehensive overview of these approaches with the hope of narrowing the gap between science and implementation. Looking to the future, greater investment of time and energy into collaborative decision-analytic processes may help ensure conservation practitioners have tools to confront uncertainty and management trade-offs when identifying invasive species management. Collaborative engagement in such processes can build trust, shared understanding, and improve the quality of management outcomes.

2.6 ACKNOWLEDGEMENT

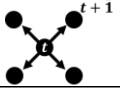
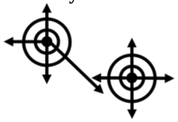
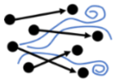
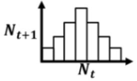
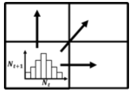
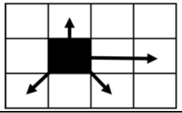
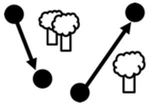
We thank two anonymous reviewers whose comments greatly improved the paper. Funding support for Brielle K.T. was provided by the U.S. Geological Survey Invasive Species Program, the Washington Cooperative Fish and Wildlife Research Unit, and the College of the Environment, University of Washington. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

2.7 TABLES & FIGURES

Table 2.1 Classification of each invasive species management model (reaction-advection-diffusion models, integrodifference equations, gravity models, particle transport models, non-spatial and spatial discrete-time population growth models, cellular automata, and individual-based models) regarding various temporal, spatial, and demographic attributes, indicated by checkmarks. Model attributes were assigned based on typical representation in literature. Temporal attributes categorize models as temporally explicit, continuous in time, and capturing dynamic environmental conditions. Models that are temporally explicit and not continuous in time are discrete in time. Spatial attributes categorize models as spatially explicit, continuous in space, and can model stochastic (random) spread and heterogeneous environments. Models that are spatially explicit and not continuous in space are discrete in space. Demographic attributes categorize models with the capability to include growth terms, simulate individuals that follow (general or simple) ecological rules or complex (individualized or local) rules. The asterisk symbol in the classification of individual-based models indicates that space and time can be discrete or continuous and the ecological rules governing this model type can range from simple to complex

	Temporal Attributes			**Spatial Attributes**				**Demographic Attributes**		
Model	**Temporally Explicit**	**Continuous in Time**	**Dynamic Environment**	**Spatially Explicit**	**Continuous in Space**	**Stochastic Spread**	**Models Heterogeneous Environments**	**Includes Growth Terms**	**Simulated individuals follow rules**	**Simulated individuals follow complex rules**
Reaction-Advection Diffusion Models	✓	✓	✓	✓	✓		✓	✓		
Integrodifference Equations	✓		✓	✓	✓		✓	✓		
Gravity Models			✓	✓	✓	✓	✓			
Particle Transport Models	✓	✓	✓	✓	✓	✓	✓			
Non-Spatial Discrete-Time Population Growth Models	✓							✓		
Spatial Discrete-Time Population Growth Models	✓		✓	✓		✓	✓	✓		
Cellular Automata	✓		✓	✓		✓	✓	✓	✓	
Individual-Based Models	✓	✓ *	✓	✓	✓ *	✓	✓	✓	✓ *	✓ *

Figure 2.1 Types of invasive species management models (reaction-advection-diffusion models, integrodifference equations, gravity models, particle transport models, non-spatial and spatial discrete-time population growth models, cellular automata, and individual-based models). For each model type we provide an icon that symbolizes model dynamics, a short description, an explanation of mathematical formulas and respective parameters, and examples from literature where the model was used to study invasive species dynamics and/or management

Model/ Icon	Description	Formula	Literature
Reaction-Advection-Diffusion Models 	Models population growth and continuous spread of an invader from areas of high concentration to areas of low concentration (diffusion), and directionally based movement (advection) in continuous time.	$\frac{\partial N}{\partial t} = \nabla D \nabla N - \nabla \boldsymbol{v} N + f(N)$ N = density of organisms at x, y, and time t, ∇ = mathematical symbol to represent changes in 3-D, D = diffusion coefficient, $\boldsymbol{v}$ = advection coefficient, $f(N)$ = population growth function	Baker 2017 Baker and Bode 2016 Baker and Bode 2013 Bonneau et al. 2017 Carrasco et al. 2010 Epanchin-Niell and Liebhold 2015
Integrodifference Equations 	Models discrete time growth and continuous spread. Can use a broad range of dispersal mechanisms (i.e. accelerating movement rates and large movement jumps) with its dispersal kernel parameter.	$N_{t+1}(x) = \int K(x-y) f\big(N_t(y)\big) dy$ N_t = population growth at time t, x = current location, y = source population, $K(x-y)$ = dispersal kernel, $f(N_t(y))$ = population growth function	Caplat et al. 2012 Gharouni et al. 2015 Gilbert et al. 2014 Neubert and Caswell 2000 Neubert and Parker 2004
Gravity Models 	Models both local and long-distance jump-dispersal in patchy or heterogeneous environments by relating the force of attraction between an invaded location and a non-invaded location as a function of the distance between locations and weighted by suitability for species establishment.	$N_{ij} = \frac{A_i O_i W_j}{{d_{ij}}^{\alpha}}$ N_{ij} = number of individuals moving from location i to j, A_i = scalar that ensures all individuals at i reaches a destination, O_i = individuals at i, W_j = attractiveness of j, d_{ij} = distance from i to j, α = distance coefficient.	Bossenbroek et al 2001 Fischer et al. 2020 Leung and Mandrak 2007 MacIsaac et al. 2004 Muirhead and MacIsaac 2005 Prasad et al. 2010
Particle Transport Models 	Models the change in invasive species concentration as a function of passive spread (i.e. drift through air or water) in 3-dimensions in continuous time and space.	$\frac{\partial c}{\partial t} = \nabla K \nabla c - \nabla \boldsymbol{v} c + Q$ c = concentration of the population in 3-D, ∇ = mathematical symbol to represent changes in 3-D, $\boldsymbol{v}$ = velocity vector, K = diffusivity tensor in 3-D, Q = locations of sources and sinks	Beletsky et al. 2017 Byers and Pringle 2006 Isard et al. 2005 Michalak et al. 2013 Tilburg et al. 2011
Non-Spatial Discrete-Time Population Growth Models 	Models changes in invasive species abundance in equal, regular time steps, where the population in the future depends on the current abundance and where space is not explicitly represented. Can integrate the density and age/stage structure of a population.	$\boldsymbol{N}_{t+1} = \boldsymbol{L}\boldsymbol{N}_t$ $\boldsymbol{N}_t$= population abundance at time t, $\boldsymbol{L}$ = matrix describing population vital rates of ages or stages of a population	Govindarajulu et al. 2005 Hastings et al. 2006 Melero et al. 2015 Shyu et al. 2013 Taylor and Hastings 2004
Spatial Discrete-Time Population Growth Models 	Models population growth by representing invasive species spread with a generalized dispersal function in a grid-based environment. This model type is the spatial extension of non-spatial discrete-time population growth models.	$\boldsymbol{N}_{t+1,s} = \boldsymbol{L}_s \boldsymbol{N}_{t,s}$ $\boldsymbol{N}_{t,s}$ = population abundance at time t and spatial cell s, $\boldsymbol{L}_s$= s x s matrix describing population vital rates at each cell	Blackwood et al. 2010 Erikson et al. 2018 Jongejans et al. 2011 Link et al. 2018
Cellular Automata 	Models changes in invasive species occupancy across a landscape according to discrete, equally sized cells that are given initial discrete states. Invaded vs. not invaded state of the cells are updated in discrete time and space by local, uniform rules that govern growth, spread or management, that are based on the current state of the cell and neighboring cells.	$X_{s,t+1} = f\big(X_{s,t}, S\big)$ $X_{s,t}$ = the state of cell s at time t (from a finite set of states), t = time step, f = transition function, influenced by the current state of the cell and the state of neighboring cells S	Arii and Parrot 2006 Crespo-Pérez et al. 2011 Huang et al. 2007 Kovacs et al. 2014 Marco et al. 2002
Individual-Based Models 	Models population growth, spread, and complex ecological dynamics where space and time can be discrete or continuous. It is a simulation model that separates a population into distinct states as individuals or agents and evaluates the interaction of states with each other and a dynamically changing environment by following a set of individualized rules governing growth, spread, or management.	$f_{i,t}: S_t \longrightarrow x_{i,t+1}$ $f_{i,t}$= transition function for each individual $x_{i,t}$ to update to a new state(s), $x_{i,t+1}$, based on neighboring and current states S_t, where $P_{i,t}$= probability space that $f_{i,t}$ is selected	Carrasco et al. 2012 Rebaudo and Dangles 2013 Lustig et al. 2019 Messager and Olden 2018 Tonini et al. 2013

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CHAPTER 3. EVALUATING SPATIALLY EXPLICIT MANAGEMENT ALTERNATIVES FOR AN INVASIVE SPECIES IN A RIVERINE NETWORK

Publication history: This study was co-authored with Julian D. Olden and Sarah J. Converse. At the time this dissertation was published, this chapter was not in review with a journal.

3.1 ABSTRACT

Identifying optimal spatial allocation of removal effort is critical for effective management of invasive species. Here, we used a simulation model to assess spatially explicit removal strategies for invasive rusty crayfish (*Faxonius rusticus*) in the John Day River, USA. We assessed strategies in terms of their performance on three management objectives: suppression (minimize the overall population abundance), containment (minimize the spatial extent of invasion), and prevention (minimize spread into a specific area, i.e., the Columbia River). We developed four spatial removal strategies to achieve those objectives, denoted as: Target Abundance (removal at locations with the highest population abundance), Target Growth (removal at locations with the highest population growth), Target Edges (removal at the most distal locations in the river), and Target Random (removal at randomly selected locations). Each strategy was assessed at various effort levels, referring to the percentage of the river in which removals were conducted, after seven years of management. We identified the alternative that best achieved each objective based on decision criteria for risk-neutral and risk-averse decision makers and further evaluated strategies based on Pareto efficiency. We found that Target Abundance and Target Growth strategies best achieved suppression, for risk neutral and risk averse decision makers respectively, and Target Downstream was always best in achieving prevention across both types of decision makers. No single strategy consistently performed best in terms of the containment

objective. In terms of all three objectives, Target Downstream was consistently Pareto efficient across all levels of management effort and both decision criteria. The modeling framework we provided is adaptable to a variety of riverine aquatic invasive species to help assess spatial management strategies.

3.2 INTRODUCTION

Invasive species are a primary threat to global biodiversity, economies, and human health (Pyšek and Richardson 2010; Early et al. 2016; Diagne et al. 2021). Managers of invasive species often seek to reduce two of the main contributors to negative invasive species impacts: population abundance and range extent (Parker et al. 1999). However, desired management outcomes can be challenging to achieve due to imperfect detection, the ineffectiveness of available management actions, and invasive species whose rapid growth and spread can largely nullify the effect of management (Rendall et al. 2021; Cuthbert et al. 2022). In addition, with widespread invasions and constrained budgets, natural resource managers are frequently limited in when and where they can manage (Donlan et al. 2015; Wenger et al. 2018). Therefore, identifying effective spatiotemporal allocation of management effort is often a primary need of managers.

Predicting the effectiveness of alternative spatial allocations of management effort is not straightforward, yet choosing the most effective allocation can mean the difference between successful population suppression or containment for an abundant invader (Eppinga et al. 2021; Travis and Park 2004). Various alternative spatial allocation rules of thumb have been posited for invasive species management to achieve objectives of suppressing and limiting the spread of invasive species. For example, to suppress population size, the “targeting the source” rule involves allocating management effort in locations where the invasive population is the most abundant (Baker 2016), and to limit invasive species spread, the “managing the edges" rule involves expending effort at the invasion front (Bradley 1988; Moody and Mack 1988; Bossard et al. 2000). Ultimately, however, in any given case, the optimal spatial allocation of effort will depend on management objectives, the ecology of the invader, and the characteristics of the invaded system. For instance, if dispersal of the invasive species is small relative to population growth, removal at the edges of the invasion may be a more successful approach in reducing spread of an invader because efforts to remove at the core of the population may be overwhelmed by population growth (Baker 2016).

Quantitative population models are useful tools for evaluating invasive species management strategies in a virtual environment before management is implemented (Büyüktahtakın and Haight 2018; García-Díaz et al. 2019; Thompson et al. 2021). Simulation models can be efficiently used to compare a variety of alternatives under varying ecological and management assumptions without the substantial time and expense of on-the-ground experiments. In particular, spatially explicit population models are powerful tools for modeling population growth and spread and evaluating alternative spatial allocations of management effort (Epanchin-Niell and Hastings 2010; Bertolino et al. 2020; Goodenberger et al. 2020). By accounting for space in invasion processes, we can more accurately quantify management impacts, for example, by considering the strength of invasion pressure from a nearby invaded area (Pepin et al. 2019).

While a number of spatially explicit population models have been developed to evaluate spatial allocation of management effort in terrestrial invasion contexts (e.g., Epanchin-Niell et al. 2012; Baker and Bode 2016; Pepin et al. 2020), these models have rarely been implemented in riverine contexts (but see Albers et al. 2018, Kallis et al. 2023). Spatially explicit population models in rivers are difficult to parameterize due to challenges in collecting and analyzing movement data (Corrales et al. 2020; Caradima et al. 2021), and movement, in addition to population growth, is a key process in spatially explicit population models. For instance, compared to terrestrial wildlife, it is rare to observe marked individuals in aquatic systems (Ogburn et al., 2017), limiting the utility of tools such as multi-state mark-recapture models (Arnason 1973) for understanding movement. In addition, software for mechanistic modeling of animal movement has primarily been developed for terrestrial systems, and only recently has been advanced for modeling animal movements in rivers (Quaglietta and Porto 2019). However, as technology for studying movement continues to develop for aquatic species, spatially explicit population models may be increasingly developed and used to inform management in river systems.

In this study, we used a spatially explicit population model to assess removal alternatives for the management of invasive rusty crayfish (*Faxonius rusticus*) in the John Day River (JDR) of Oregon, USA, a major tributary of the Columbia River. The JDR is one of the largest free-flowing rivers in the United States and holds high conservation importance as it supports a variety of salmon species of significant cultural and economic value, such as endangered spring Chinook salmon (*Oncorhynchus tshawytscha*) and threatened steelhead (*Oncorhynchus mykiss*). The presence of rusty crayfish in the JDR remains a significant concern because they are spreading rapidly (18 km/year), reaching high local abundances (up to 50/m^2), and have the potential to inflict severe ecological impacts due to polytrophic and generalist feeding habits (Olden et al. 2011; Twardochleb et al. 2013).

Using our spatially explicit population model for rusty crayfish, we assessed alternative management strategies involving different spatial allocations of removal effort over a seven-year management time horizon. We evaluated the alternatives based on performance on three management objectives that capture commonly held values of natural resource managers concerned with invasive species: suppression (minimize the overall population abundance), containment (minimize the spatial extent of invasion), and prevention (minimize spread into a particular area). Our results can inform managers in the JDR identify efficient management strategies for rusty crayfish, and more broadly our methods provide a template for the evaluation of invasive species management strategies in branching river systems.

3.3 METHODS

3.3.1 STUDY SYSTEM AND MANAGEMENT CONTEXT

The rusty crayfish in the JDR has the potential to cause a variety of ecological problems due to its high population growth and generalist feeding habits. Rusty crayfish have already been implicated in the decline of macrophytes, aquatic insects, snails, and fishes (Twardochleb et al. 2013). We considered alternative strategies for managing rusty crayfish in a portion of the JDR where it is anticipated to negatively impact the ecosystem (Falke et al., 2013, McHugh et al., 2017; Figure 3.1). We divided this portion of the JDR into 35 20-km river segments, henceforth segments, and the locations where crayfish management occurred corresponded to specific segments selected annually (Figure 3.1).

Management efforts targeting invasive species involve a range of objectives, including – broadly – eradication, suppression (i.e., minimizing total abundance), containment (i.e., minimizing range size or total spatial extent), and prevention (i.e., minimizing spread into a particular geographic location) (Gherardi et al. 2011; Rytwinski et al., 2019). We assumed these objectives would be of interest to managers in the JDR. However, we focused on the latter three – suppression, containment, and prevention – as eradication does not appear to be achievable based on our results and other studies (Messager and Olden 2018).

We developed management strategies with suppression, containment, and prevention in mind (Table 3.1). We developed the strategy Target Abundance primarily to address the suppression objective, with removal effort in segments where total crayfish abundance was highest. We also developed the Target Growth strategy primarily to address the suppression objective, with removal effort in segments with the highest population growth. We created the Target Edges strategy to address the containment objective, with removal effort at the invasion edges with the highest abundance and at segments adjacent to invasion edges depending on the number of segments receiving removal effort, again prioritized by abundance. An invasion edge refers to the most upstream invaded segment on the Mainstem, North Fork, Middle Fork, South Fork, and Murderer's Creek, and the most downstream invaded segment on the Mainstem (Figure 3.1). We developed the strategy Target Downstream to address both the prevention and containment objectives; in this strategy, removal effort occurred at the most downstream segments in the Mainstem of the JDR with crayfish present. We also evaluated a Target Random strategy, in which removal occurred at segments that were randomly selected each year. Given random selection under this strategy, segments with no crayfish could be selected for management. Finally, we evaluated a No Removals strategy to represent the status quo in the JDR.

For each of the broad management strategies (except No Removals), we evaluated various levels of removal effort, which corresponded to the number of segments where removal occurred (Table 3.1). We assumed removal of crayfish via trapping and physical removal, which is the most common method for crayfish (Manfrin et al. 2019, Gherardi et al. 2011, Freeman et al. 2010). We tested four levels of removal effort, such that removal was simulated at 1, 4, 8, or 16 segments out of the total 35 segments (~3%, 11%, 23%, and 45% of the total segments in the system). Thus, with five broad removal strategies, each with four levels of effort, plus the No Removals strategy, we evaluated 21 total management alternatives. The segments selected for removal remained fixed during a year and were updated annually according to the management strategy. In addition, given high-flow conditions during the autumn and winter months that limit accessibility, we assumed that removals could only occur during June through September, with removals occurring over ten trap nights in each of those months. We evaluated management strategies over a seven-year management time horizon.

3.3.2 *MODEL STRUCTURE*

We developed a spatially explicit population model to simulate rusty crayfish removal, growth, and movement. Our simulation model largely follows the ecological process described by Link et al. (2018) in their model for estimating abundance, growth, movement, and detection efficiency using spatially referenced counts of removals from an invasive population; the primary difference is our addition of age structure. That is, we track abundance of the population by spatial unit (i.e., a river segment), and allow the population to grow and move, and to be removed as a function of removal effort. We assumed that removals occur on ten consecutive trap nights each month, during the months of June through September each year, and that all population growth and movement occurred between each removal period. The time step in the simulation model is primarily a monthly time step, but switches to a daily time step during periods of removal, when the population is otherwise closed.

Messager and Olden (2018) previously simulated the spread and removal of rusty crayfish in the JDR with a spatially explicit individual-based model. We drew many parameter values from that study as well as the literature (see 3.9 *Appendix 3* for parameter value descriptions). In our model, segments of 20-km length were indexed by $i = 1, 2, . . . , I$ ($I = 35$

segments), months were indexed by $j = 1, 2, \ldots J$ ($J = 84$ months), and trap nights within months were indexed by $k = 1, \ldots, K$ ($K = 10$ trap nights). In the model, only females were modeled, and age class was indexed by $a = 0, 1, 2$, and 3 (where 0 = 0-1 year olds, 1 = 1-2 year olds, 2 = 2-3 year olds, and 3 = older than 3). In the following sections we describe the specific modeling structures for the removal, population growth, and movement sub-models.

Removal sub-model – The removal sub-model allowed for simulation of the trapping and removal of crayfish. We defined $N_{i,j,k,a}$ as the population abundance at segment *i* before the *k*th trap night during month *j*, for age a, and $Y_{i,j,k,a}$ as the number of crayfish removed. We assumed age-0 individuals were too small to be removed by typical trapping methods (Ogle and Kret 2008). Hence, crayfish abundance and removals for age classes $a = 1, 2, 3$ and for trap nights $k = 2, \ldots, K$ were:

$$N_{i,j,k,a} = N_{i,j,(k-1),a} - Y_{i,j,(k-1),a} \tag{1}$$

$$Y_{i,j,k,a} \sim \text{Binomial}\left(N_{i,j,k,a}\,, p\right) \quad .(2)$$

with effective removal probability, p, modeled as:

$$p = \frac{n^{\text{traps}}}{8{,}000}\theta \quad ,(3)$$

with n^{traps} the number of traps in a river section and θ was the probability of capture for a crayfish within the trappable area around a trap. We assumed that the trappable area around a single trap was 25 m^2 and given that a river segment had an area of 200,000 m^2, 8,000 traps would provide full coverage. No information was available with which to estimate this parameter, so we defined a Uniform (0.1, 0.5) distribution to represent our (uncertain) judgment about this parameter, i.e., $p = 0.25 * \theta$ and $\theta \sim$ Uniform(0.1, 0.5. We assumed $n^{traps} = 2{,}000$, which is a reasonable maximum number of traps that a resource manager could deploy in a 20-km river segment over 4 months).

The calculation of $N_{i,j,k,a}$, for *j* > 1 and *k* = 1, i.e., abundance on the first trap night in all removal months after the first month, is described further in the movement sub-model section, and initial population $N_{i,j,k,a}$ for *j* = 1 and *k* = 1 is described in section 3.3.3 *simulation study implementation.*

Given our expression for p (Eq. 3) and estimate for θ*,* we obtained low values of effective removal probability. Therefore, in a subset of simulations, we modified the equation for p in two ways to simulate scenarios with higher effective removal probability. In one scenario, we set n^{traps} = 8,000, such that p = θ and θ ~ Uniform(0.1, 0.5). In another, we set n^{traps} = 2,000 and fixed θ = 0.5, such that p = 0.25*0.5 = 0.125.

Population growth sub-model – After K = 10 trap nights, we calculated $R_{i,j,a}$, the population remaining after removal as:

$$R_{i,j,a} = N_{i,j,K,a} - Y_{i,j,K,a} \tag{4}$$

We then initiated the population change sub-model based on $R_{i,j,a}$. Since the model was age structured, we calculated $D_{i,j,a}$, defined as the number in the population after population growth. $D_{i,j,a}$was based on a time-varying Leslie matrix, $\boldsymbol{L_j}$, containing survival probabilities and fecundity rates for each age class. Since survival was applied monthly, while age transitions and reproduction occurred yearly, we created two Leslie matrices, one for all months excluding June and one for June, when age transitions and reproduction occurred. For months excluding June, $\boldsymbol{L_j}$ was:

$$\begin{pmatrix} \varphi_0 & 0 & 0 & 0 \\ 0 & \varphi_1 & 0 & 0 \\ 0 & 0 & \varphi_2 & 0 \\ 0 & 0 & 0 & \varphi_3 \end{pmatrix} \tag{5}$$

where φ_a were monthly survival rates for each age class. In June, the population underwent age transition and reproduction, and the post-breeding census matrix was:

$$\begin{pmatrix} \varphi_0 f_1 m_1 & \varphi_1 f_2 m_2 & \varphi_2 f_3 m_3 & \varphi_3 f_3 m_3 \\ \varphi_0 & 0 & 0 & 0 \\ 0 & \varphi_1 & 0 & 0 \\ 0 & 0 & \varphi_2 & \varphi_3 \end{pmatrix} \tag{6}$$

where f_a represented age class-specific fecundity rates and m_a represented the fraction of mature females in each age class, for a = 1, 2, and 3 (Messager and Olden 2018). The first row provides each age class's contribution to the age-0 crayfish entering the population on June 1.

We sampled rates φ_a, f_a, and m_a from normal distributions. Survival rate φ_a, had mean values of 0.81, 0.97, 0.94, and 0.72 with a standard deviation of 0.1 for a = 0, 1, 2, and 3 respectively, with a lower limit of 0.0001 and upper limit of 0.9999 (Table S3.3; Messager and Olden 2018). The fecundity rates, f_a, had mean values of 80, 120, and 150 with standard deviations of 10, 20, and 40 for a = 1, 2, and 3, respectively (Table S3.3; Messager and Olden 2018). The fraction of mature females, m_a, had mean values of 0.1, 0.8, and 0.9 for a = 1, 2, and 3, respectively, with a standard deviation of 0.1 and bounded between 0 and 1 (Table S3.3; Messager and Olden 2018). $D_{i,j,a}$ was calculated as:

$$D_{i,j,a} = \boldsymbol{L}_j \times R_{i,j,a} \tag{7}$$

and rounded upwards.

We assumed that the number of crayfish in each segment could at most be 12,166,668, which was calculated as twice the maximum density (30.4 crayfish/m^2) observed in a 2016 field study for a population assumed to be at the stable age structure (Messager and Olden 2018). If the number of crayfish in a segment was greater than the carrying capacity, the excess number of crayfish was first subtracted from age class 0 individuals, $D_{i,j,0}$, since that age class would likely be the most negatively impacted by density-dependent processes. Any remaining crayfish were subtracted from the other age classes, in order of increasing age.

Movement sub-model – After population growth, we modeled the monthly movement of crayfish between adjacent segments. We first calculated the number of crayfish that remained in each segment. The probability of staying in each segment was:

$$m_{\text{stay}} = 1 - 0.5\pi\left(1 - u_{i,j}\right) \qquad .(8)$$

In this expression, the 0.5 indicated that only one half of the crayfish population in any segment was available to move because the size of a single segment was 20 km and crayfish do not disperse more than 5 km in a single month (Message and Olden 2018). The parameter π is the probability of moving, and was assumed to be either 0.05, 0.1, 0.15, 0.2, or 0.25 to capture a range from low to high movement probabilities (Messager and Olden 2018, Table S3.3). Next, $u_{i,j}$ represented the proportion of crayfish that stayed in a current segment due to temperature constraints. To calculate this proportion, we obtained segment-level temperature data and calculated the fraction of days each month in which temperature was less than 6°C, such that crayfish movement is physiologically infeasible (Hamr 1997; Messager and Olden 2018). Hence, the term 1- $u_{i,j}$ represented the probability that crayfish were not restricted in their movement by temperature constraints. Then, for *a* = 1, 2 and 3, the number of crayfish that stayed in a segment was calculated as:

$$D_{i,j,a}^{\text{stay}} \sim \text{Binomial}\left(D_{i,j,a},\ m_{\text{stay}}\right) \qquad .(9)$$

Next, we calculated crayfish that moved downstream:

$$D_{i,j,a}^{\text{down}} \sim \text{Binomial}\left(D_{i,j,a} - D_{i,j,a}^{stay},\ m_{\text{down}}\right) \qquad (10)$$

where $D_{i,j,a} - D_{i,j,a}^{\text{stay}}$ was the number of crayfish that did not stay in segment *j* and the probability of moving downstream conditional on moving was m_{down}, which was drawn from Uniform(0.5, 1) (Messager and Olden 2018). Then, for segments not adjacent to a river fork, we calculated the number of individuals moving upstream as

$$D_{i,j,a}^{\mathrm{up}} = D_{i,j,a} - D_{i,j,a}^{\mathrm{stay}} - D_{i,j,a}^{\mathrm{down}} \qquad .(11)$$

Crayfish in some segments could move upstream within the same tributary and move upstream to a new fork (i.e., segments 6, 8, 25, and 31, Figure S3.7) and we needed to implement a bifurcation movement process. Due to the hydrology of the JDR, we only needed to incorporate the bifurcation process in upstream movement. In these segments, we assumed upstream movement within the same fork and to a different fork had equal probability. Therefore, we calculated the number of individuals that moved upstream as

$$D_{i,j,a}^{\mathrm{up}} = \frac{D_{i,j,a} - D_{i,j,a}^{\mathrm{stay}} - D_{i,j,a}^{\mathrm{down}}}{2} \qquad ,(12)$$

rounded downwards, and the number of crayfish that moved to a new fork as

$$D_{i,j,a}^{\mathrm{fork}} = D_{i,j,a} - D_{i,j,a}^{\mathrm{stay}} - D_{i,j,a}^{\mathrm{down}} - D_{i,j,a}^{\mathrm{up}} \qquad .(13)$$

Finally, we redistributed crayfish in the river according to their recent movement. However, for a = 0, $D_{i,j,a} = N_{i,j,a}^{\mathrm{redistribute}}$ since we assume that age-0 individuals do not move (Messager and Olden 2018). Hence, we calculated the redistributed population as:

$$N_{i,j,a}^{\mathrm{redistribute}} = D_{i,j,a}^{\mathrm{stay}} + \sum_{h \in \mathrm{down}_i} D_{h,j,a}^{\mathrm{down}} + D_{up_i,j,a}^{\mathrm{up}} + D_{\mathrm{fork}_i,j,a}^{\mathrm{fork}} \qquad ,(14)$$

where the first term represented the population that stayed in segment *i*. The second term is the population that moved downstream into *i* from segments $h \in \mathrm{down}_i$, where down_i was the set of segments from which crayfish could move downstream to *i*. The third term represents the number of crayfish that moved into *i* from upstream segment up_i. Finally, the fourth term is the number of crayfish that moved upstream into *i* from a segment in a different fork, fork_i (see Figure S3.8 for a graphical representation of each river segment in the JDR and downstream movement directions). We assumed that in the most upstream segments in all forks, no crayfish could move upstream out of that fork. We also assumed that crayfish in the most downstream segment in the mainstem could move out of the JDR, which allowed us to calculate the number of crayfish that entered the Columbia River.

Once we completed the movement process, we calculated abundance at the beginning of the next month $j + 1$ as $N_{i,(j+1),1,a} = N_{i,j,a}^{\text{redistribute}}$. For the months June, July, August, and September, crayfish removals occurred and for all other months only population growth, and movement occurred. At the end of May, before June crayfish removal, the abundance of total crayfish in a = 1, 2, and 3 (i.e., excluding a = 0) at each segment was assessed and the locations where removal would occur the next month were informed by the simulated management strategy.

3.3.3 *SIMULATION STUDY IMPLEMENTATION*

Population simulations were coded in R (R version 4.3.1, R Core Team). We simulated each of the 21 management alternatives under the same 20 parameter sets to represent parametric uncertainty for each parameter (e.g., survival, fecundity, and movement rates) and ran 50 simulations for each parameter set to represent process uncertainty. To create the parameter sets, we performed 20 independent draws from the parametric distributions provided in the model descriptions (Table S3.3).

Each simulation under each alternative was initialized with the same segment-level population, which was informed by an intensive crayfish survey in 2016 (Figure S3.1, Messager and Olden 2018). Since rusty crayfish were likely introduced to the JDR in 1999, we assumed that by 2016 the population had reached a stable age distribution and for each parameter set we calculated an annual Leslie matrix and then calculated the stable age distribution as the eigenvector associated with the largest eigenvalue of the annual Leslie matrix:

$$\begin{pmatrix} \varphi_0^{12} f_1 m_1 & \varphi_1^{12} f_2 m_2 & \varphi_2^{12} f_3 m_3 & \varphi_3^{12} f_3 m_3 \\ \varphi_0^{12} & 0 & 0 & 0 \\ 0 & \varphi_1^{12} & 0 & 0 \\ 0 & 0 & \varphi_2^{12} & \varphi_3^{12} \end{pmatrix} \quad .(15)$$

Therefore, although the segment-level population was the same across parameter sets, the distribution of each age class at each segment differed between parameter sets.

3.3.4 *EVALUATION OF ALTERNATIVES*

We evaluated the performance of each objective – suppression, containment, and prevention – for each alternative. We only considered adults (*a* = 1, 2, and 3) in our calculation of management outcomes because of the demonstrated ecological effects of adult crayfish. We expressed management outcomes for the suppression objective for each simulation as the total crayfish population size after 7 years of management (month $J = 84$), $\sum_{i=1}^{I} \sum_{a=1}^{A} N_{i,J,a}^{\text{redistribute}}$ (with the objective of minimizing this quantity). We expressed management outcomes under the containment objective for each simulation as the proportion of segments in which rusty crayfish abundance exceeded a threshold after 7 years of management (with the objective of minimizing this quantity). We defined this threshold as 10% of the average abundance for *a* = 1, 2, and 3 under the No Removals strategy, and assumed that a segment-specific abundance below this threshold would represent functional eradication (sensu Green and Grosholz 2020) in this system, and values above this threshold would indicate the segment “contained” crayfish. We expressed management outcomes under the prevention objective for each simulation as the cumulative number of crayfish that moved out of the JDR and entered the Columbia River (with the objective of minimizing this quantity). This was calculated as $\sum_{j=1}^{J} \sum_{a=1}^{A} D_{i,j,a}^{\text{down}}$ for the most downstream segment *i* in the mainstem of the JDR (Figure S3.8).

We considered two decision criteria: expected value and mini-max. The expected value criterion, used for risk-neutral decision makers, selects for the management alternative with the best expected performance (i.e., average simulated value) over simulations. The mini-max criterion is a risk-averse decision criterion that selects for the alternative that minimizes the maximum possible loss given uncertainty (i.e., the worst outcome over all simulations) (Savage 1951).

3.3.5 *MULTIPLE OBJECTIVE ASSESSMENT*

Multiple objective decisions are common in natural resources management (Converse 2020), and we were interested in evaluating strategies across our three objectives simultaneously. Pareto-efficient alternatives, or non-dominated alternatives, are the alternatives within a set under which the outcome on one objective cannot be improved without a reduction in another objective (Kennedy et al. 2008; Cohon, 1978). Non-optimal alternatives, or dominated alternatives, are clearly inferior because some other alternative in the set performs at least as well as the dominated alternative on all objectives and performs strictly better on at least one. We found the Pareto front, the set of Pareto-efficient alternatives, using both the expected value and mini-max criteria, across our three objectives: suppression, containment, and prevention.

3.4 RESULTS

The Target Abundance strategy performed best on the suppression objective with respect to expected value, regardless of the number of segments receiving removal effort (Figure 3.2A, Table 3.2). The final population distribution further revealed that this strategy led to overall population suppression in the JDR (Figure 3.3; with 16 segments of removal effort). However, this strategy was not optimal under the risk-averse mini-max criterion for the suppression objective (Table 3.2, Table 3.3). In addition, the Target Abundance performed poorly on the containment and prevention objectives across all levels of removal effort (Table 3.2, Table 3.3).

The Target Growth strategy, across all levels of removal effort, performed the best on the mini-max criterion for the suppression objective (Table 3.3), yet was the worst in terms of expected value (Table 3.2, Figure 3.2A). Target Growth had the best expected performance for the containment objective given 1 segment of removal effort and was the second-best strategy for this objective given 4, 8, or 16 segments of effort (Table 3.2). This strategy was never optimal with respect to the prevention objective given either the expected value or the mini-max criteria and any level of removal effort (Table 3.2, Table 3.3).

The Target Edges strategy did not perform well on the suppression objective across any level of removal effort (Table 3.2, Table 3.3). However, with 16 segments of effort, this strategy did suppress crayfish population at the "edges" of invasion, as there were low final populations in all major tributaries of the JDR and in the most upstream and downstream segments of the mainstem of the JDR (Figure 3.3). Therefore, this strategy had the best expected value for the containment objective for 16 segments of effort (Table 3.2, Figure 3.2B).

Target Downstream was the best strategy on the prevention objective regardless of the decision criterion and regardless of the number of segments of removal effort (Table 3.2, Table 3.3, Figure 3.2C, Figure 3.3). In addition, this strategy performed the best in terms of expected value for the containment objective for 4 or 8 segments of effort (Table 3.2). Overall, the Target Downstream strategy did not perform well on the suppression objective (Table 3.2, Table 3.3).

The Target Random strategy, in terms of the mini-max criterion, was the worst strategy for both suppression and prevention objectives and performed equally as bad as all other strategies on the containment objective, across all numbers of segments receiving removal effort

(Table 3.3). Compared to other strategies, Target Random was neither the optimal nor the worst strategy in terms of the expected value criterion across all objectives. Overall, the Target Random strategy had variable outcomes on all objectives, as shown by the various outlier values (Figure 3.2). However, Target Random did perform better than No removals. In fact, across all strategies, the No removals strategy performed the worst across every objective and criterion (Table 3.2, Table 3.3).

The Pareto efficient strategies, in terms of expected value, included Target Abundance, Target Downstream, and Target Random across all levels of removal effort (Table 3.2). For 4 and 8 segments of effort, the dominated strategies (Target Growth and Target Edges) were dominated by the Target Downstream strategy, and for 16 segments of effort, the dominated strategy (Target Growth) was dominated by Target Edges (Table 3.2). In terms of the mini-max criterion, Target Growth and Target Downstream were Pareto efficient regardless of the level of removal effort (Table 3.3). For 4, 8, and 16 segments of effort, the Target Random strategy was dominated by every other strategy (Table 3.3).

Incorporating modifications on effective detection probability, p, did not substantially improve outcomes for suppression and prevention objectives (Figure S3.2-Figure S3.4). However, when evaluating strategies with 16 segments of removal effort under the containment objective, we found that making either of the two modifications to p (i.e., setting n^{traps} = 8,000 and $\theta \sim$ Uniform(0.1, 0.5), or setting n^{traps} = 2,000 and $\theta = 0.5$) made the Target Abundance strategy the best alternative in terms of expected value (Figure S3.4).

Since all the objectives were based on either final population abundance (suppression), final distribution (containment), or cumulative abundance (prevention), we did not focus on changes in the population over time. However, under all alternatives, the abundance of crayfish slightly increased over time (Figure S3.6-Figure S3.7).

3.5 DISCUSSION

We used a spatially explicit population model to simulate rusty crayfish population growth, movement, and removal in the JDR and evaluated different management strategies across various effort levels (i.e., number of locations receiving management). We evaluated the performance of all alternatives in meeting objectives of suppression (i.e., minimize the overall population size or total abundance of rusty crayfish), containment (i.e., minimize the range size or spatial extent of rusty crayfish in the JDR), and prevention (i.e., minimize the number of crayfish entering the Columbia River). Our results point to three major outcomes with respect to comparing spatially explicit management alternatives for an invasive species.

First, all strategies involving crayfish removal performed better than No Removals on every objective in terms of both decision criteria, yet the optimal strategy often varied by objective, decision criteria, or the level of removal effort. For example, in terms of expected value, the Target Abundance strategy performed the best on the prevention objective, but in terms of the mini-max criterion, the Target Growth strategy performed the best on this objective, across all levels of effort (Table 3.2, Table 3.3, Figure 3.2). The optimal strategy for the containment objective in terms of expected value varied across the number of segments that received management (Table 3.2). However, Target Downstream was consistently the best strategy on the prevention objective across all number of segments that received management and across the two decision criteria, yet this strategy performed poorly on the suppression objective (Table 3.2, Table 3.3, Figure 3.2). The Target Downstream strategy is similar to other efforts in freshwater invasive species management to reduce spread rates into an uninvaded area

(Rytwinski et al., 2019). For example, to minimize stone moroko (*Pseudorasbora parva*) spread in England and Wales, resource managers targeted management at lakes that were located on the floodplain (Britton et al., 2011). In addition, a study of invasive signal crayfish (*Pacifastacus leniusculus*) in Europe revealed that removing crayfish at the leading front of the invasion may delay colonization to new areas (Moorhouse and Macdonald 2011).

Second, because no single management strategy performed the best across every objective and decision criterion, tradeoffs amongst objectives must be made. However, we found that the Target Downstream strategy was the only strategy that was Pareto efficient (i.e., not dominated by another strategy) regardless of the number of segments receiving removal effort and regardless of the decision criterion (Table 3.2, Table 3.3, Figure 3.2). This is because the Target Downstream strategy was always the best strategy on the prevention objective. This result differs from findings in terrestrial invasive species contexts that suggest targeting the core of invasion (e.g., Baker 2016, Lustig et al. 2019), equivalent to the Target Abundance strategy here. However, our result is similar to findings for invasive weed management, in which targeting outlier invasions can be effective (Bossard et al. 2000). In many invasive species management contexts, preventing invasion of a new area is an objective, especially when eradication is not feasible (Green and Grosholz 2020). For example, a primary objective of Bigheaded carp (*Hypophthalmichthys spp.*) management in the midwestern US is to minimize spread of invasive carp into the Great Lakes (MacNamara et al., 2016). In addition, the U.S. Forest Service developed a campaign for invasive spongy moth (*Lymantria dispar*) called “Slow the Spread” to minimize new invasions (Grayson and Johnson 2017).

Third, as expected, it is better to conduct management at a higher intensity. We found there was a small difference in expected value outcomes when we compared No Removals with any alternative receiving removal effort in just 1 segment, especially for the suppression and containment objectives (< 2% improvement with management, Table 3.2). When we compared the best expected value alternative across 4 to 16 segments of removal effort, we found that for the suppression objective there was a 37% improvement in outcomes, for the containment objective a 17% improvement, and for the prevention objective a 69% improvement (Table 3.2). However, on the prevention objective, removing at 1 segment under the Target Downstream strategy performed better than any other strategy with 4 segments of removal effort (Table 3.2). The finding that higher intensity removals achieve better management results is supported by a variety of invasive crayfish management studies (Resinger et al., 2024; Perales et al., 2021; Hansen et al., 2013). For example, a whole lake invasive rusty crayfish removal study in Wisconsin, USA, showed that intensive trap efforts could suppress rusty crayfish populations (Hein et al., 2007). Cost is a major consideration in management (Epanchin-Niell 2017). To account for this, we considered alternatives with varying intensities (i.e., number of segments with removal effort) as a proxy for cost. Implementing a "proxy" for cost is a simple and effective way to help identify the degree to which management outcomes may improve if budget is increased. Here, we showed that increasing the number of segments that received management from 4 to 16 segments greatly improved outcomes in suppressing the population, yet there were only marginal benefits in improving outcomes for the prevention objective under this increase in investment or budget (Figure 3.2).

We relied on a population model to conduct this study, and with all models, there were some limitations. In terms of the ecology of rusty crayfish, in our model, temperature was the only covariate included, but other environmental factors may be important. For example, river flow likely impacts dispersal of crayfish (Ehrlén and Morris 2015). In addition, we assumed that every location was available for removal, which may not be the case in reality due to restrictions in access. Bertolino et al. (2021) showed that restricting access of natural resource managers to private property can cause delays and lead to more costly management. In addition, we only considered removal of crayfish via physical trapping and other management techniques might more effectively reduce the population. For example, accounting for techniques that allow for all ages of crayfish to be removed could improve management outcomes (Manfrin et al. 2019).

We selected segments for management based on perfect knowledge of the system, which will not be the case in real applications. If we do not have perfect knowledge of the state of the system, we would need to rely on monitoring data to identify removal segments. If we have monitoring data and are using this information to update predictive models, then we could implement adaptive management (Lyons et al. 2008; Williams and Brown, 2014). We attempted to create this case study in an adaptive management context, which relied on creating a Bayesian estimation model using a robust design model similar to Link et al. (2018) to estimate abundance. However, we were unable to produce accurate estimates of abundance for this specific study, likely because we were collecting data from only a subset of segments at each time period. If management were to occur more frequently than four months per year or additional data streams were integrated (e.g., detection-non/detection or radio telemetry data) an adaptive management framework may be appropriate, as abundance and other parameters could be better estimated.

The JDR represents a particularly challenging system, both in terms of the extent of the system, making it challenging to accurately monitor the entire basin, and in terms of the extent of invasion in the system. Although we showed that removing crayfish resulted in better management outcomes than No Removals, on average, no strategies resulted in eradication, successful containment, or prevention of crayfish entering the Columbia River. Therefore, rusty crayfish invasion in the JDR can serve as a precautionary tale, as management outcomes would have likely improved if management had begun earlier in the invasion process (as shown by Messager and Olden 2018). Therefore, we emphasize the value of early detection and rapid response for minimizing the impacts of invasive species before the invasion becomes too large for management to be effective (Reaser et al., 2019).

In conclusion, we provided an approach to simulate an aquatic invasive species in a complex riverine environment. In general, there are very few applications of population models that evaluate spatially explicit management in riverine contexts (Corrales et al. 2020). We described a flexible modeling framework that integrated different spatial management strategies and is broadly appliable to different species and regions of interest. Spatially explicit population models can offer natural resource managers a cost effective tool to examine management alternatives. Future studies should consider implementing a similar modeling approach to help determine effective invasive species management practices.

3.6 ACKNOWLEDGEMENT

This research was funded through support of B.K. Thompson by the U.S. Geological Survey Invasive Species Program and the U.S. Geological Survey Science Support Program in collaboration with the U.S. Fish and Wildlife Service’s Pacific Region. Funding was facilitated by, and additional funding was provided by, the Washington Cooperative Fish and Wildlife Research Unit at the University of Washington. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We would like to thank Theresa Thom and Paul Heimowitz for guidance in developing this chapter.

3.7 TABLES & FIGURES

Table 3.1 Twenty-one management alternatives that were simulated for removal of rusty crayfish in the John Day River System, including the broad removal strategy, the number of segments (and percentage of the modeled system) receiving removal effort, and the specific objectives targeted by the management strategy: suppression (i.e., minimize total abundance), containment (i.e., minimize total spatial extent), and prevention (i.e., minimize spread into the Columbia River). Removals were assumed to occur in June through September for ten trap-nights per month. Segments receiving removal effort were selected annually given the alternative and the simulated system state.

Management Strategy	**No. Segments Receiving Removal Effort (% of the JDR managed)**	**Objective(s) Targeted**
No removals	0 (0%)	None
Target Abundance: remove at segments where total crayfish abundance was the highest	1 (3%), 4 (11%), 8 (23%), 16 (46%)	Suppression
Target Growth: remove at segments where crayfish population growth was the highest	1 (3%), 4 (11%), 8 (23%), 16 (46%)	Suppression
Target Edges: remove at edges of invasion with the highest abundance (i.e., invaded segments most downstream on the Mainstem and most upstream on the Mainstem, North Fork, Middle Fork, South Fork, or Murderer's Creek)	1 (3%), 4 (11%), 8 (23%), 16 (46%)	Containment
Target Downstream: remove at the most downstream segments on the mainstem with crayfish abundance	1 (3%), 4 (11%), 8 (23%), 16 (46%)	Containment/ Prevention
Target Random: remove at randomly selected segments	1 (3%), 4 (11%), 8 (23%), 16 (46%)	Suppression/ Containment/ Prevention

Table 3.2 Consequence table of simulation results for rusty crayfish removal in the John Day River, Oregon, USA, based on the expected value decision criterion. The first column indicates the alternative, and the second to fourth columns represent the expected value for that alternative under each of three objectives, with M representing millions of crayfish. The light green cells represent the minimum (i.e., preferred) expected value for each objective, for a given number of segments receiving removal effort. The fifth column indicates the alternative, if any, that dominated the alternative in the row, again for a given number of segments receiving removal effort. An alternative is Pareto efficient if no alternative dominates that alternative, indicated with "None." We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream, and Target Random as Random.

Alternative management strategy, no. segments of removal effort	Objective (expected value)			
	Suppression (in millions)	**Containment** (%)	**Prevention** (in millions)	**Dominated by** X **Alternative**
No removal, 0	21.13 M	90.3%	1.15 M	None
Abundance, 1	20.52 M	90.2%	1.15 M	None
Growth, 1	20.83 M	89.7%	1.15 M	None
Edges, 1	20.68 M	90%	0.83 M	None
Downstream, 1	20.81 M	90.1%	0.48 M	None
Random, 1	20.61 M	90%	1.10 M	None
Abundance, 4	18.82 M	89.6%	1.14 M	None
Growth, 4	20.05 M	87.2%	1.01 M	Downstream, 4
Edges, 4	19.24 M	88.1%	0.48 M	None
Downstream, 4	19.37 M	86.2%	0.18 M	None
Random, 4	19.00 M	88.6%	0.96 M	None
Abundance, 8	16.67 M	85.7%	1.02 M	None
Growth, 8	18.34 M	83.1%	0.58 M	Downstream, 8
Edges, 8	17.92 M	85.1%	0.31 M	Downstream, 8
Downstream, 8	17.32 M	81.4%	0.15 M	None
Random, 8	16.93 M	85.7%	0.83 M	None
Abundance, 16	11.81 M	74.1%	0.67 M	None
Growth, 16	14.25 M	72.9%	0.22 M	Edges, 16
Edges, 16	14.24 M	71.4%	0.22 M	None
Downstream, 16	13.17 M	73.7%	0.15 M	None
Random, 16	12.78 M	78.3%	0.56 M	None

Table 3.3 Consequence table of simulation results for rusty crayfish removal in the John Day River, Oregon, USA, based on the mini-max decision criterion. The first column indicates the alternative, and the second to fourth columns represent the maximum predicted value for that alternative under each of three objectives, with M representing millions of crayfish. The light green cells represent the minimum (i.e., preferred) of the maximum values for each objective, for a given number of segments receiving removal effort. The fifth column indicates the alternative, if any, that dominated the alternative in the row, again for a given number of segments receiving removal effort. An alternative is Pareto efficient if no alternative dominates that alternative, indicated with "None." We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream, and Target Random as Random.

Alternative management strategy, no. segments of removal effort	Objective (expected value)			**Dominated by** X **Alternative(s)**
	Suppression (in millions)	**Containment** (%)	**Prevention** (in millions)	
No removals, 0	80.30 M	100%	5.73 M	N/A
Abundance, 1	79.10 M	100%	5.72 M	None
Growth, 1	78.72 M	100%	5.73 M	None
Edges, 1	79.80 M	100%	3.78 M	Downstream, 1
Downstream, 1	79.58 M	100%	2.45 M	None
Random, 1	79.91 M	100%	5.72 M	Abundance, 1 & Downstream, 1
Abundance, 4	75.77 M	100%	5.72 M	Growth, 4 & Edges, 4
Growth, 4	74.68 M	100%	5.31 M	None
Edges, 4	75.52 M	100%	2.45 M	None
Downstream, 4	76.11 M	100%	1.76 M	None
Random, 4	76.84 M	100%	5.72 M	All
Abundance, 8	72.32 M	100%	4.53 M	Edges, 8 & Downstream, 8
Growth, 8	69.91 M	100%	5.00 M	None
Edges, 8	70.08 M	100%	2.10 M	None
Downstream, 8	71.49 M	100%	1.70 M	None
Random, 8	73.30 M	100%	5.72 M	All
Abundance, 16	63.04 M	100%	3.54 M	Growth, 16 & Edges, 16 & Downstream, 16
Growth, 16	59.64 M	100%	1.75 M	None
Edges, 16	59.80 M	100%	1.85 M	Growth, 16
Downstream, 16	62.13 M	100%	1.70 M	None
Random, 16	63.61 M	100%	4.61 M	All

Figure 3.1 A map of the John Day River (JDR) basin and tributaries (Mainstem, North Fork, Middle Fork, South Fork, and Murderer's Creek). The dark blue region of the JDR represents the spatial extent of this study (35 segments). The light blue regions of the JDR Basin are not included in our simulations.

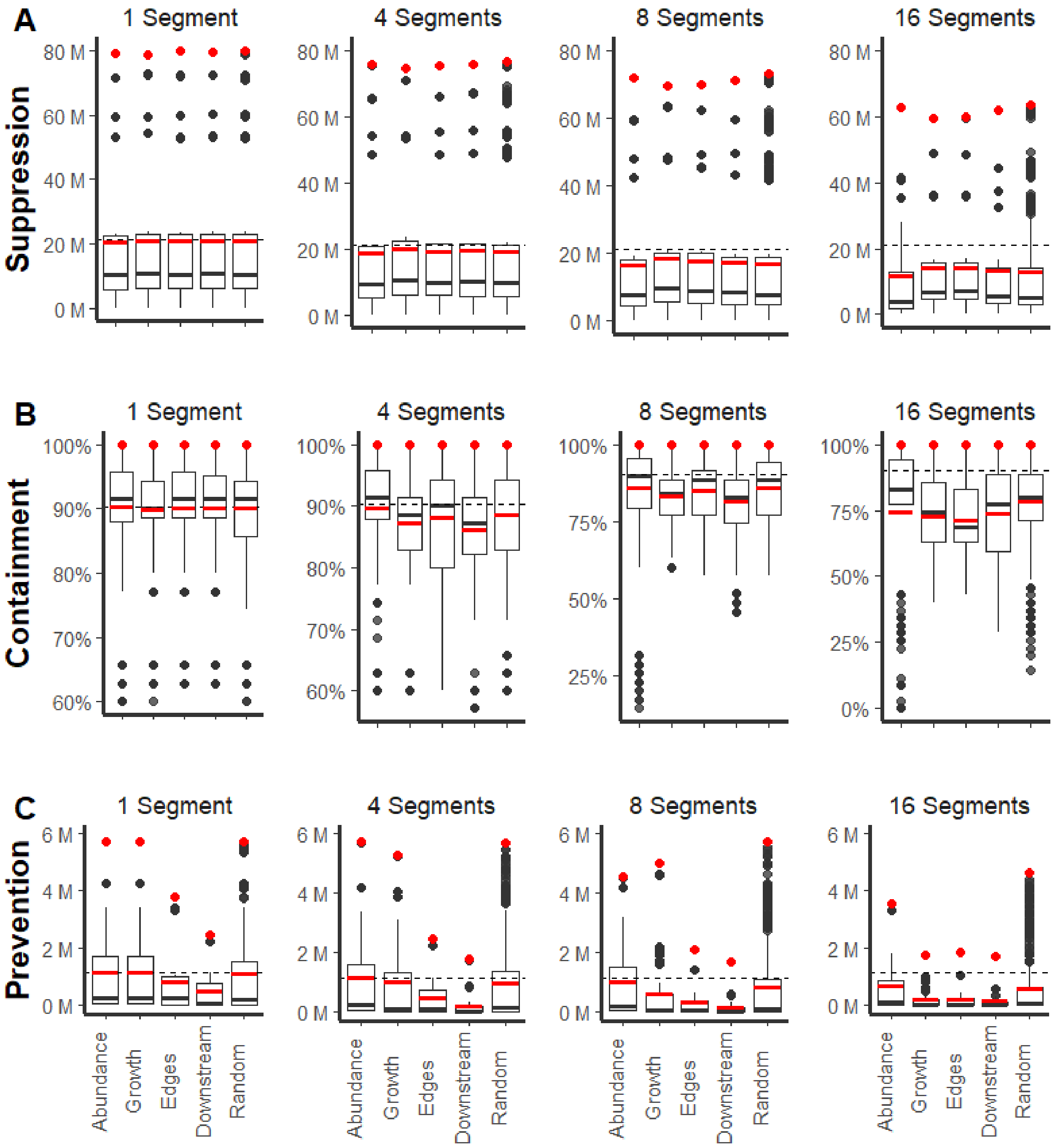

Figure 3.2 Boxplots displaying the performance of each crayfish removal alternative, except No Removals, across all parameter sets and simulations for each objective, A) Suppression: final total crayfish abundance (millions), B) Containment: percent invaded, and C) Prevention: total crayfish in the Columbia River (millions). The horizontal black dotted line represents the expected value outcome under No Removals. In each boxplot, the red line is the mean, the black line is the median, and the red point is the maximum value. In subfigures A, B, and C, the facet plots represent 1, 4, 8, and 16 segments receiving removal effort. We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream, and Target Random as Random.

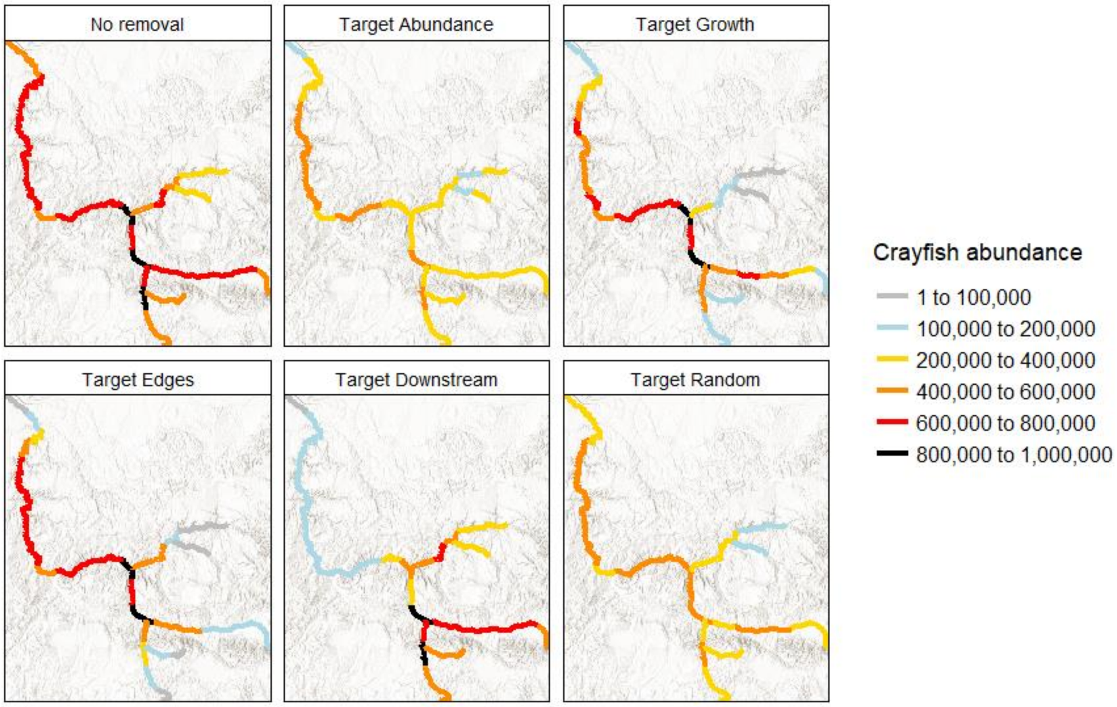

Figure 3.3 Segment-level total crayfish abundance after 7 years of management, averaged across simulations and parameter sets for each strategy (No removal, Target Abundance, Target Growth, Target Edges, Target Downstream, and Target Random) with 16 segments of removal effort. The colors show segment level abundance.

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3.9 APPENDIX 3

Table S3.1 Notations of parameters used in the model structure for rusty crayfish (see Table S3.2 for descriptions of indices).

Parameter	**Notation**
Abundance	$N_{i,j,k,a}$
Removal data	$Y_{i,j,k,a}$
Effective removal probability	p
Number of traps per segment	n^{traps}
Capture efficiency	θ
Population remaining after removal	$R_{i,j,a}$
Population available for dispersal	$D_{i,j,a}$
Leslie matrix	L_j
Monthly survival	φ_a
Fecundity rate	f_a
Fraction of mature females	m_a
Crayfish available to move after population growth	$D_{i,j,a}$
Probability of staying	m_{stay}
Proportion that stayed in the current segment due to temperature	$u_{i,j}$
Population that stayed in a segment *i*	$D^{\text{stay}}{}_{i,j,a}$
Population that moved downstream from segment *i*	$D^{\text{down}}{}_{i,j,a}$
Probability of moving downstream conditional on moving	m_{down}
Population that moved upstream from segment *i*	$D^{\text{up}}_{i,j,a}$
Population that moved to a different fork from segment *i*	$D^{\text{fork}}_{i,j,a}$
Population redistributed after movement occurred	$N^{\text{redistribute}}_{i,j,a}$

Table S3.2 Explanation of parameter indices used in the rusty crayfish study

Indices	**Notation**
Segment	i {1,..,I = 114}, h {1,...,35}
Month	j {1,...,J = 84}
Trap night	k {1,.., K = 10}
Age	a {0,1,2,3}

Table S3.3 Explanation of values and references for the model parameters for rusty crayfish. Each of the parameters were drawn from its respective distribution 20 times to create the 20 different parameter sets.

Parameter	**Value and Distribution**	**Distribution**	**Sources**
The capture probability, θ	The capture probability θ was informed by an author (JDO), which was a probability range between 0.1 and 0.5 that a single crayfish would be trapped within a 25m^2 area.	Uniform(0.1, 0.5)	Olden
monthly survival rate, φ_a	Mean values for φ_a were calculated using the mean monthly survival rates from Messager & Olden 2018.The mean, $\overline{\varphi_a}$, values for a = 0-3 were: 0.8101974, 0.9707145, 0.9356233, 0.7218038 and standard deviation of 0.1.	Normal($\overline{\varphi_a}$, 0.1)	**Messager & Olden 2018**
Fraction of mature females, m_a	Mean values for m_a were calculated using the fraction of mature females from Messager & Olden 2018. The mean values, $\overline{m_a}$, for a = 1-3 were: 0.1, 0.8, 0.9 and standard deviation of 0.1.	Normal($\overline{m_a}$, 0.1)	**Messager & Olden 2018**
Fecundity, f_a	The fecundity rates were expressed as a normal distribution using mean and standard deviations from Messager & Olden 2018. The mean, $\overline{f_a}$, values for a = 1-3 were: 80, 120, 150, the standard deviation values, sd_{f_a} , for a = 1-3 were: 10, 20, 40	$Normal(\overline{f_a}, sd_{f_a})$	**Messager & Olden 2018**
Probability of moving π	The original movement probability π was informed by Messager & Olden (0.85), and we created four additional probabilities to reflect uncertainty in this estimate to project high and low levels of movement. We changed the stationary probability (probability of staying), 1- π, by a 0.05 and 0.1 increase, and a 0.05 and 0.1 decrease in the stationary probability. The various π were: (0.15, 0.1, 0.05, 0.2, 0.25)	Each kernel was randomly drawn with equal probability	**Messager & Olden 2018**
Downstream movement,m_{down}	Moving downstream is more probable than moving upstream, m_{down} could be between 0.5 and 1	Uniform(0.5, 1)	**Messager & Olden 2018**

Table S3.4 Data used in the crayfish population model

Data:	Description	Source
Monthly fraction degree days for each segment that is < 6C (minimum thermal tolerance for movement, Hamr 1997), parameter $u_{i,j}$	If u_{ij} = 1 then all crayfish stay, if 0, then all undergo the dispersal process where some crayfish still stay in each segment -but not because of temperature	River segment temperature data was from **Messager & Olden 2018** We averaged the 2000-2017 temperature data to get average temperature for each month. However, that study expressed river segments at various lengths. So, we averaged the temperature across space to get segment level temperature data for our study (See details below on how we manipulated the temperature data in ArcGIS to clean the data).
Initial population abundance, $N_{i,1,1,a}$	See Figure S3.1 below	Olden 2016 survey

Parameter references:

Hamr, P. 1997. The potential for the commercial harvest of the exotic rusty crayfish (*Orconectes rusticus*). A feasibility study OW Crayfish Enterprises. Keene, Ontario.

Messager, M. L., & Olden, J. D. (2018). Individual-based models forecast the spread and inform the management of an emerging riverine invader. Diversity and Distributions, 24(12), 1816-1829.

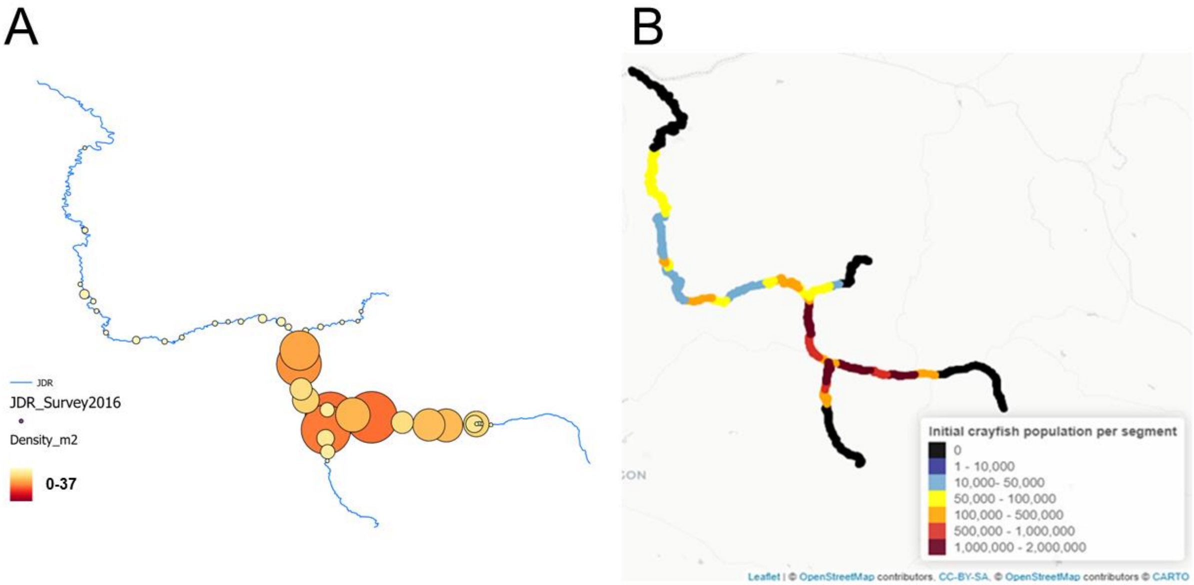

Figure S3.1 Initial population figures. A: 2016 crayfish density survey data. B: Initial population crayfish abundance in the model. Using data from the 2016 intensive crayfish survey.

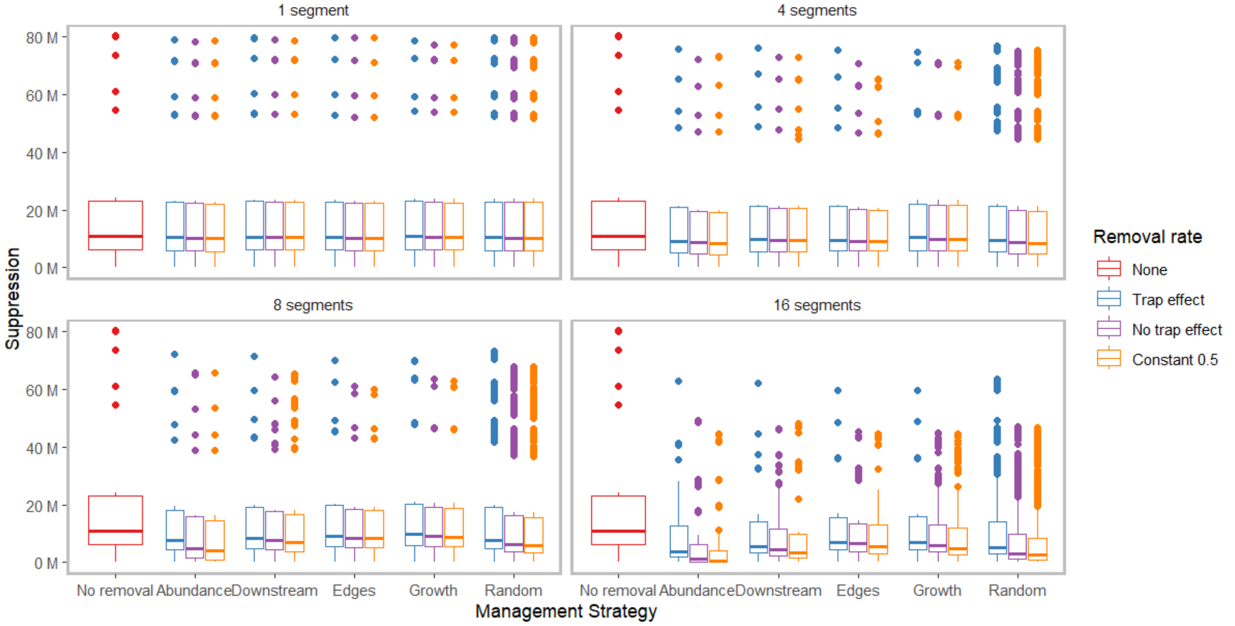

Figure S3.2 Box plots of the performance of the suppression objective, measured as final total crayfish abundance (in Millions). Each facet of the figure shows a different number of segments with removal effort, 1,4,8, or 16 segments. The colors depict the different effective removal scenarios, none (for no removal), trap effect (where n^{traps} = 2,000 and $\theta \sim$ Uniform(0.1, 0.5)), no trap effect (where n^{traps} = 8,000 and $\theta \sim$ Uniform(0.1, 0.5)), and a constant 0.5 (where n^{traps} = 2,000 and θ = 0.5). We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream, and Target Random as Random

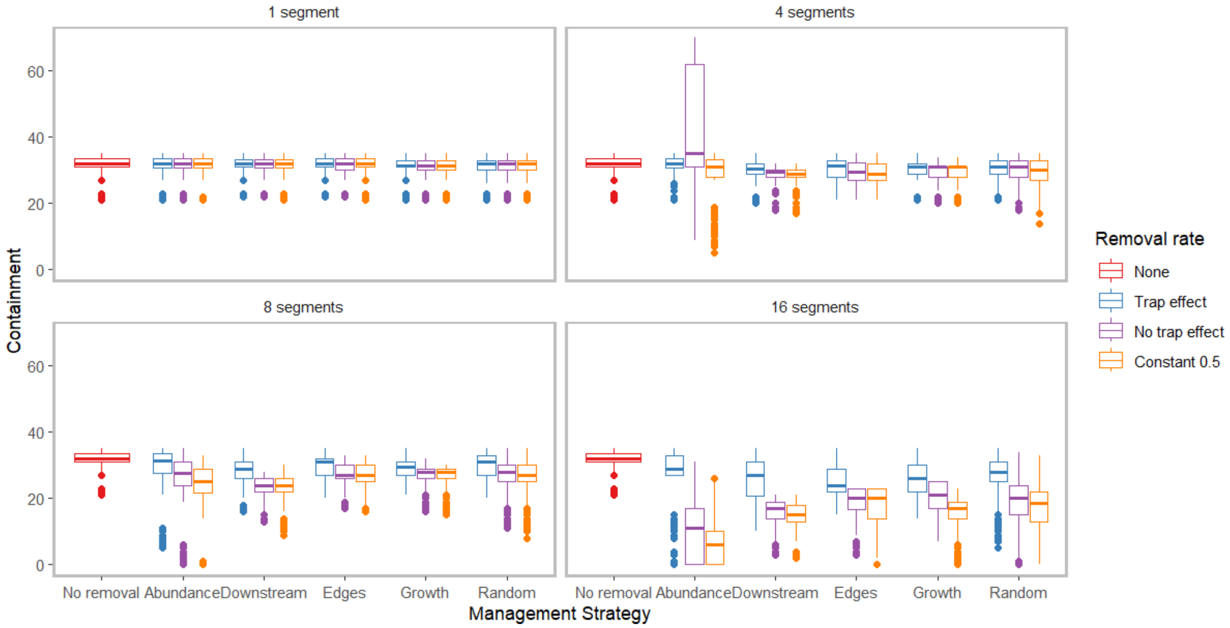

Figure S3.3 Box plots of the performance of the Containment objective, measured as percentage invaded. Each facet of the figure shows a different number of segments with removal effort, 1,4,8, or 16 segments. The colors depict the different effective removal probabilities, none (for no removal), trap effect (where n^{traps} = 2,000 and $\theta \sim$ Uniform(0.1, 0.5)), no trap effect (where n^{traps} = 8,000 and $\theta \sim$ Uniform(0.1, 0.5)), and a constant 0.5 (where n^{traps} = 2,000 and θ = 0.5). We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream, and Target Random as Random

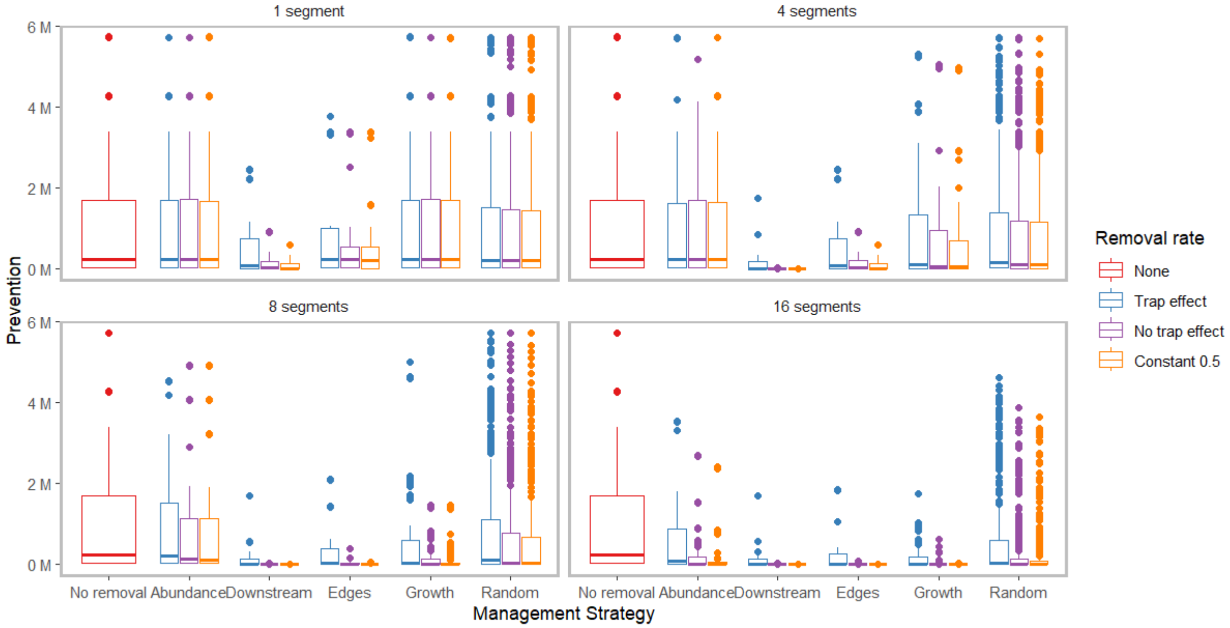

Figure S3.4 Box plots of the performance of the Prevention objective, measured as total crayfish that entered the Columbia River. Each facet of the figure shows a different number of segments managed, 1,4,8, or 16 segments. The colors depict the different effective removal scenarios, none (for no removal), trap effect (where n^{traps} = 2,000 and $\theta \sim$ Uniform(0.1, 0.5)), no trap effect (where n^{traps} = 8,000 and $\theta \sim$ Uniform(0.1, 0.5)), and a constant 0.5 (where n^{traps} = 2,000 and θ = 0.5). We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream, and Target Random as Random

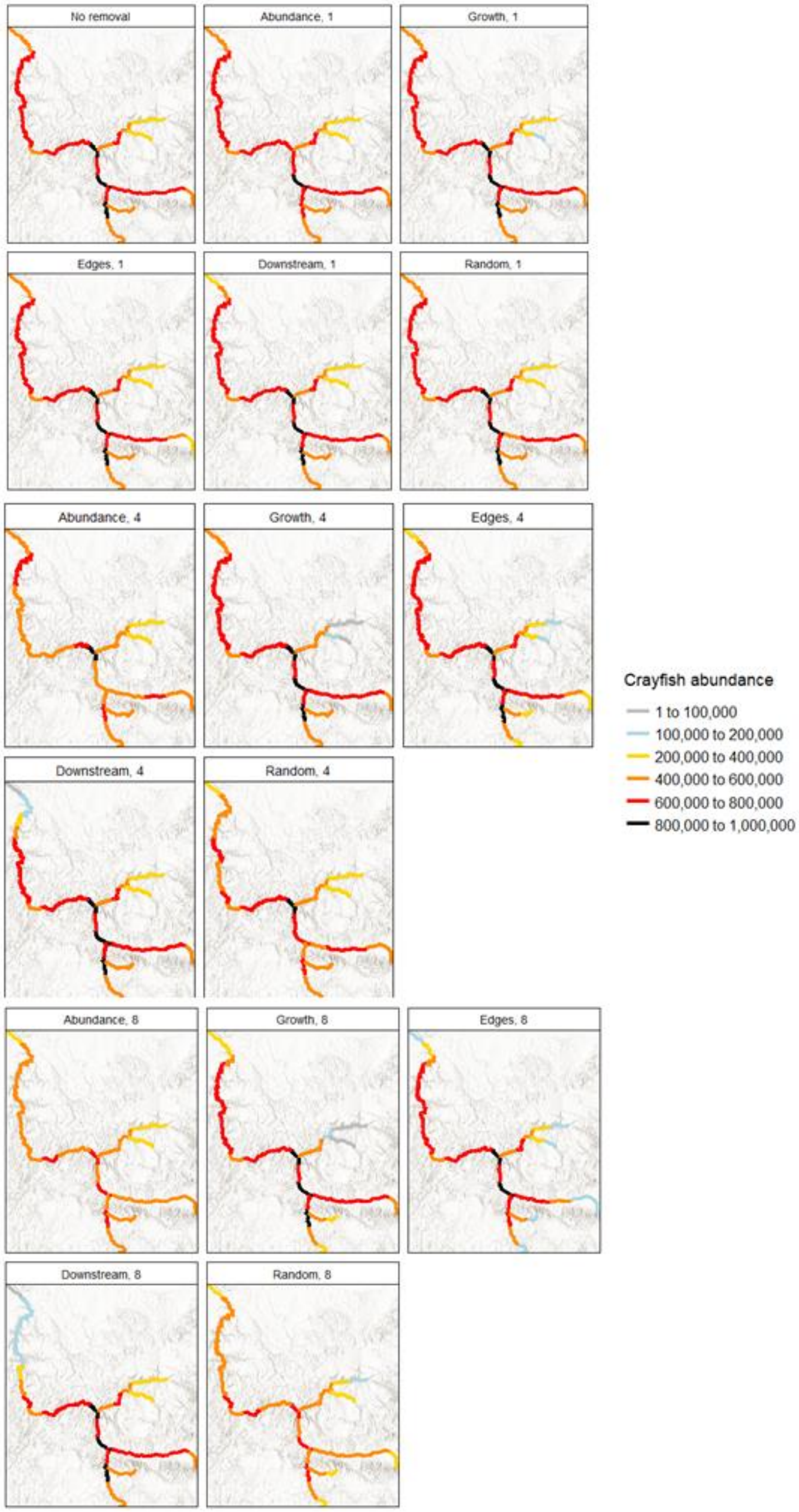

Figure S3.5 Segment level final crayfish abundance after 7 years of management, averaged across simulations and parameter sets for each alternative where 1, 4, and 8 segments managed. The colors show segment level abundance

Figure S3.6 Plots of total crayfish abundance through time. The colors depict the different effective removal scenarios: none (for no removal), trap effect (where $n^{traps} = 2{,}000$ and $\theta \sim \text{Uniform}(0.1,\ 0.5)$), no trap effect (where $n^{traps} = 8{,}000$ and $\theta \sim \text{Uniform}(0.1,\ 0.5)$), and a constant 0.5 (where $n^{traps} = 2{,}000$ and $\theta = 0.5$). Grey bars are the lower and upper 90% values) We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream, and Target Random as Random

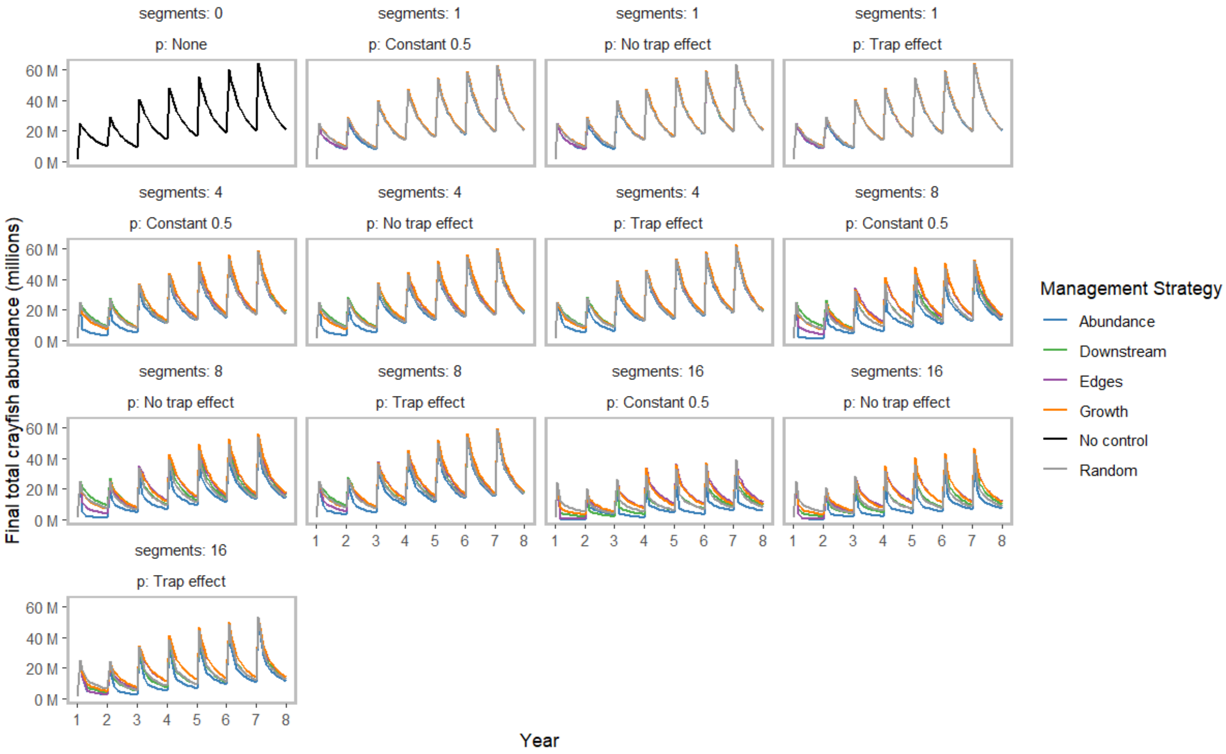

Figure S3.7 Plots of average total crayfish abundance through time, averaged across parameter sets and simulations. The colors depict the different management strategies. The facet plots represent different numbers of segments of removal effort and effective removal scenarios: none (for no removal), trap effect (where n^{traps} = 2,000 and $\theta \sim$ Uniform(0.1, 0.5)), no trap effect (where n^{traps} = 8,000 and $\theta \sim$ Uniform(0.1, 0.5)), and a constant 0.5 (where n^{traps} = 2,000 and $\theta = 0.5$). We express strategies Target Abundance as Abundance, Target Growth as Growth, Target Edges as Edges, Target Downstream as Downstream, and Target Random as Random

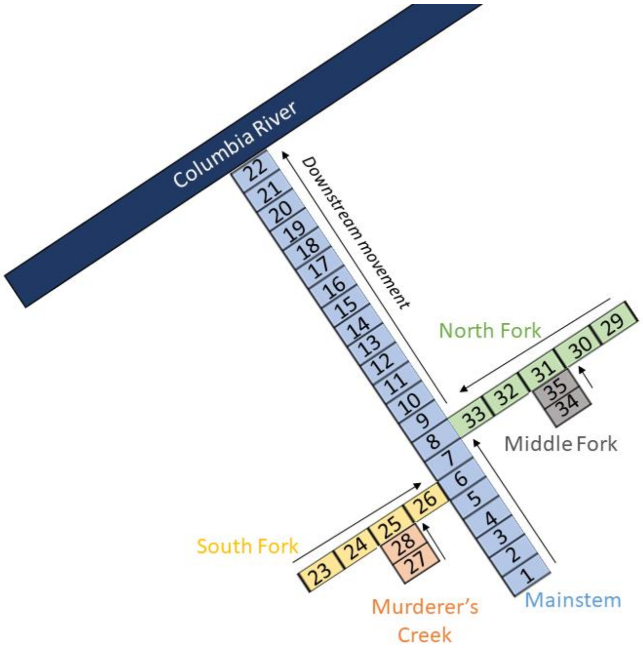

Figure S3.8 Graphical representation of all 35 segments in this study. The arrows depict the direction of downstream river flow. The colors signify the different forks of the John Day River

CHAPTER 4. BALANCING RESOURCES TOWARDS MONITORING AND CONTROL FOR AN AQUATIC INVASIVE PLANT ADAPTIVE MANAGEMENT PROGRAM

Publication history: This study was co-authored with Julian D. Olden and Sarah J. Converse. At the time this dissertation was published, this chapter was not in review with a journal.

4.1 ABSTRACT

Optimally allocating resources towards monitoring and management can improve the effectiveness of invasive species management. We developed a management strategy evaluation framework for adaptive management of invasive flowering rush (*Butomus umbellatus*) in the Columbia River, USA, to compare outcomes of different monitoring and management alternatives. We compared alternatives under two invasion conditions: a well-established invasion and an emerging invasion. Generally, we found that prioritizing monitoring and management in highly invaded areas (*High invasion* prioritization) resulted in better management outcomes for an emerging invasion, whereas it was beneficial to allocate effort at spatially fixed areas (*Linear* prioritization) for a well-established invasion. In addition, management outcomes improved under the emerging invasion scenario with the addition of community science data, which helped identify locations where management could be focused. Across both invasion conditions, we found management outcomes improved when more resources were allocated towards removal effort than monitoring effort. In addition, we found that actions that led to the best management outcomes often did not produce the most accurate and precise estimates of parameters describing system function. The modeling framework we present can be adapted to a variety of invasive species management contexts in which ongoing monitoring allows management strategies to be updated over time.

4.2 INTRODUCTION

Species invasions are increasing rapidly (Sardain et al. 2019; Seebens et al. 2021), and the associated ecological, environmental, and economic damage is growing (Doherty et al., 2016; Diagne et al., 2021). Natural resource managers have opportunities to help thwart the negative consequences of invasions by implementing management to suppress or eradicate invasive species. However, given that effective invasive species management approaches are context specific, questions regarding how best to prevent and control invasive species in particular situations are ubiquitous (van Poorten and Beck 2020). Despite this, there is emerging consensus that an accurate understanding of invasive species population dynamics, including population growth and spread rates, is vital for making decisions regarding optimal allocation of management resources (Crystal-Ornelas and Lockwood 2020).

Ecologists have long struggled with understanding demographic processes in invasive populations. Much of this challenge can be attributed to limited field surveys during the invasion process and the inability to depend on demographic data from species' native ranges (Liu et al. 2011; Franklin et al. 2017). However, novel insights into invasive population dynamics can be gained from spatially structured monitoring data (van Rees et al., 2022). For instance, occupancy, colonization, and extinction can be inferred from detection/non-detection data (MacKenzie et al. 2003), abundance can be estimated with count (Royle and Nichols 2003) and removal data (Link et al. 2018), and survival and movement rates can be measured with radio-telemetry and mark-recapture data (Anderson et al., 2022).

Monitoring data can be used to inform initial decisions and to update management based on information gained from the data in an iterative process known as adaptive management (Walters 1986; Nichols and Williams, 2006). Adaptive management involves using models to make predictions regarding which actions are likely to result in the best outcomes in terms of management objectives, acting based on these predictions, and then updating models of the system through the integration of monitoring data, such that future decisions are better informed by data. Monitoring data allows decision makers to manage simultaneous with learning, thereby improving performance on management objectives over the long term (Lyons et al., 2008; Pepin et al. 2020). Despite the importance of monitoring data for adaptive management, data collection is often costly, time intensive, and involves the arduous task of balancing limited resources allocated for monitoring versus management (Hauser and McCarthy 2009; Bogich et al., 2008; Baker et al., 2017).

Advancing methods to determine optimal prioritization of resources towards monitoring and management is now considered paramount in invasive biology (Koch et al., 2020; Yemshanov et al., 2020; Nguyen et al., 2023). Numerous studies have explored the question of how to optimally balance surveillance and control efforts across space and time (Hauser and McCarthy 2009; Regan et al. 2011; Rout et al. 2017). For example, Bogich et al. (2008) determined optimal trap densities to monitor and manage invasive spongy moths (*Lymantria dispair*) in the United States and found that a proactive monitoring program alongside removal was more cost effective than a post-eradication monitoring program. In another example, Rout et al. (2014) developed a modeling framework to determine allocation of management and surveillance for invasive black rats (*Rattus rattus*) in Australia and showed that it was better to manage under uncertainty regarding the presence of rats than to spend substantial resources towards confirming the presence of rats.

Past investigations have largely considered the question of how one decision-making entity can optimally monitor and manage an invasive species. However, for a given invasive species, there are often many data collection programs administered by different agencies and the public (Crall et al., 2006; Graham et al. 2007; Crall et al., 2010). Community science programs in particular offer a cost-effective approach for surveillance of invasive species (Larson et al., 2020). For instance, natural resource agencies who are actively controlling invasive species could collect some monitoring data but also rely on community scientists to search for a species (e.g., Sipe et al. 2023). By using data integration techniques, it may be possible to make more efficient and effective use of various data streams to estimate key demographic parameters (Zipkin and Saunders, 2018; Fletcher et al., 2019; Isaac et al., 2020) resulting in more accurate and precise parameter estimates (Dorazio 2014; Doser et al. 2022) and allowing inference across larger spatial extents (Zipkin et. al., 2021). In short, data integration has the potential to be a powerful tool for invasive species management where several monitoring data streams can be used to jointly inform key parameters (Baker & Bode, 2021; Zipkin et al. 2017).

Data integration for invasive species management has the potential to merge various data sources, such as removal data (i.e., individuals removed from an area), count data, and detection/non-detection data (e.g., eDNA). For invasions covering a large spatial extent or where management and monitoring does not give rise to discrete individual counts, detection/non-detection data and occupancy modeling can serve as a proxy for the abundance of invasive species (MacKenzie et al., 2002). In invasive plant monitoring, detection/non-detection data is used less than methods such as cover estimation and point intercept methods (Elzinga et al., 2001), though it offers a cost-effective approach to understand plant invasion (Middleton and Vining 2022; Al-Chokhachy et al. 2013). Detection/non-detection data can be used to estimate whether an area is occupied (invaded) or unoccupied by an invasive plant. More detailed data can also be collected, allowing for modeling of additional states, such as invaded, occupied at low density, or occupied at high density (i.e., multi state detection/non-detection data; MacKenzie et al., 2009). Using data integration to combine multiple types of data could enhance our understanding of invasions, identify new invasions, and inform the management of invasions.

Here, we focus on the problem of invasive flowering rush (*Butomus umbellatus*) at its leading edge of invasion in the Columbia River, USA, as a case study. Invasive flowering rush was introduced to North America in 1897 as an ornamental plant for water gardens in Montreal, Canada. It was found in the Snake River, a major tributary of the Columbia River, in 1949 (Anderson et al., 1974; Madsen et al. 2016). Flowering rush is a significant concern in the Columbia River watershed because it can greatly alter ecosystems through sediment accretion, rapidly disperse, colonize, and produce dense stands of emergent and submerged growth that displace native vegetation and can provide habitat for invasive predator fish species that impact salmon populations and cause negative food web consequences (Cooper et al. 2008; Gunderson et al. 2016). Since flowering rush is currently expanding in the Columbia River, there is a pressing need to evaluate alternative management strategies for control (Columbia Basin CWMA 2019).

We developed spatial simulations to explore optimal adaptive approaches for invasive flowering rush control, including different monitoring strategies, allowing us to estimate whether management outcomes improve as a function of the amount or type (e.g., single- or multi-state detection/non-detection data) or monitoring data. We simulated population dynamics and management outcomes for a fixed time under various spatial allocation strategies, and for different investment conditions (i.e., budget) and invasion conditions. The results from this study point to optimal management alternatives that are specific to the invasion condition. In addition to potentially informing flowering rush management and monitoring, the modeling framework presented here is readily applicable to a variety of invasive species management contexts for which monitoring data make it possible to iteratively update management through time.

4.3 METHODS

4.3.1 MANAGEMENT CONTEXT

Resource managers in the Columbia River Basin aim to manage flowering rush populations to reduce the negative ecological and economic effects (Columbia Basin CWMA 2019). For the past decade, flowering rush has been established in Washington State along the Columbia River and Yakima River. The current leading edge of flowering rush invasion in the mainstem of the Columbia River is projected to be downstream of McNary Dam (Columbia Basin CWMA 2019). Therefore, this study focused on simulating removal and monitoring of flowering rush between McNary Dam and 40 miles downstream of the dam (Figure 4.1).

Guided by conversations with natural resource managers in the area, we assumed a management objective of minimizing the overall level of infestation of flowering rush across the study area; we refer to this as the “suppression” objective. Natural resource managers are often concerned with the cost of conducting monitoring and management. We therefore developed alternatives involving different investment levels, defined by a fixed number of available labor hours per week (labor is the primary contributor to management costs).

We simulated management actions conducted at 1-mile long river management units, henceforth referred to as “segments”. Following current management practices, we assumed that monitoring and management (via hand removals) would be conducted at the end of the growing season, for a four-week period starting August 1st, and repeated annually for a total of 10 years. We envisioned a setup in which, over this four-week period, segments along the river would be visited and some effort would be put into searching for the plant in that segment. Two independent searchers would search for a fixed number of hours, allowing for the estimation of detection probability in an occupancy framework. If the plant was found, a fixed number of hours of effort would be put into removing the plant. Then, the next segment would be visited, and so on, until the total effort available for the week was expended (or until all segments had been visited and searched).

The management and monitoring alternatives we developed and simulated were a function of four key elements: (1) spatial priority, referring to the locations of segments that were prioritized for monitoring and management; (2) target detection and eradication probabilities, referring to targeted probabilities of flowering rush detection and eradication by segment; (3) investment, referring to the hours of labor per week deployed to monitor and manage flowering rush; and (4) types of monitoring data gathered (Table 4.1).

First, spatial priority describes the order in which segments were “visited” in the simulation during the four-week removal period each year. We developed three prioritization approaches: *Linear*, *High invasion*, and *Epicenter*. The *Linear* approach prioritized segments according to location, starting from the most upstream segment closest to the McNary Dam. The *High invasion* approach prioritized segments according to the predicted state of flowering rush invasion. Under *High invasion*, we organized the segments into three bins according to estimated invasion state and visited segments in the most invaded bin first, with segments ordered within each bin to minimize travel distance. Under *Epicenter*, we prioritized segments by distance from the estimated epicenter of invasion (i.e., the segment with the highest estimated invasion state), with segments closest to the epicenter visited first. In each of the alternatives we simulated, we assumed that the *Linear* prioritization would be applied during the first three years of management, to allow for learning, as described below, and after that, either the *Linear* prioritization would be continued, or the *High invasion* or *Epicenter* prioritization would be implemented, depending on the particular management alternative. Under the *High invasion* and *Epicenter* prioritizations, the prioritization list was updated annually based on predicted system state (see 4.3.3 *management strategy evaluation*).

Second, target detection and eradication probabilities refer to target probabilities of detection and eradication for flowering rush at visited segments. We assumed that detection and eradication probabilities were a function of the number of hours spent searching for and removing flowering rush (see 4.3.4 *modeling framework*). Since flowering rush is a relatively new invasive species in the Columbia River system, there is substantial uncertainty regarding the amount of time that it takes to achieve particular detection and eradication probabilities. Therefore, to meet targets, managers must first learn about the relationship between detection probability at a segment and the number of hours spent searching for flowering rush in that segment, and the relationship between eradication probability at a segment and the number of hours spent removing the plant in that segment. Therefore, during the first three years of simulated management, when *Linear* prioritization was conducted, we assigned random search and removal hours from a Uniform(0.1, 10) distribution, which allowed us to estimate the relationships between effort and probabilities of detection and eradication. Then, after three years of management, we found the number of search hours and removal hours that allowed us to achieve each of the six sets of the target detection, p, and eradication, ϵ, probabilities (Table 4.1). We assumed goal detection probabilities were either 0.25, 0.5, and 0.75 and goal eradication probabilities were 0.5 and 0.75. Due to the difficulty of detecting and achieving eradication of flowering rush (Columbia Basin CWMA 2019), we did not evaluate probabilities beyond 0.75.

Since we used a multi-state occupancy model (see 4.3.4 *modeling framework*) that included invasion states of no invasion, low invasion, and high invasion, we solved for the hours required to achieve detection and eradication for both the low and high states, and we took the average of the required monitoring and removal hours across these states.

Third, investment refers to different budget levels, expressed as the maximum labor hours available each week: 20, 40, and 60 hours. Budget was negatively impacted by hours spent searching for and removing flowering rush, and the hours spent traveling between segments. We assumed that the boats with agency workers would travel at a speed of 10 knots (18.5 km/hour) between segments, and adjacent segments were assumed to be 1 mile apart. Prior to the first week of removal, the spatial priority list was made, and segments were visited in that order. Visitation ended each week if all the segments were visited or if the budget was exhausted. If the budget was exhausted, the locations for monitoring and removal at the start of the next week would begin at the next segment on the spatial priority list.

Fourth, the types of monitoring data gathered included either (1) only the data collected during detection and management, or (2) included the data collected during detection and management as well as additional community science data (see 4.3.2 *data collection procedure*). We aimed to determine whether the addition of community science data would help achieve the management objective by contributing to the ability to predict invasion state of segments. This was tested through the integration of community science data on alternatives that included *High invasion* and *Epicenter* prioritization. We only evaluated the value of community science data for the detection and eradication targets that best achieved the management objective on average for each investment level (Table 4.1). Once the target probabilities were identified, we simulated those alternatives with the addition of community science data to determine if community science data could produce better outcomes.

In total we evaluated 54 management alternatives in which the agency was collecting all of the monitoring data (3 spatial prioritizations, 6 sets of target probabilities (for detection and eradication), and 3 investment levels) and we evaluated 6 additional alternatives with the addition of citizen science data (2 spatial priortizations, 1 set of target probabilities, and 3 investment levels). We also simulated a No-removals alternative where no monitoring or removal of flowering rush occurred (Table 4.1).

4.3.2 DATA COLLECTION PROCEDURE

In the process of searching segments for flowering rush, we assumed that two agency observers independently collected data (i.e., resulting in replicate observations at each visited segment). We assumed that the observers had equal training on detecting flowering rush (i.e., no variation in detection by observer) and both independently evaluated each river segment for the detection of flowering rush in three states: absent, low invasion (≤ 10 clusters of plants), or high invasion (>10 clusters of plants). Then, after the specified search time, the two observers compared their observations. If at least one observer detected an invasion (either low or high invasion), the two observers spent a specified amount of time removing flowering rush. The predefined times spent searching and removing flowering rush were calculated from the target detection and removal probabilities for each alternative (Table 4.1). Therefore, we assumed that all the management alternatives – other than the no removal alternative – generated monitoring data in addition to removing flowering rush (Table 4.1).

The volunteers collecting community science data were assumed to go out in pairs (i.e., to have two replicate observations) and independently collected detection/non-detection (i.e., single-state) data on flowering rush in each visited segment. The two volunteers were assumed to have the same level of knowledge on flowering rush, i.e., no variability in detection probability by observer. We assume that community science observers do not remove flowering rush if detected. We simulated volunteers visiting 8 randomly selected segments each week, where the locations were selected without knowledge of where the management agency was also collecting data and removing flowering rush. The identity of the segments was kept constant across alternatives to facilitate comparisons. At the end of the four-week data collection period, we integrated those data into the estimation process (see 4.3.4 *modeling framework*). We assumed that the time volunteers spent collecting data was not a factor in the budget calculations for the agency.

4.3.3 MANAGEMENT STRATEGY EVALUATION

Adaptive management may be applied in cases involving iterative decisions and when monitoring data are collected to help reduce critical uncertainties regarding system function (Walters 1986; Williams 2011). Hence, we developed an adaptive management framework for flowering rush. We used a Management Strategy Evaluation (MSE), sometimes referred to as "forward simulation" approach, to simulate the process of managing and learning (Punt et al. 2016).

The process of MSE involves four main steps (Siple et al. 2021, Figure 4.2). First, under multiple alternative management strategies, simulate realistic population dynamics and management of the species using an operating model based on distributions of parameter values representing the current state of knowledge; second, gather simulated monitoring data from the operating model; third, analyze the monitoring data using an estimation model and potentially use informed priors generated through Bayesian updating, then predict population dynamics; and fourth, based on the estimated model predictions, update the allocation of management effort, which subsequently influences the realistic population dynamics of the species in the operating model (Figure 4.2). Hence, this process involves the use of two models. One model (the operating model) simulates “reality,” or what is truly happening in the simulated system of interest, while the other model (the estimation model) simulates what a manager would have available to them to inform their decision making at a given point in time. The results of the estimation model (e.g., level of invasion status) will be used to determine management actions, which consecutively affects the operating model, which projects population dynamics and management outcomes. In the *High invasion* and *Epicenter* prioritization actions, the segment prioritization lists are updated based on information. This does not occur under *Linear* prioritization since the segment priority list is fixed. However, the Bayesian updating process occurs in all three types of prioritizations, as learning in the first three years is used to determine the amount of effort to expend on detection and management, and parameters (e.g., invasion growth and spread rates) are updated throughout to improve predictions of system function, allowing for more effective prediction of system state.

4.3.4 MODELING FRAMEWORK

A dynamic multi-state occupancy model was developed for this study (MacKenzie et al. 2009, Kéry and Royle 2020). Dynamic multi-state occupancy models have previously been used to model invasive plants and other species (Bled et al 2011; Yackulic et al. 2012; Pepin et al. 2019). Both the operating and estimation models were dynamic multi-state occupancy models, except the operating model simulated the true latent population process using the true latent parameter values, while the estimation model relied on the simulated data to estimate parameters.

An extension of the estimation model was developed to allow for the integration of community science data.

In the dynamic multi-state occupancy model, each river segment was in one of three invasion states at each point in time: no invasion, referred to as empty (denoted as $E = 0$), low invasion ($L = 1$) which represented ≤ 10 plant clusters, and high invasion ($H = 2$) which represented > 10 plant clusters, together invaded states L and H are sometimes denoted as the collective occupied states, S. We indexed segments with i ($1, 2, ..., I = 40$), removal weeks with w ($1, 2, ..., W = 5$), and years with y ($1, 2, \ldots, Y = 10$). The timing of events in this model is important due to the seasonal growth of flowering rush, and because monitoring and removal only occur during four weeks a year. Therefore, our modeling framework was divided into two periods. The first period was developed for the four weeks when monitoring and removal occurred, known as the “data weeks.” The second period described the 48-week period between monitoring and removal, the “non-data weeks” (Figure 4.3A).

During the “data weeks” at the outset of the study (week 1 year 1, in August) and given the initial state of the river (see 4.3.5 *simulation procedure* for description of initial invasion states), the agency observes/removes flowering rush and depending on the alternative, the community scientist volunteers collect data. Then at the end of week 1, state transitions occur. For three more weeks, we generate data, simulate removals and state transitions, and model state transitions until the start of week 5, during which no removals occur. Throughout this entire four-week period, we assume that population change does not occur other than through removals, because by late summer, the vegetation of flowering rush has reached its maximum value for the year and remains dormant until it senesces during the winter months (Columbia

Basin CWMA 2019). Thus, a segment in state E = 0 in week 1 will remain in E = 0 throughout the "data weeks" period.

We modeled the state transition (for both agency and community science data) between weeks as:

$$z_{i,w+1,y} | z_{i,w,y} \sim \text{Categorical}\left(\boldsymbol{\Phi}^{D}{}_{i,w,y}\right) \quad , (1)$$

where $z_{i,w,y}$ is the invasion state at segment i, in week w (w = 2 to 5), during year y (y = 1 to 10), which is either E, L, or H (with numerical values of 1,2, or 3). The transition probability matrix, $\boldsymbol{\Phi}^{D}{}_{i,w,y}$, describes the probability of moving from $z_{i,w,y}$ in week w to state $z_{i,w+1,y}$ in week w + 1, where D denotes the "data weeks" period. $\boldsymbol{\Phi}^{D}{}_{i,w,y}$ was described as:

$$\boldsymbol{\Phi}^{D}{}_{i,w,y} = \begin{array}{c c} & \begin{array}{ccc} E & L & H \end{array} \\ \begin{array}{c} E \\ L \\ H \end{array} & \begin{pmatrix} 1 & 0 & 0 \\ \epsilon_{i,w,y}{}^{L} & 1 - \epsilon_{i,w,y}{}^{L} & 0 \\ \epsilon_{i,w,y}{}^{H} & \left(1 - \epsilon_{i,w,y}{}^{H}\right)\left(1 - \varphi_{i,w,y}{}^{H}\right) & \left(1 - \epsilon_{i,w,y}{}^{H}\right)\varphi_{i,w,y}{}^{H} \end{pmatrix} \end{array} \quad .(2)$$

We modeled eradication probability, or the transition probability from invaded state S (L or H) to the empty state E as:

$$\text{logit}\left(\epsilon_{i,w,y}{}^{S}\right) = \beta_0{}^{\epsilon^{S}} + \beta_1{}^{\epsilon^{S}} X_{i,w,y} \quad , (3)$$

where $\beta_0{}^{\epsilon^{S}}$ is logit-scale state-specific eradication probability when no removal effort is conducted, $\beta_1{}^{\epsilon^{S}}$ is the state-specific effect of per-hour removal effort on eradication probability, and $X_{i,w,y}$ is the removal effort (hours) expended at segment i during week w and year y. We modeled the probability of remaining in state H as:

$$\text{logit}\left(\varphi_{i,w,y}{}^{H}\right) = \beta_0{}^{\varphi^{H}} + \beta_1{}^{\varphi^{H}} X_{i,w,y} \quad , (4)$$

where ${\beta_0}^{\varphi^H}$ is the logit-scale probability of staying in state H (i.e., not transitioning to L) given no removal effort, and ${\beta_1}^{\varphi^S}$ is the effect of per-hour removal effort on this probability (such that ${\beta_1}^{\varphi^S}$ is expected to be negative).

Next, we describe the observation process (i.e., imperfect detection of invasion states) for both agency and citizen science data streams during the "data weeks" period. Agency multi-state detection/non-detection data, denoted as ${y^A}_{i,w,y}$, can take values of 0 for non-detection, 1 for detecting the state as L, and 2 for detecting the state as H. We describe these data with a categorical distribution:

$$ {y^A}_{i,w,y} \mid z_{i,w,y} \sim \text{Categorical}\left({\boldsymbol{P}^A}_{i,w,y}\right) \quad , (5)$$

where ${\boldsymbol{P}^A}_{i,w,y}$ is the detection probability matrix for the agency data,

$$\begin{array}{c} \\ E \\ L \\ H \end{array} \begin{array}{c} \begin{array}{ccc} 0 & 1 & 2 \end{array} \\ \begin{pmatrix} 1 & 0 & 0 \\ 1 - {p^{L,A}}_{i,w,y} & {p^{L,A}}_{i,w,y} & 0 \\ 1 - {p^{H,A}}_{i,w,y} & {p^{H,A}}_{i,w,y}(1-\delta) & {p^{H,A}}_{i,w,y}\,\delta \end{pmatrix} \end{array} \quad , (6)$$

We defined the agency's detection probability of invaded states S as:

$$ \text{logit}\left({p_{i,w,y}}^{S,A}\right) = {\beta_0}^{p^{S,A}} + {\beta_1}^{p^{S,A}} \log\left(M^A_{i,w,y}\right) \quad , (7)$$

where ${\beta_0}^{p^{S,A}}$ is the state-specific (L and H invasion states) logit-scale detection probability when search effort is zero. Here, we assumed a logarithmic relationship between hours spent monitoring and detection probability. Hence, ${\beta_1}^{p^{S,A}}$ is the state-specific effect of log(search hours), i.e., $\log\left(M^A_{i,w,y}\right)$, on detection probability. In row 3 of the detection probability matrix, δ is the probability of observing the high state given the species has been detected and the true state is high.

Single state detection/non-detection community science data, denoted as ${y^C}_{i,w,y}$, can take values of 0 for non-detection and 1 for detection, and are modeled as:

$$ {y^C}_{i,w,y} \mid z_{i,w,y} \sim \text{Categorical}\left({\boldsymbol{P}^C}_{i,w,y}\right) \qquad , (8)$$

where ${\boldsymbol{P}^C}_{i,w,y}$ is the detection probability matrix for the community science data:

$$\begin{array}{cc} & \begin{array}{cc} 0 & 1 \end{array} \\ \begin{array}{c} E \\ L \\ H \end{array} & \begin{pmatrix} 1 & 0 \\ 1 - {p_{i,w,y}}^{L,C} & {p_{i,w,y}}^{L,C} \\ 1 - {p_{i,w,y}}^{H,C} & {p_{i,w,y}}^{H,C} \end{pmatrix} \end{array} \qquad . (9)$$

We assumed the agency and community scientists had different detection probabilities. Hence, the detection probability for community science data if in invaded state *S* (*L* or *H*) was modeled as:

$$\text{logit}\left({p_{i,w,y}}^{S,C}\right) = {\beta_0}^{p\,S,C} + {\beta_1}^{p\,S,C} \log\left(M^C_{i,w,y}\right) \qquad , (10)$$

where ${\beta_0}^{p\,S,C}$ is the logit-scale detection probability from community science sampling when search effort is zero and ${\beta_1}^{p\,S,C}$ is the effect of log(hours), i.e., $\log\left(M^C_{i,w,y}\right)$, on detection for invasion states (*L* and *H*) for community science data. Since we assumed $M^C_{i,w,y}$ = 1 hour, the detection equation (Eq 10) simplified to $\text{logit}\left({p_{i,w,y}}^{S,C}\right) = {\beta_0}^{p\,S,C}$.

Next, we describe the “non-data weeks” period (48 weeks) wherein no data collection or removals occurred (between the start of week 5 and the beginning of week 1 in the next year). During this period, state transitions occurred, including, population growth during the seasonal growth period (Figure 4.3B). We modeled the transition of the invasion state from the end of data collection (*w* = 5, *y* – 1) in the previous year to the initiation of management and data collection in the current year (*w* = 1, *y*) as:

$$z_{i,1,y} \mid z_{i,5,y-1} \sim \text{Categorical}\left({\boldsymbol{\Phi}^B}_i\right) \qquad , (11)$$

where ${\boldsymbol{\Phi}^{B}}_{i}$ is the transition probability matrix during this period, where *B* denotes state transitions occurring between management periods (i.e., different from Eq 2):

$$\begin{array}{cccc} & E & L & H \\ \begin{matrix} E \\ L \\ H \end{matrix} & \multicolumn{3}{c}{\begin{pmatrix} 1-\gamma_i & \gamma_i(1-g) & \gamma_i g \\ {\epsilon_B}^L & 1-{\epsilon_B}^L & (1-{\epsilon_B}^L)(1-{\varphi_B}^L) \\ {\epsilon_B}^H & (1-{\epsilon_B}^H)(1-{\varphi_B}^H) & (1-{\epsilon_B}^H)(1-{\varphi_B}^H) \end{pmatrix}} \end{array} \quad , (12)$$

Invasion probability, the probability of segment *i* transitioning from state *E* to invaded state *S*, is modeled as:

$$\text{logit}(\gamma_i) \; = {\beta_0}^{\gamma} + {\beta_1}^{\gamma}\, h_i + {\beta_1}^{\gamma}\, N_{i,y-1} \quad , (13)$$

where ${\beta_0}^{\gamma}$ is the logit-scale eradication probability, ${\beta_1}^{\gamma}$ is the effect of segment habitat (h_i) on invasion, and ${\beta_2}^{\gamma}$ is the effect of the state of neighboring segments at week 5 in the previous year. The state of neighboring segments was expressed as:

$$N_{i,y-1} = \frac{\sum_{l\,\in\,n(i)} z_{l,5,y}}{|n(i)|} \quad ,(14)$$

where *n*(*i*) is the set of segments neighboring segment *i*, *l* is an element of that set, and |*n*(*i*)| describes the size of that set. Prior to simulation, h_i, representing whether a segment has habitat characteristics that promote establishment of flowering rush, with a value of 1 indicating ideal conditions, was drawn from a Uniform(0, 1) distribution and was held constant throughout all simulations. Parameter *g* in the transition matrix (Eq 12) the probability of transitioning to state *H* given colonization occurred. The eradication probability for invaded state *S* (*L* or *H*) during this period is ${\epsilon_B}^S$ and the probability of remaining in the invaded state is ${\varphi_B}^S$. Since there was no removal effort during this period, the eradication probability is equivalent to natural local extinction.

At the end of the "non-data weeks" period we have an estimate of the states at each segment in week 1 of the next management year (Eq 11). Using this information we generate our segment prioritization list (Table 4.1), and then we conduct the data collection and removal process for the following 4 weeks (Eq 1, 5, 8). We then project the 48 week "non-data weeks" transitions again (Eq 11) and continue this process (Figure 4.2).

For the estimation portion of our MSE (Figure 4.3), we defined the likelihood for alternatives with only agency data as: $\mathcal{L}^A\left(\boldsymbol{\Phi}^D{}_{i,w,y}, \boldsymbol{\Phi}^B{}_i, \boldsymbol{P}^A{}_{i,w+1,y} \middle| y^A{}_{i,w+1,y}\right)$, and for management alternatives with both agency and community science data we used an integrated model by defining a joint-likelihood: $\mathcal{L}^A\left(\boldsymbol{\Phi}^D{}_{i,w,y}, \boldsymbol{\Phi}^B{}_i, \boldsymbol{P}^A{}_{i,w+1,y} \middle| y^A{}_{i,w+1,y}\right) \times \mathcal{L}^C\left(\boldsymbol{\Phi}^D{}_{i,w,y}, \boldsymbol{\Phi}^B{}_i, \boldsymbol{P}^C{}_{i,w+1,y} \middle| y^C{}_{i,w+1,y}\right)$, where both $\boldsymbol{\Phi}^D{}_{i,w,y}$ and $\boldsymbol{\Phi}^B{}_i$ were shared between data streams.

4.3.5 SIMULATION PROCEDURE

Simulations were coded in R (version 4.3.1; R Core Team, 2023), with an embedded MCMC estimation process coded in JAGS (Plummer 2003). In the MCMC process, we used 20,000 iterations and a burn-in value of 2,000, for a posterior distribution of 18,000 iterations. We evaluated model convergence by confirming that model parameters had a Gelman-Rubin diagnostic value of less than 1.1. We additionally tested convergence by visually evaluating trace plots and density plots. Due to the need to estimate the transition between the weeks where data is collected and when data is not collected, we were required to first run our estimation model with two years of monitoring data (Figure S4.1). Then for subsequent years, we ran the estimation model for just a year at a time and updated our segment prioritization list based on estimated results.

We used both our knowledge of flowering rush and support from the literature to specify the statistical distributions for the parameters within the operating model for all alternatives. Table S4.1 depicts the statistical distributions, and we drew each parameter value from the respective distribution 200 times to create 200 unique parameter sets. Each alternative was run under each of the 200 parameter sets. These values represented “truth” and with each of the 200 parameter sets, the initial priors for every parameter in the first run of the estimation model (i.e., year 1 and year 2) was drawn from the distribution depicted in Table S4.1. After the first run of the estimation model (i.e., starting with year 3), all parameter priors were updated via Bayesian updating (Applestein et al. 2022).

In addition, since initial flowering rush biomass is an important factor for management outcomes (Carter et al. 2018), we tested all alternatives under two different invasion conditions in place at the beginning of the management simulation. Condition 1, “established invasion,” represented an invasion with the invasive plant distributed across multiple segments, and condition 2, “emerging invasion,” represented an invasion with the species concentrated in a few segments (Figure 4.4). In condition 1, 35% of the river was initially in state *E*, 37.5% was initially in state *L*, and 27.5% was initially in state *H*. In condition 2, 80% of the river was initially in state *E*, 10% was initially in state *L*, and 10% was initially in state *H*.

4.3.6 EVALUATION OF ALTERNATIVES

After running our estimation model with three years of data, we identified the search hours and removal hours to achieve the detection and eradication targets (Table 4.1, Figure S4.4).

Then, after an additional 7 years of running each management alternative, we evaluated our alternatives in terms of our management objective. We calculated performance on our objective, “suppression” (i.e., to minimize overall invasion), for each simulation as the average state of the system at week 5 after 10 years of management, $\sum_{i=1}^{I} \frac{z_{i,5,10}}{I}$ We found the expected value and the maximum value across parameter sets for each alternative. We then identified optimal alternatives based on two criteria: maximum expected value and mini-max. The alternative that maximizes expected value is the alternative with the best average outcome for an objective across simulations and is commonly used for risk neutral decision makers. The mini-max criterion selects the alternative that has the "best worst outcome" for the objective, which accounts for risk-aversion (Runge and Converse 2020). That is, since our management objective was to minimize invasion, we identified the maximum invasion outcome for each alternative across simulations, and then we identified the alternative with the minimum of these maximum values as the alternative that performed best on the mini-max criterion.

We were interested in the relationship between management performance and estimation performance and so we examined estimation performance under each alternative for various parameter values by calculating relative bias for each simulation, i , of a single management alternative, a:

$$\text{relative bias}_{i,a} = (\text{estimated value}_{i,a} - \text{true value}_{i,a}) \,/\, \text{true value}_{i,a} \qquad .(15)$$

We evaluated what we refer to as "state relative bias," which is the bias in the estimated state of each segment at the start of week 5 in each year; "p relative bias," which is the average relative bias across the estimated agency detection parameters, $\beta_0^{p^{L,A}}$, $\beta_1^{p^{L,A}}$, $\beta_0^{p^{H,A}}$, and $\beta_1^{p^{H,A}}$; and "ϵ relative bias," the average relative bias across the estimated eradication parameters $\beta_0^{\epsilon^L}$, $\beta_1^{\epsilon^L}$, $\beta_1^{\epsilon^H}$, and $\beta_1^{\epsilon^H}$.

4.4 RESULTS

Under an established invasion, *Linear* prioritization with a detection probability (p) of 0.5 and an eradication probability (ϵ) of 0.75 was always the optimal alternative for risk-neutral decision makers (i.e., based on the expected value criterion, Figure 4.5Ai, Table S4.2, Figure S4.2). However, under this invasion condition, the decision for risk-averse decision makers (i.e., based on the mini-max criterion) varied across investment levels (budget). For instance, *Linear* prioritization with target probabilities of 0.25 and 0.75, for p and ϵ respectively, was preferred for a 20-hour budget. For a 40-hour budget, *Linear* prioritization with target probabilities of 0.75 and 0.75 and *Epicenter* prioritization with target probabilities of 0.25 and 0.75 were equally preferred. Finally, for a 60-hour budget, *High invasion* prioritization with target probabilities of 0.75 and 0.75 was preferred (Figure 4.5Aii, Table S4.2, Figure S4.2). We also found that integrating community science data did not improve management performance for a well-established invasion (Figure 4.5A, Table 4.2).

However, we found that under an emerging invasion, integrating community science data under *High invasion* prioritization improved management outcomes with high investment (Figure 4.5B, Table S4.2, Figure S4.3). *High invasion* prioritization with target detection and eradication probabilities of 0.5 and 0.75, respectively (Figure 4.5Bi) and with the addition of community science data was preferred for a risk-neutral decision maker with a 60-hour budget. This alternative was also preferred for both 40- and 60-hour budgets for a risk-averse decision maker (Figure 4.5Bii).

Across both invasion conditions, alternatives with a detection probability (p) of 0.5 and an eradication probability (ϵ) of 0.75 generally performed the best (Figure 4.5, Table S4.2, Figure S4.2-Figure S4.3, see Figure S4.4 for the relationship between hours of effort and detection and eradication probabilities). In addition, across all alternatives except No removals, *Epicenter* prioritization generally performed the worst under both invasion conditions (Figure 4.5, Table S4.2; No removals consistently performed the worst overall (Table S4.2).

The relationship between management outcomes and statistical model performance was generally weak; the best performing alternative in a given situation (i.e., for a given management investment, invasion condition, and decision criterion) was rarely the alternative that demonstrated the lowest relative bias (Table S4.2). For instance, although *Linear* with target probabilities of 0.5 and 0.75, for p and ϵ respectively, was generally the best alternative in terms of expected value, this alternative did not have the lowest relative bias for invasion state, detection, or eradication parameter estimates (Table S4.2). In addition, although data integration does not always improve management outcomes, data integration did greatly improve detection parameter estimates, especially under *High invasion* prioritization (Table 4.2). Across all alternatives, we found that on average, our model overestimated the invasion state and underestimated eradication parameters (Table 4.2, Table S4.2).

Overall, we found that alternatives with *Linear* prioritization allowed the manager to visit the most segments with a relatively low average cumulative distance traveled each week (Figure 4.6). In addition, *Epicenter* prioritization had the largest weekly distance traveled compared to the other prioritizations (Figure 4.6). We also found that the weekly percentage of segments visited, and the weekly distance traveled, declined with increasing detection (p) and decreasing eradication (ϵ) (Figure 4.6). These results are consistent across both sets of invasion conditions (Figure S4.5).

Through time, we found that parameter estimates and spatially explicit invasion state estimates generally improved under some management alternatives due to our Bayesian updating process (Figure 4.7, Figure S4.6-Figure S4.11). For instance, relative bias on the detection parameters, p, generally improved through time for the *High invasion* prioritization for an established invasion (Figure 4.7).

4.5 DISCUSSION

We simulated monitoring and adaptive management of invasive flowering rush in the Columbia River, USA (Columbia Basin CWMA 2019). We analyzed different alternatives that were a function of management location prioritization (i.e., the order in which segments were visited), target detection and eradication probabilities, and investment level (budget hours). We also evaluated a subset of alternatives with the addition of community science data, which we had anticipated would help achieve management outcomes. We assessed all alternatives under two invasion conditions: an established invasion and an emerging invasion. From our management simulations, we identified four key lessons.

First, we found that alternatives involving learning alongside the integration of community science data were preferred when there was an emerging invasion and investment was high (i.e., *High invasion* prioritization, Figure 4.5, Table 4.2, Table S4.2). This outcome supports the value of both adaptive management and designing early detection and rapid response (EDRR) protocols, because learning about management effectiveness and the location of the invasion is important at the onset of an invasion (Rout et al., 2017; Reaser et al., 2020). For example, Sepulveda et al (2023) found that eDNA tools for detecting invasive brittle naiad (*Najas minor*) were useful in lake environments with high invasion potential compared to already invaded lakes. In another example, Marchessaux et al., (2023) suggested EDRR methods (e.g., integrating immediate overfishing measures) should be promptly used to mitigate invasive blue crab populations (*Callinectes sapudus* and *Portunus segnis)* from establishing in the Mediterranean Sea.

Second, for established invasions, and in contrast to emerging invasions, the value of adaptive management and data integration was low (Figure 4.5A, Table 4.2). For a well-established invasion, the *Linear* prioritization method was the preferred approach, as it allowed the manager to visit a large percentage of the river each week without losing time traveling longer distances between sites (Figure 4.6). Hence, for a well-established invasion, managers may consider implementing a strategy that maximizes removal effort and detection opportunities. For example, a previous simulation study of Burmese python (*Python bivittatus*) management showed that management and monitoring methods with high detection probabilities could help control a widespread invasion (Bonneau et al., 2016). In addition, suggestions to manage an established invasion include using methods that capture a wide spatial extent, such as using aerial shooting to manage wild pig populations (Ditchkoff and Bodenchuk 2020) or implementing large-scale mowing and fire management for invasive plants (Weidlich et al., 2020).

Third, we found that management outcomes improved if less time was spent monitoring, and instead, more effort was directed towards removing flowering rush (Figure 4.5, Table S4.2). That is, the target detection and eradication probabilities that were most often optimal were, respectively, $p = 0.5$ and $\epsilon = 0.75$. When target detection probabilities were lower, the manager was spending less time searching for flowering rush (Figure 4.5) and could use their budget to explore a higher percentage of segments (Figure 4.6). Other resource allocation studies support the claim that under a constrained budget, more time should be spent on removal than surveillance (Rout et al., 2014; Moore and McCarty 2016; Liu et al., 2021). For example, a simulation study involving invasive emerald ash borer (*Agrilus planipennis*) found that optimal management to suppress populations involved implementing a strategy wherein more sites were visited for management and where the detection methods involved a cheaper, yet less effective, trapping approach (Yemshanov et al., 2020). Therefore, managers with an objective to suppress an invasive population might consider strategies involving more removal compared to strategies involving more surveillance.

Fourth, we found no clear positive relationship between optimal management outcomes and unbiased parameter estimates (Table 4.2, Table S4.2). In fact, the alternative that performed the best in terms of suppressing the invasive population was often the alternative that performed the worst in terms of relative bias for invasion and parameter estimates (e.g., *Linear* prioritization with target probabilities of $p = 0.5$ and $\epsilon = 0.75$; Table 4.2, Table S4.2). This outcome contradicts other studies that suggest that uncertainty in parameter values is a major impediment to invasive species management (Li et al., 2021; Pepin et al., 2022). However, this result is highly context dependent. For instance, for the case of invasive knotweed management (*Fallopia japonica*), managers acknowledged that action on knotweed removal should be taken immediately, and uncertain invasion properties can be examined after management is implemented (Cottet et al., 2015). However, Baxter and Possingham (2011) suggested that invasive red fire ant management (*Solenopsis invicta*) could benefit from learning about spread rates prior to management. Thus, future studies should individually assess the value of learning using a decision analysis concept called value of information which evaluates the difference between management outcomes with and without new information (Runge et al., 2011, Canessa et al., 2015).

Although we found that integrating community science data only improves outcomes under emerging invasions (Table 4.2), the benefits of community science data in terms of educating the public should not be overlooked (Encarnação et el., 2021). For example, Nanayakkara et al (2018) conducted a survey to assess stakeholders' aquatic invasive species knowledge in Saskatchewan, Canada and found that many survey respondents were not aware of the negative consequences of flowering rush. A public education component to flowering rush management could help prevent flowering rush from establishing in new areas via human dispersal (Columbia Basin CWMA 2019). In addition, in a review, Anđelković et al (2022) identified that volunteer invasive species management programs can inspire greater commitment to protecting native species and their habitats. In general, including a community science component in a removal program can at minimum aid in education about invasive species, which may reduce invasive species spread (Crall et al. 2013; Phillips et al. 2021).

Although EDRR is currently being integrated in invasive species management (Kaiser et al., 2010; Reaser et al., 2020; Martinez et al., 2020), adaptive management is rarely implemented (Williams and Brown 2013; Lewandoski et al., 2021). The paucity of adaptive management applications may be due to poor institutional buy-in; the need to collect and maintain monitoring data; and because the analytical approaches needed to identify optimal adaptive strategies are complex, not easily customized, time-consuming, and requiring specialized quantitative skills (Foxcroft 2004; Richardson et al., 2020; Nicol et al., 2022). However, we argue that adaptive management could be useful for an emerging invasion, wherein management and detection alternatives could be updated based on new information about the system (Figure 4.2, Figure 4.7). In addition, we attempted to overcome analytical adaptive management barriers by providing an approach that can be customized for a variety of invasion contexts.

Future studies could improve upon our modeling and adaptive management approach. First, the biological and management rates for flowering rush in this specific region are unknown and we had to rely on defining various statistical distributions to sample parameter values (Table S4.1). Future studies could benefit from the addition of local experiments and surveys to inform the parameters used in models. Second, we did not account for potential multi-control methods of flowering rush. Combining mechanical hand removals with chemical treatments is an effective management approach (Turnage et al., 2019), however chemical treatments are currently limited in this region due to management being conducted on National Wildlife Refuges (Columbia Basin CWMA 2019). In the future, biocontrol agents may be used in the region (Columbia Basin CWMA 2019), and future modeling methods could account for this additional management method. Third, we assumed that community scientists would not remove flowering rush, even if detected. In fact, without training, flowering rush may be removed incorrectly, producing plant fragments that can facilitate the spread of flowering rush (Johnson et al., 2009). However, if volunteers are trained for flowering rush removal, management outcomes may improve with this additional source of removal effort.

Identifying optimal allocation of effort to monitoring and management is key to efficient use of conservation resources. We provide a framework to test different management and monitoring approaches in an adaptive management context, wherein management was iteratively updated through time as monitoring and learning occurred. Future studies could implement a similar adaptive management framework to help identify management and monitoring strategies.

4.6 ACKNOWLEDGEMENT

This research was funded through support of B.K. Thompson by the U.S. Geological Survey Invasive Species Program and the U.S. Geological Survey Science Support Program in collaboration with the U.S. Fish and Wildlife Service's Pacific Region. Funding was facilitated by, and additional funding was provided by, the Washington Cooperative Fish and Wildlife Research Unit at the University of Washington. We would also like to thank the U.S. Fish and Wildlife Mid-Columbia National Wildlife Refuge Complex for inviting B.K. Thompson to join flowering rush removal efforts in 2023. We would like to thank Katherine Maikis, Theresa Thom, and Paul Heimowitz for guidance in developing this chapter. Any use of trade, firm, or

product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

4.7 TABLES & FIGURES

Table 4.1 Description of alternatives in simulated monitoring and management of flowering rush in the Columbia River. The alternatives were a combination of spatial priority (which segments were prioritized for visits); target detection, p, and eradication, ϵ, probabilities; management investment (maximum labor hours per week); and the type of monitoring data gathered (indicated with None if no monitoring data were collected, A if just agency data were collected, and A+C if agency and community science data were collected).

Spatial Priority	**Target detection and eradication probabilities** (p, ϵ)	**Investment** (hours/week)	**Data**
None: no segments are visited (a.k.a No removals)	(0,0)	0	None
Linear: prioritized in order by space	(0.25, 0.5), (0.25, 0.75), (0.5, 0.5), (0.5, 0.75), (0.75, 0.5), (0.75, 0.75)	20 40 60	A
High invasion: segments are placed in one of three bins that describe invasion size, then segments are prioritized by highest estimated invasion bin and visited in order by distance	(0.25, 0.5), (0.25, 0.75), (0.5, 0.5), (0.5, 0.75), (0.75, 0.5), (0.75, 0.75)	20 40 60	A, A+C
Epicenter**:** prioritized by epicentral distance (distance from the single highest invaded segment, a.k.a adaptive sampling)	(0.25, 0.5), (0.25, 0.75), (0.5, 0.5), (0.5, 0.75), (0.75, 0.5), (0.75, 0.75)	20 40 60	A, A+C

Table 4.2 Results under both invasion conditions for a subset of alternatives with the addition of data integration. We display results first for an established invasion (condition 1), followed by results for an emergent initial invasion (condition 2). We show the performance of data integration (noted by Data A + C) and without data integration (A) and compare outcomes against the best expected value result, *Linear* (0.5, 0.75). For each alternative, for a given investment level, the best outcome is colored in green, and the worst outcome is colored in gray. The outcomes identified from the model simulations included the mean and maximum outcome in the suppression objective (final average invasion state) across simulations, and the mean outcome in relative bias for invasion state (State bias), detection probabilities (*p* bias), and eradication probabilities (ϵ bias) across simulations for each alternative. Each alternative was denoted by the spatial priority action, target detection and eradication probabilities (Target probabilities) whether citizen science data was included (Data), and the investment hours (Investment).

Alternative				Objective		Model performance: relative bias		
				Suppression *aim to minimize*		State bias *aim for* 0	*p* bias *aim for* 0	ϵ bias *aim for* 0
Investment	**Spatial priority**	**Target probabilities (*p*, ϵ)**	**Data**	**Mean outcome**	**Max outcome**	**Mean outcome**	**Mean outcome**	**Mean outcome**
***Condition* 1:**								
20 hours	*High invasion*	(0.5, 0.75)	A	0.638	1.180	0.166	-0.589	-0.071
		(0.5, 0.75)	A+C	0.636	1.300	0.216	0.014	-0.12
	Epicenter	(0.5, 0.75)	A	0.647	1.180	0.190	-0.566	-0.066
		(0.5, 0.75)	A+C	0.650	1.230	0.214	-0.582	-0.111
	Linear	(0.5, 0.75)	A	0.618	1.120	0.167	-0.898	-0.066
40 hours	*High invasion*	(0.5, 0.75)	A	0.416	0.975	0.129	0.046	-0.172
		(0.5, 0.75)	A+C	0.417	1.050	0.148	-0.014	-0.21
	Epicenter	(0.5, 0.75)	A	0.443	1.050	0.126	-0.694	-0.158
		(0.5, 0.75)	A+C	0.430	0.975	0.153	-0.614	-0.199
	Linear	(0.5, 0.75)	A	0.416	0.950	0.131	-0.438	-0.178
60 hours	*High invasion*	(0.5, 0.75)	A	0.299	0.950	0.121	-0.401	-0.208
		(0.5, 0.75)	A+C	0.320	0.900	0.139	0.0313	-0.227
	Epicenter	(0.5, 0.75)	A	0.340	0.900	0.130	0.026	-0.211
		(0.5, 0.75)	A+C	0.318	0.975	0.144	-0.186	-0.233
	Linear	(0.5, 0.75)	A	0.290	0.800	0.115	0.057	-0.210
Condition 2:								
20 hours	*High invasion*	(0.5, 0.75)	A	0.631	1.100	0.178	-0.395	-0.052
		(0.5, 0.75)	A+C	0.635	1.100	0.199	-0.0691	-0.115
	Epicenter	(0.5, 0.75)	A	0.647	1.350	0.168	-1.400	-0.046
		(0.5, 0.75)	A+C	0.654	1.250	0.204	-0.313	-0.108
	Linear	(0.5, 0.75)	A	0.612	1.150	0.175	-0.698	-0.048
40 hours	*High invasion*	(0.5, 0.75)	A	0.415	0.950	0.132	-0.306	-0.156
		(0.5, 0.75)	A+C	0.415	0.925	0.150	0.142	-0.206
	Epicenter	(0.5, 0.75)	A	0.439	1.120	0.125	-0.373	-0.143
		(0.5, 0.75)	A+C	0.450	1.080	0.152	-0.137	-0.198
	Linear	(0.5, 0.75)	A	0.407	1.050	0.134	-0.275	-0.158
60 hours	*High invasion*	(0.5, 0.75)	A	0.297	0.875	0.103	0.050	-0.175
		(0.5, 0.75)	A+C	0.285	0.800	0.119	0.266	-0.201
	Epicenter	(0.5, 0.75)	A	0.332	0.875	0.110	-0.136	-0.180
		(0.5, 0.75)	A+C	0.314	0.925	0.126	0.332	-0.207
	Linear	(0.5, 0.75)	A	0.296	0.825	0.106	0.094	-0.174

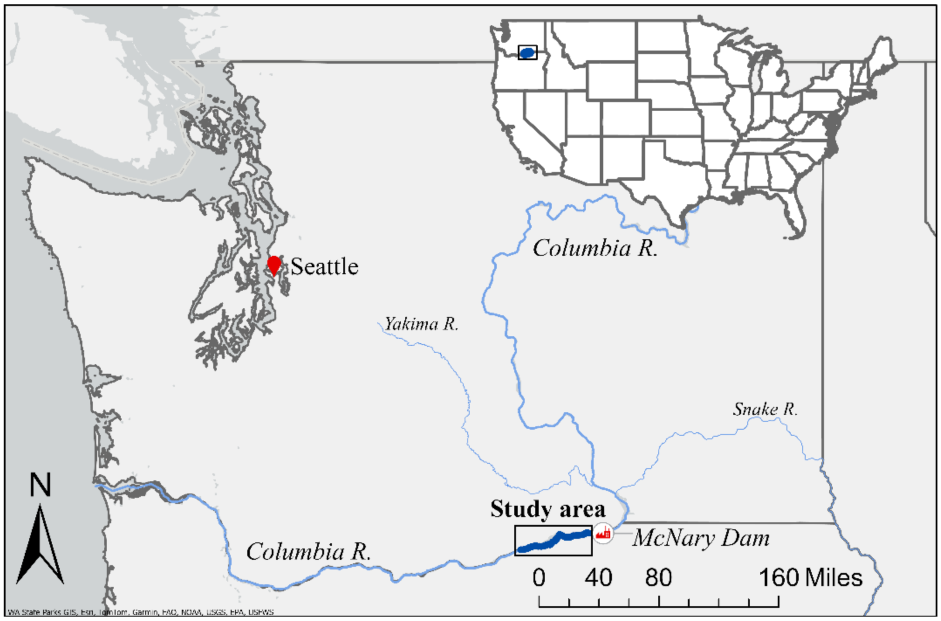

Figure 4.1 Map of the mainstem of the Columbia River, in light blue, and location of the study area, in dark blue and indicated with a box. The study area is a subset of the Columbia River that spans 40 miles downstream of the McNary Dam.

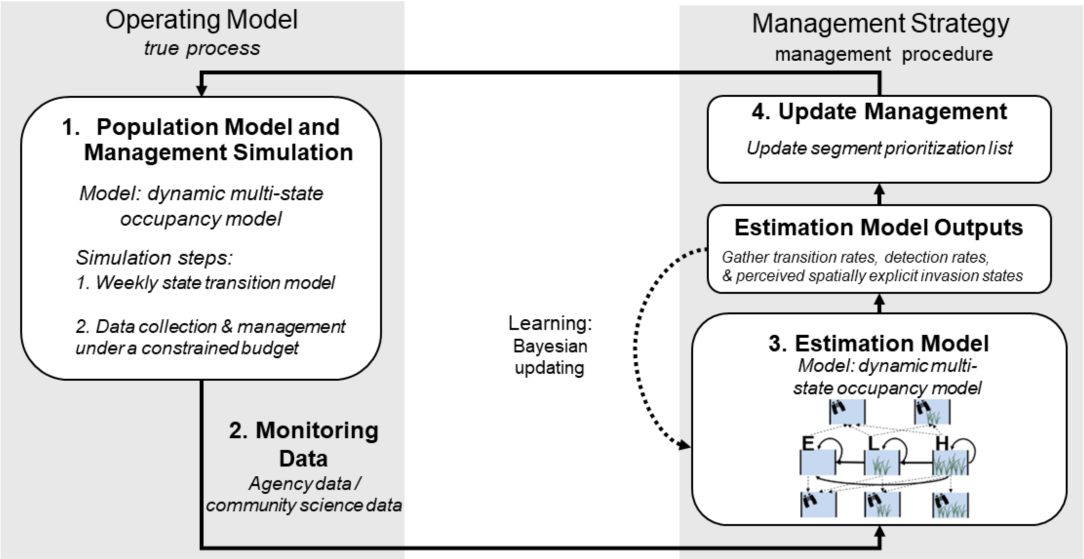

Figure 4.2 Depiction of Management Strategy Evaluation (MSE): 1. under multiple alternative management strategies, simulate realistic population dynamics and management of the species using an operating model based on distributions of parameter values representing the current state of knowledge; 2. gather simulated monitoring data from the operating model; 3. Analyze the monitoring data using an estimation model and potentially use informed priors generated through Bayesian updating, then predict population dynamics; 4. based on the estimated model predictions, update the allocation of management effort, which subsequently influences the realistic population dynamics of the species in the operating model. The details in italics are specific to this study. Figure was adapted from Siple et al. 2021.

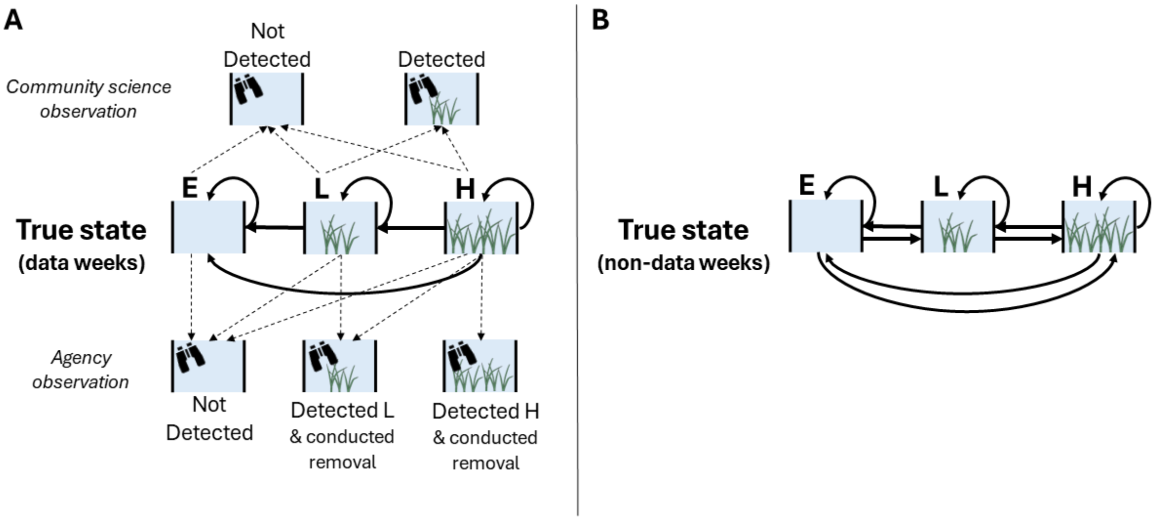

Figure 4.3 Graphical representation of the modeling framework for this study, where the thick arrows represent the true state transition process, and the dotted arrows and binocular icons represent the observation process. Box A depicts the modeling process during "data weeks" and box B depicts the modeling process during "non-data" weeks. (Plant icons reference: ian.umces.edu/media-library)

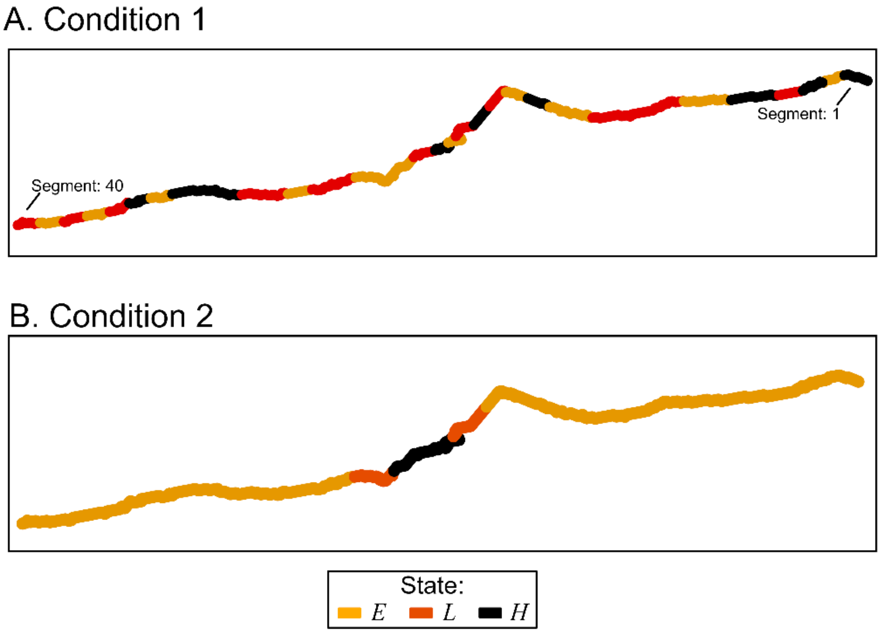

Figure 4.4 Two initial invasion conditions of flowering rush simulated across the 40-segment state space for the case study, including A: initial invasion states by segment under condition 1, an established invasion, and B: initial invasion states by segment under condition 2, an emerging invasion. The colors depict the initial true invasion state at each segment with orange depicting E, empty, red depicting L, low invasion, and black depicting H, high invasion. Segment 1 is the most upstream segment in the region and Segment 40 is the most downstream segment.

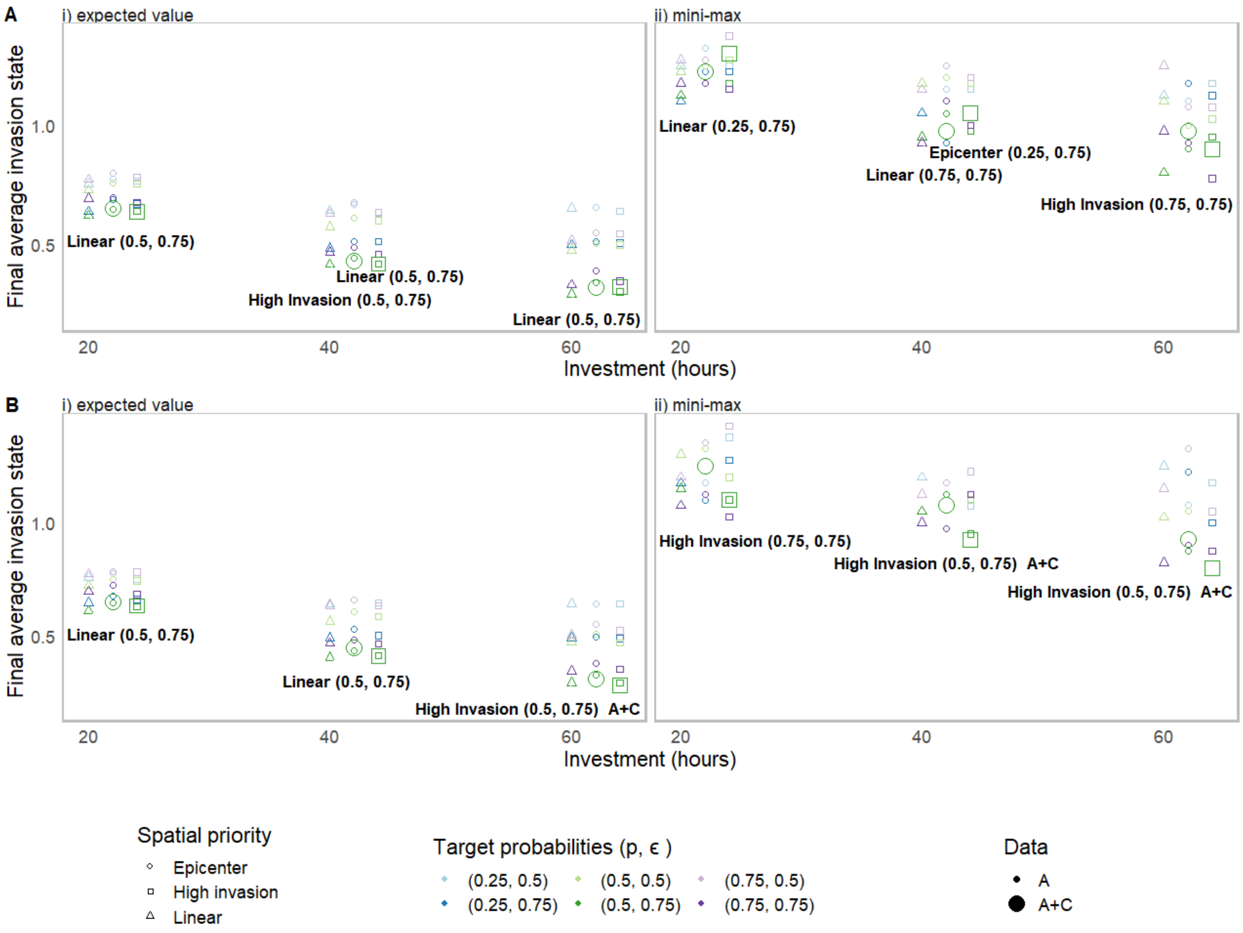

Figure 4.5 Performance of each alternative in meeting the management objective to minimize the final average invasion state of flowering rush in the simulated Columbia River study area, displayed across the three investment levels (20, 40, and 60 hours of effort per week). A final average invasion state of 0 indicates eradication while a final average invasion state of 3 indicates that all segments are in the high invasion state. In Box A, outcomes are displayed for an established invasion, and in box B, outcomes are displayed for an emerging invasion. In plots A and B, subplot i) displays the expected-value outcome for each alternative across simulations for each investment level, the bolded text displays the alternative that performed best in terms of expected value. The expected value criterion is used for risk-neutral decision makers. In plots A and B, the right plot displays the maximum outcome for each alternative across simulations and for each investment level, the bolded text displays the alternative that performed best in terms of minimizing the maximum potential invasion outcome, or the “mini-max” criterion. This criterion is used for risk-averse decision makers. The alternatives are a function of spatial priority (shown with the shapes), target detection and eradication probabilities (shown with colors), and the data used in estimation (shown with the size of the points) where “A” indicates just agency were collected, and “A+C” indicates agency and community science data were collected. In the bolded text, we indicate whether the top alternative included citizen science data with “A+C.”

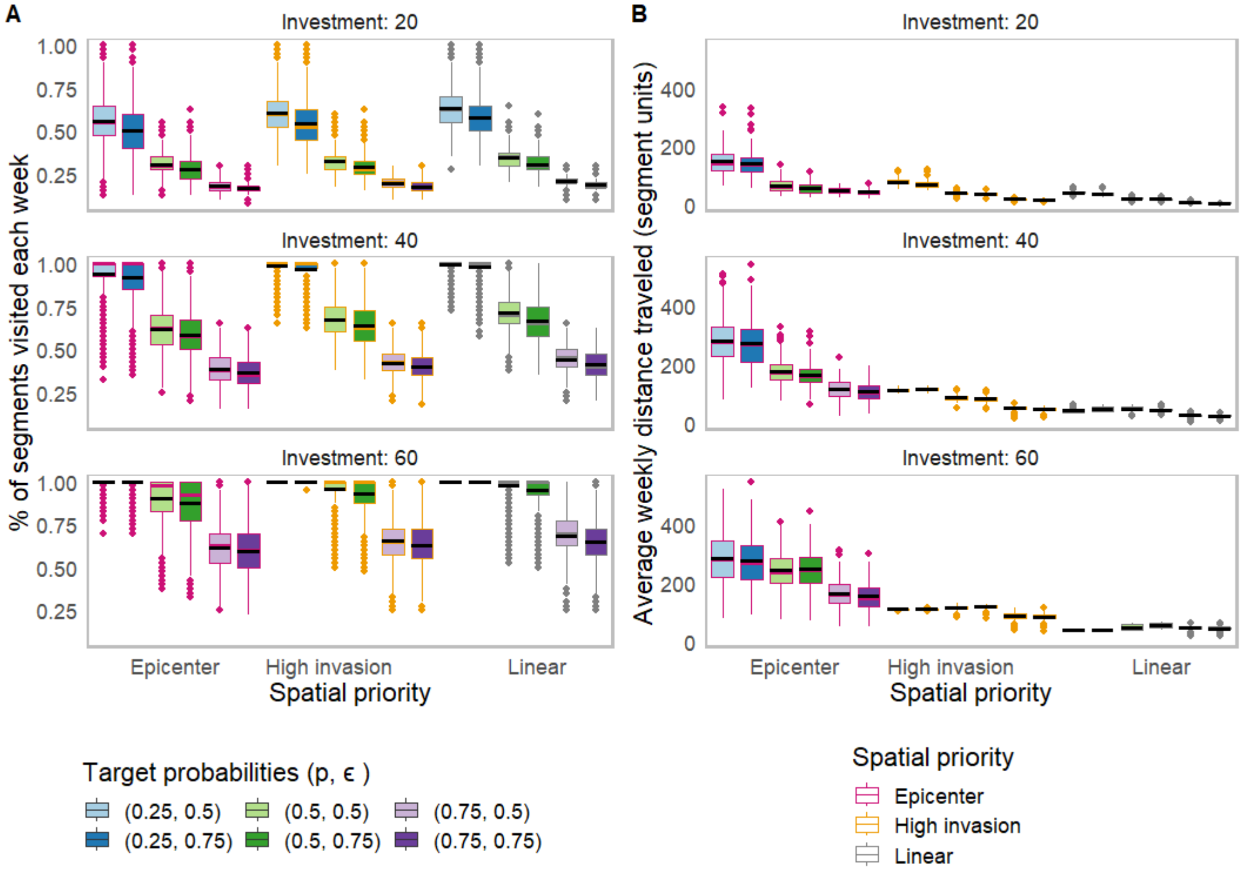

Figure 4.6 A) Results of average percentage of segments visited for either detection or detection and removal for each alternative and investment level and B) Average weekly distance traveled (in terms of segment level units) for an established initial invasion (condition 1) for each alternative and investment level. In both plots, the boxplots represent outcomes from each alternative, the outline color of each box plot represents the spatial priority action, and the fill color represents the target (detection and eradication) probabilities. In each boxplot, the colored line represents the median value, the black line is the mean value, the box displays the interquartile range, the lines indicate variability beyond the first and third quartiles, and the points represent outliers (See Figure S4.5 for outcomes under an emerging initial invasion).

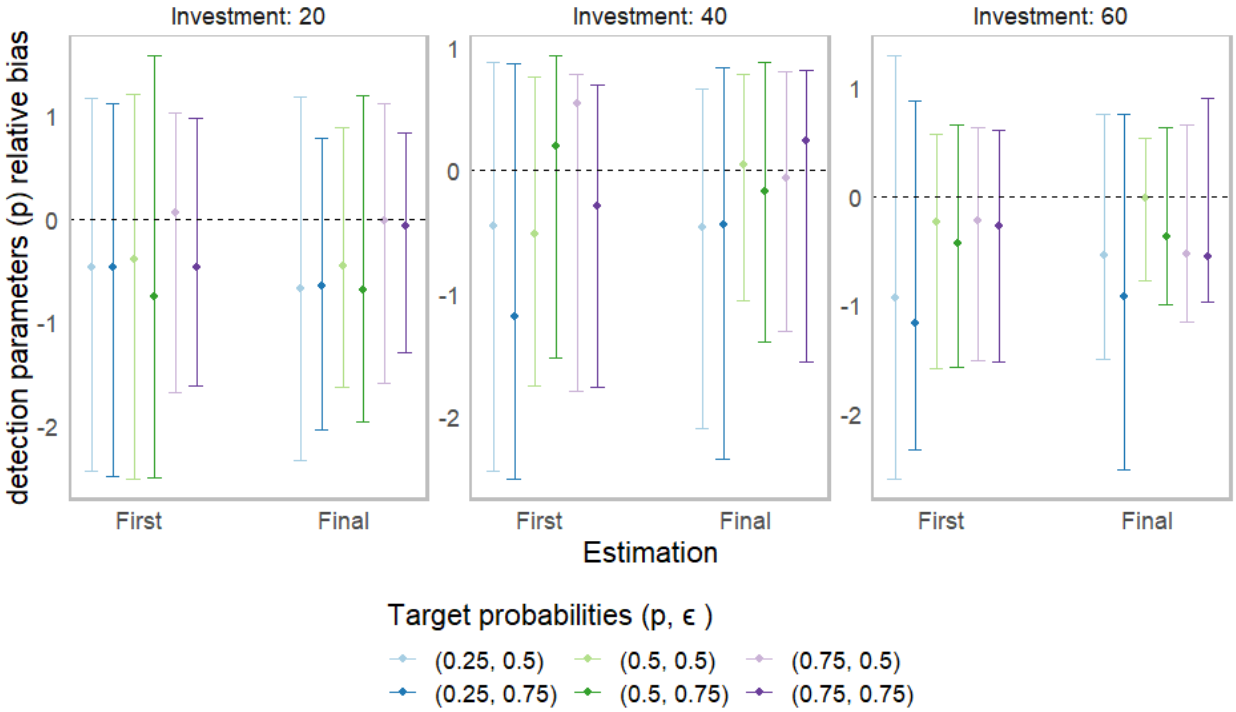

Figure 4.7 Results of relative bias estimates for detection parameters p for the High invasion prioritization under the established initial invasion (condition 1) for the three investment levels in terms of the first and final time the estimation model was run. The colors represent the different target probability pairings (p = detection, ϵ = eradication). The points represent average values across parameter sets and the error bars represent the upper and lower 5% quantile values.

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4.9 APPENDIX 4

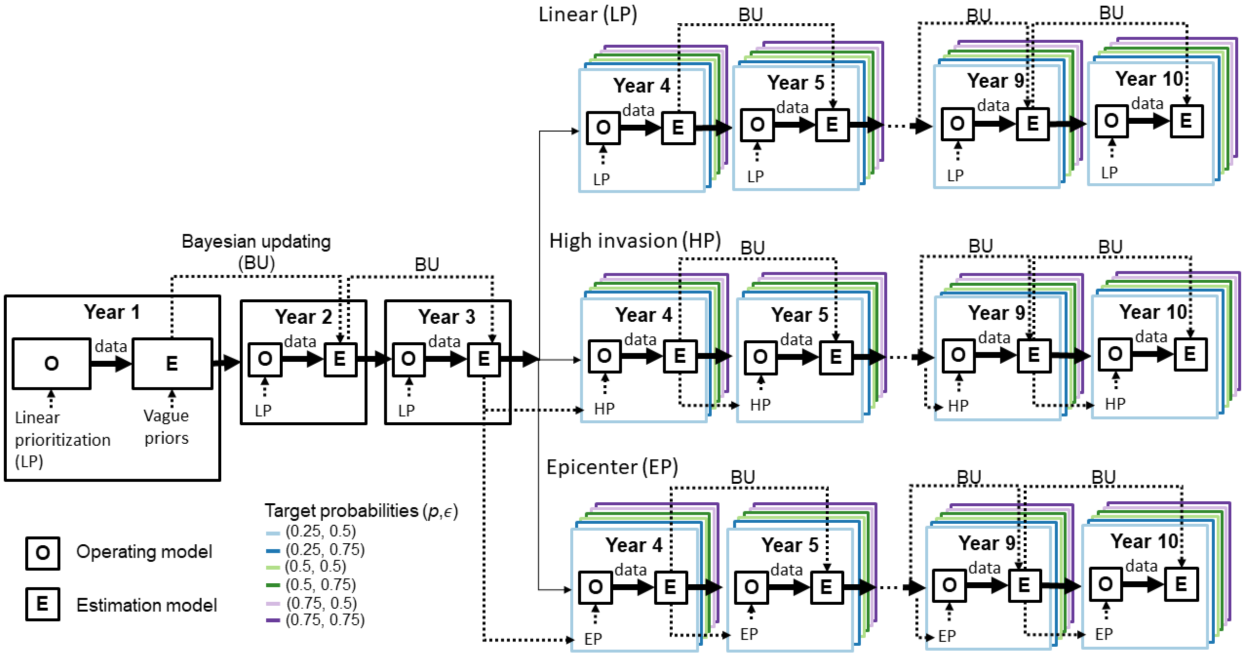

Figure S4.1 Depiction of the MSE process for this study. The O boxes represent the operating model, and the E boxes represent the estimation model. During the first three years, removal locations were prioritized linearly, removal and search hours were randomized, the estimation model was fit using simulated monitoring data, and after year 1, Bayesian updating was used to update priors in the estimation model. After year 3, the Linear (LP), High invasion (HP), and Epicenter (EP) spatial priority actions were tested under the six target probability pairings, indicated by the different colored boxes, where removal locations were prioritized according to the certain strategy and informed by results from the estimation model. Each operating and estimation model was run under 200 parameter sets to reflect different ecological and management assumptions.

Table S4.1 Description of parameter values

Parameter	**Meaning**	**Distribution**	**Rationale** (literature source)
$\beta_0^{\epsilon^S}$	Logit eradication probability for state *S* without management	$S = L$: Normal(-2, 0.5) $S = H$: Normal(-3, 0.5)	Large infestations are likely to persist (Columbia Basin CWMA 2019)
$\beta_1^{\epsilon^S}$	Effect of removal on eradication probability	$S = L$: Normal(3, 0.5), > 0 $S = H$: Normal(2, 0.5), > 0	Removal will lead to reduced biomass (Columbia Basin CWMA 2019)
$\beta_0^{\varphi^H}$	Logit probability of staying in state *H* without management	Normal(2, 0.5)	Biomass growth is rapid (Gunderson et al. 2016)
$\beta_1^{\varphi^H}$	Effect of removal on the probability of staying in state *H*	Normal(1, 0.5), < 0	Removal will lead to reduced biomass, but difficult to remove all fragments (Columbia Basin CWMA 2019)
β_0^{γ}	Logit invasion probability without management	Normal(0, 0.5)	Highly suitable to many environments (Banerjee et al. 2020)
β_1^{γ}	Effect of habitat on invasion probability	Normal(1, 0.5)	Habitat dependent invasion (Madsen et al. 2016; Gebhart and Wersal 2024)
β_2^{γ}	Effect of adjacent invasion state on invasion probability	Normal(2, 0.5)	Neighboring propagule size leads to high invasion (Carter et al. 2018)
ϵ_B^{S}	Between period eradication probability	$S = L$: Beta(2, 15) $S = H$: Beta(1, 20)	Biomass can remain during the non-growing season (Columbia Basin CWMA 2019). During growing season, growth is rapid (Gunderson et al. 2016)
φ_B^{S}	Between period probability of staying in state *S*	$S = L$: Beta(2, 15) $S = H$: Beta(14, 6)	Biomass can remain during the non growing season (Columbia Basin CWMA 2019). During growing season, growth is rapid (Gunderson et al. 2016)
g	Probability of being state *H* if invaded	Beta(12,12)	Rhizome density is highly variable (Madsen et al. 2012)
$\beta_0^{p^{S,A}}$	Logit detection probability for state *S* for agency data, *A*, without search effort	$S = L$: Normal(0, 0.5) $S = H$: Normal(0, 0.5)	Detection is low (Columbia Basin CWMA 2019)
$\beta_1^{p^{S,A}}$	Effect of search effort on detecting state *S* for agency data *A*	$S = L$: Normal(2, 0.5), > 0 $S = H$: Normal(3, 0.5), > 0	Higher invasions are easier to detect (Columbia Basin CWMA 2019)
δ	Probability of correctly detecting state *H* if detected	Beta(1, 1)	Certainty of invasion status is variable (Columbia Basin CWMA 2019)
$\beta_0^{p^{S,C}}$	Logit detection probability for state *S* for community science data, *C*, without search effort	$S = L$: Normal(0, 0.5) $S = H$: Normal(0, 0.5)	Detection is low (Columbia Basin CWMA 2019)

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Table S4.2 Results for every alternative which is a function of investment, spatial priority, and target detection and eradication probabilities (denoted as Target Probabilities) . We display results first, for an established invasion (condition 1), followed by results for an emergent initial invasion (condition 2). For each alternative, conditioned by investment level, the best outcome is colored in green, and the worst outcome is colored in gray. The results included the mean and maximum outcome in the suppression objective (final average invasion state), and mean outcome in relative bias for invasion state estimate (State bias), detection (*p* bias) and eradication (ϵ bias) probabilities.

			Objective		Model performance: relative bias		
Alternative			Suppression *aim to minimize*		State bias *aim for* 0	*p* bias *aim for* 0	ϵ bias *aim for* 0
Investment	**Spatial priority**	**Target Probabilities (*p*, ϵ)**	**Mean**	**Max**	**Mean**	**Mean**	**Mean**
***Condition* 1:**							
0 hours	None	(0,0)	0.934	1.3	NA	NA	NA
20 hours	*High invasion*	(0.25, 0.5)	0.765	1.250	0.214	-0.628	-0.074
		(0.25, 0.75)	0.668	1.230	0.232	-0.579	-0.081
		(0.5, 0.5)	0.754	1.270	0.163	-0.365	-0.070
		(0.5, 0.75)	0.638	1.180	0.166	-0.589	-0.071
		(0.75, 0.5)	0.782	1.380	0.134	0.050	-0.067
		(0.75, 0.75)	0.675	1.150	0.140	-0.138	-0.068
	Linear	(0.25, 0.5)	0.753	1.250	0.224	-0.392	-0.076
		(0.25, 0.75)	0.636	1.100	0.229	-0.656	-0.085
		(0.5, 0.5)	0.727	1.230	0.164	-0.101	-0.064
		(0.5, 0.75)	0.618	1.120	0.167	-0.898	-0.066
		(0.75, 0.5)	0.772	1.270	0.130	0.144	-0.063
		(0.75, 0.75)	0.691	1.180	0.135	0.017	-0.063
	Epicenter	(0.25, 0.5)	0.775	1.320	0.224	-0.814	-0.072
		(0.25, 0.75)	0.688	1.230	0.219	-0.604	-0.075
		(0.5, 0.5)	0.758	1.250	0.171	-0.274	-0.067
		(0.5, 0.75)	0.647	1.180	0.190	-0.566	-0.066
		(0.75, 0.5)	0.798	1.270	0.133	0.075	-0.066
		(0.75, 0.75)	0.697	1.180	0.146	-0.078	-0.068
40 hours	*High invasion*	(0.25, 0.5)	0.635	1.150	0.201	-0.439	-0.129
		(0.25, 0.75)	0.510	1.000	0.222	-0.605	-0.166
		(0.5, 0.5)	0.600	1.180	0.122	-0.080	-0.142
		(0.5, 0.75)	0.416	0.975	0.129	0.046	-0.172
		(0.75, 0.5)	0.632	1.200	0.071	0.029	-0.109
		(0.75, 0.75)	0.458	1.000	0.057	0.039	-0.113
	Linear	(0.25, 0.5)	0.641	1.150	0.198	-0.306	-0.125
		(0.25, 0.75)	0.483	1.050	0.213	-0.604	-0.167
		(0.5, 0.5)	0.572	1.180	0.139	-0.314	-0.145
		(0.5, 0.75)	0.416	0.950	0.131	-0.438	-0.178
		(0.75, 0.5)	0.630	1.150	0.065	-0.059	-0.109
		(0.75, 0.75)	0.466	0.925	0.058	0.083	-0.110
	Epicenter	(0.25, 0.5)	0.665	1.150	0.202	-0.304	-0.127
		(0.25, 0.75)	0.513	0.925	0.227	-1.120	-0.165
		(0.5, 0.5)	0.608	1.200	0.124	-0.277	-0.136
		(0.5, 0.75)	0.443	1.050	0.126	-0.694	-0.158
		(0.75, 0.5)	0.675	1.250	0.081	-0.424	-0.110
		(0.75, 0.75)	0.486	1.100	0.074	0.272	-0.112
60 hours	*High invasion*	(0.25, 0.5)	0.638	1.180	0.235	-0.660	-0.158
		(0.25, 0.75)	0.504	1.120	0.234	-0.997	-0.194
		(0.5, 0.5)	0.496	1.020	0.130	-0.022	-0.174
		(0.5, 0.75)	0.299	0.950	0.121	-0.401	-0.208
		(0.75, 0.5)	0.543	1.080	0.097	-0.439	-0.190
		(0.75, 0.75)	0.344	0.775	0.089	-0.521	-0.213
	Linear	(0.25, 0.5)	0.651	1.120	0.213	-0.880	-0.161
		(0.25, 0.75)	0.496	0.975	0.235	-0.680	-0.192
		(0.5, 0.5)	0.475	1.100	0.131	-0.415	-0.170
		(0.5, 0.75)	0.290	0.800	0.115	0.057	-0.210
		(0.75, 0.5)	0.516	1.250	0.101	-0.467	-0.192
		(0.75, 0.75)	0.329	0.975	0.106	-0.767	-0.214
	Epicenter	(0.25, 0.5)	0.656	1.100	0.218	-0.499	-0.158
		(0.25, 0.75)	0.509	1.180	0.241	-0.568	-0.192
		(0.5, 0.5)	0.502	1.000	0.131	-0.231	-0.175
		(0.5, 0.75)	0.340	0.900	0.130	0.026	-0.211
		(0.75, 0.5)	0.548	1.080	0.091	-0.476	-0.182
		(0.75, 0.75)	0.386	0.925	0.092	-0.120	-0.200

Condition 2							
0 hours	*None*	(0,0)	0.941	1.375	NA	NA	NA
20 hours	*High invasion*	(0.25, 0.5)	0.753	1.380	0.213	-0.648	-0.057
		(0.25, 0.75)	0.663	1.270	0.228	-0.876	-0.066
		(0.5, 0.5)	0.745	1.200	0.159	-0.720	-0.051
		(0.5, 0.75)	0.631	1.100	0.178	-0.395	-0.052
		(0.75, 0.5)	0.784	1.420	0.130	-0.358	-0.047
		(0.75, 0.75)	0.685	1.020	0.144	-0.526	-0.047
	Linear	(0.25, 0.5)	0.760	1.180	0.231	-0.711	-0.061
		(0.25, 0.75)	0.648	1.180	0.224	-0.822	-0.067
		(0.5, 0.5)	0.724	1.300	0.160	-0.801	-0.047
		(0.5, 0.75)	0.612	1.150	0.175	-0.698	-0.048
		(0.75, 0.5)	0.774	1.200	0.139	-0.317	-0.043
		(0.75, 0.75)	0.698	1.080	0.138	-0.723	-0.042
	Epicenter	(0.25, 0.5)	0.776	1.180	0.211	-0.538	-0.054
		(0.25, 0.75)	0.676	1.100	0.235	-0.601	-0.054
		(0.5, 0.5)	0.751	1.320	0.170	-0.522	-0.045
		(0.5, 0.75)	0.647	1.350	0.168	-1.400	-0.046
		(0.75, 0.5)	0.784	1.350	0.137	0.026	-0.048
		(0.75, 0.75)	0.726	1.120	0.129	-0.393	-0.048
40 hours	*High invasion*	(0.25, 0.5)	0.648	1.080	0.197	-0.054	-0.117
		(0.25, 0.75)	0.504	1.080	0.228	-0.361	-0.153
		(0.5, 0.5)	0.587	1.100	0.134	0.159	-0.129
		(0.5, 0.75)	0.415	0.950	0.132	-0.306	-0.156
		(0.75, 0.5)	0.634	1.230	0.072	-0.496	-0.097
		(0.75, 0.75)	0.467	1.120	0.062	0.024	-0.101
	Linear	(0.25, 0.5)	0.642	1.200	0.192	-0.026	-0.119
		(0.25, 0.75)	0.494	1.000	0.226	-0.403	-0.157
		(0.5, 0.5)	0.566	1.120	0.129	-0.134	-0.133
		(0.5, 0.75)	0.407	1.050	0.134	-0.275	-0.158
		(0.75, 0.5)	0.635	1.120	0.067	-0.173	-0.095
		(0.75, 0.75)	0.470	1.000	0.061	-0.085	-0.092
	Epicenter	(0.25, 0.5)	0.662	1.180	0.205	-0.567	-0.115
		(0.25, 0.75)	0.531	0.975	0.232	-0.291	-0.153
		(0.5, 0.5)	0.611	1.180	0.137	-0.355	-0.123
		(0.5, 0.75)	0.439	1.120	0.125	-0.373	-0.143
		(0.75, 0.5)	0.661	1.180	0.089	-0.241	-0.097
		(0.75, 0.75)	0.484	0.975	0.073	0.067	-0.095
60 hours	*High invasion*	(0.25, 0.5)	0.643	1.180	0.198	-0.109	-0.126
		(0.25, 0.75)	0.492	1.000	0.209	-0.101	-0.161
		(0.5, 0.5)	0.473	1.050	0.118	0.397	-0.135
		(0.5, 0.75)	0.297	0.875	0.103	0.050	-0.175
		(0.75, 0.5)	0.526	1.050	0.091	0.466	-0.156
		(0.75, 0.75)	0.357	0.875	0.092	-0.325	-0.177
	Linear	(0.25, 0.5)	0.644	1.250	0.190	-0.100	-0.127
		(0.25, 0.75)	0.494	1.020	0.205	-0.275	-0.162
		(0.5, 0.5)	0.477	1.020	0.115	0.236	-0.137
		(0.5, 0.75)	0.296	0.825	0.106	0.094	-0.174
		(0.75, 0.5)	0.506	1.150	0.103	-0.101	-0.153
		(0.75, 0.75)	0.348	0.825	0.097	-0.157	-0.183
	Epicenter	(0.25, 0.5)	0.644	1.080	0.194	-0.138	-0.126
		(0.25, 0.75)	0.499	1.230	0.207	-0.270	-0.164
		(0.5, 0.5)	0.511	1.050	0.121	-0.110	-0.136
		(0.5, 0.75)	0.332	0.875	0.110	-0.136	-0.180
		(0.75, 0.5)	0.554	1.320	0.086	-0.182	-0.144
		(0.75, 0.75)	0.382	0.900	0.084	-0.353	-0.167

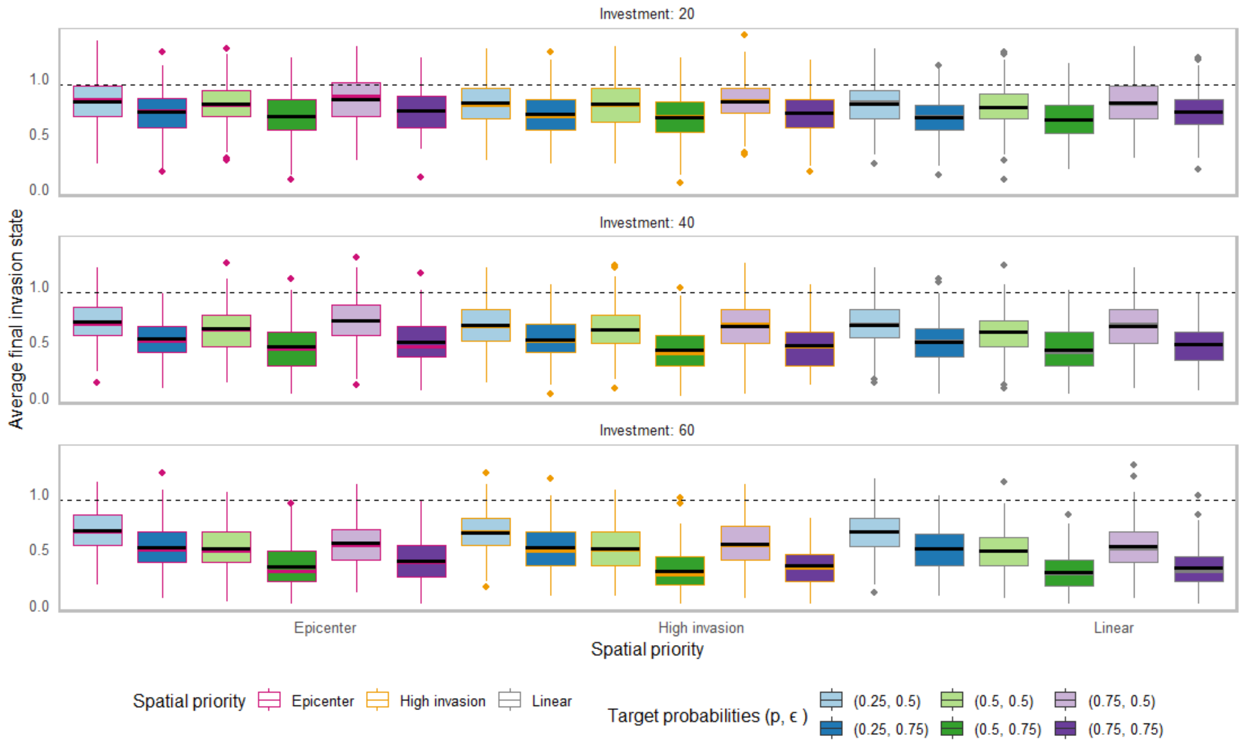


Figure S4.2 Results of the suppression objective for all alternatives under the three investment levels for an established initial invasion (condition 1). The boxplots represent outcomes from each alternative, the outline color of each box plot represents the spatial priority, and the fill color represents the target probability pairings. In each boxplot, the colored line represents the median value, the black line is the mean value, the boxplot displays the interquartile range, the lines indicate variability beyond the first and third quartiles, and the points represent outliers.

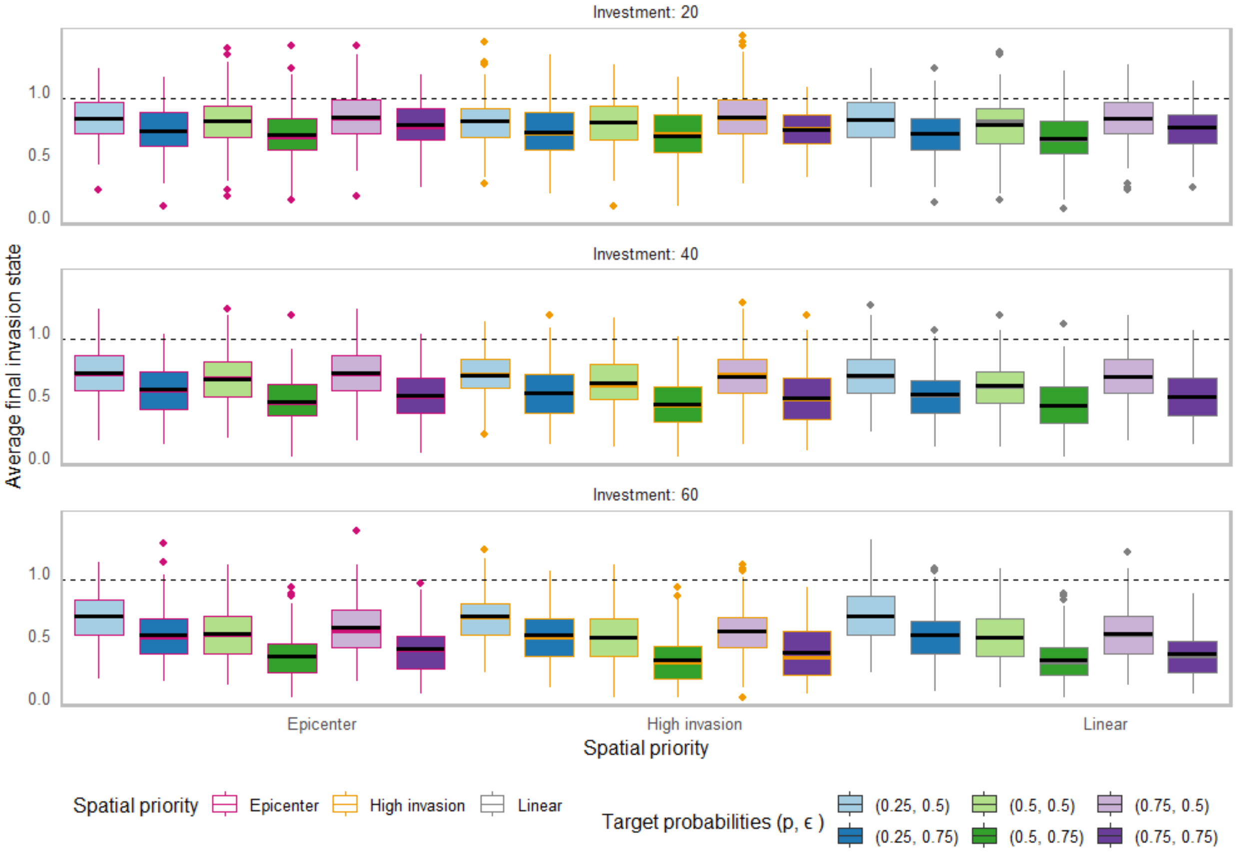


Figure S4.3 Results of the suppression objective for all alternatives under the three investment levels for an emerging initial invasion (condition 2). The boxplots represent outcomes from each alternative, the outline color of each box plot represents the spatial priority, and the fill color represents the target probability pairings. In each boxplot, the colored line represents the median value, the black line is the mean value, the boxplot displays the interquartile range, the lines indicate variability beyond the first and third quartiles, and the points represent outliers.

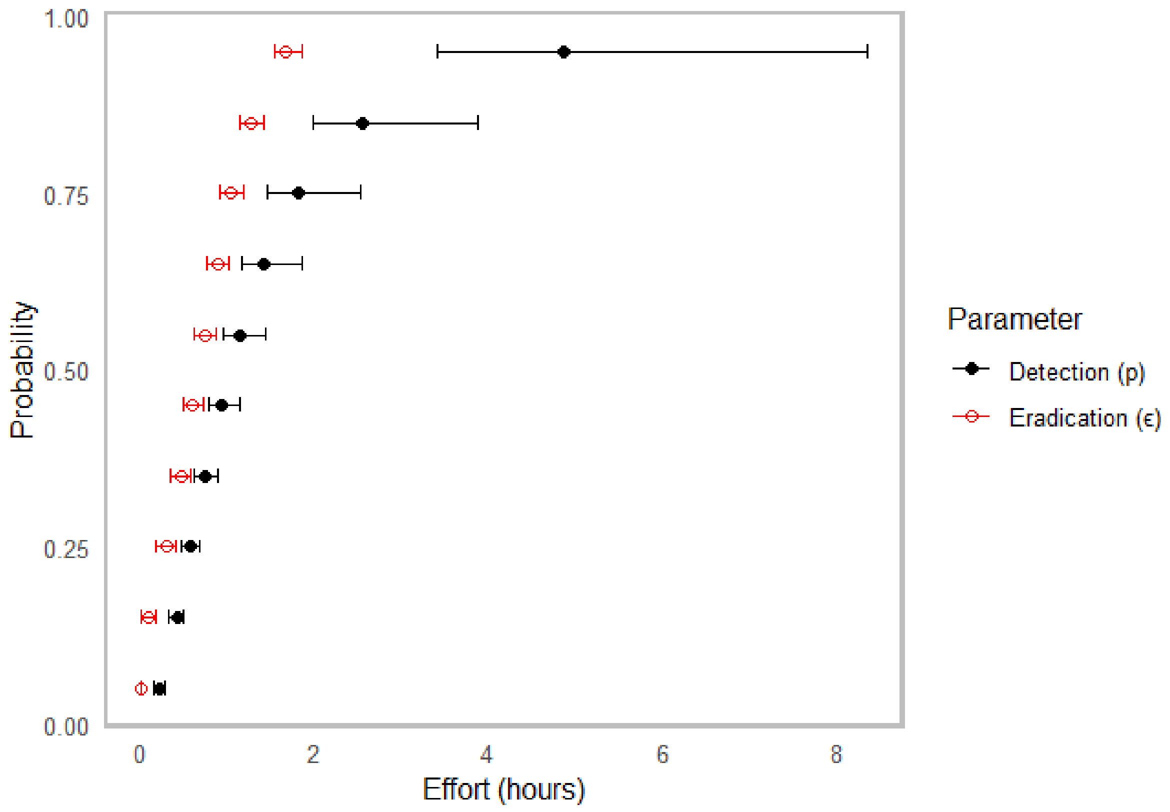


Figure S4.4 The relationship between effort and target probabilities for detection and eradication. We display detection probabilities, p, with black closed circles, and eradication probability, ϵ, with red open circles. The points represent average values across parameter sets, invasion states, investment levels, and the two initial invasion scenarios. The error bars represent the upper and lower 5% quantile values.

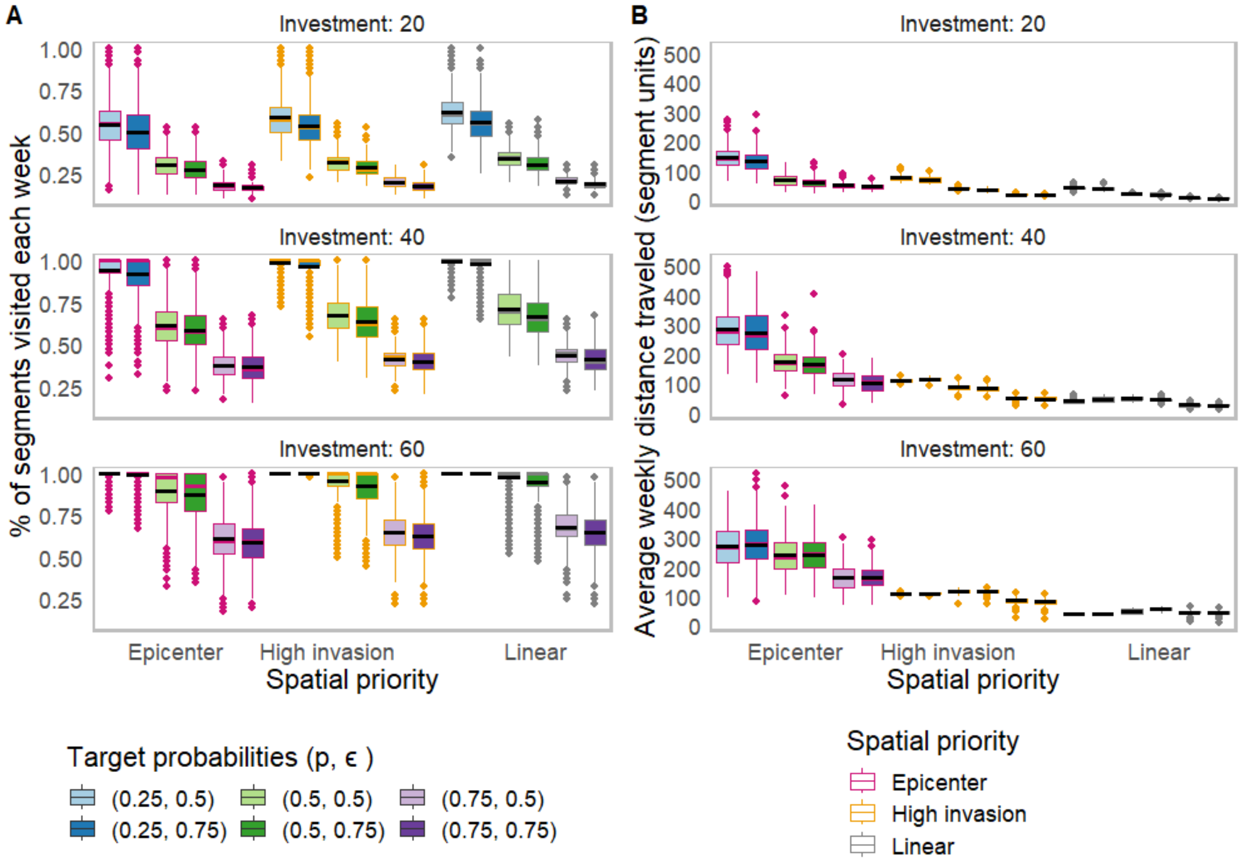


Figure S4.5 A) Results of average percentage of segments that are visited for either detection or removal for each alternative and investment level and B) Average weekly distance traveled (in terms of segment level units) for an emerging initial invasion (condition 2) for each alternative and investment level. In both plots, the boxplots represent outcomes from each alternative, the outline color of each box plot represents the spatial priority, and the fill color represents the target probability pairings. In each boxplot, the colored line represents the median value, the black line is the mean value, the boxplot displays the interquartile range, the lines indicate variability beyond the first and third quartiles, and the points represent outliers.

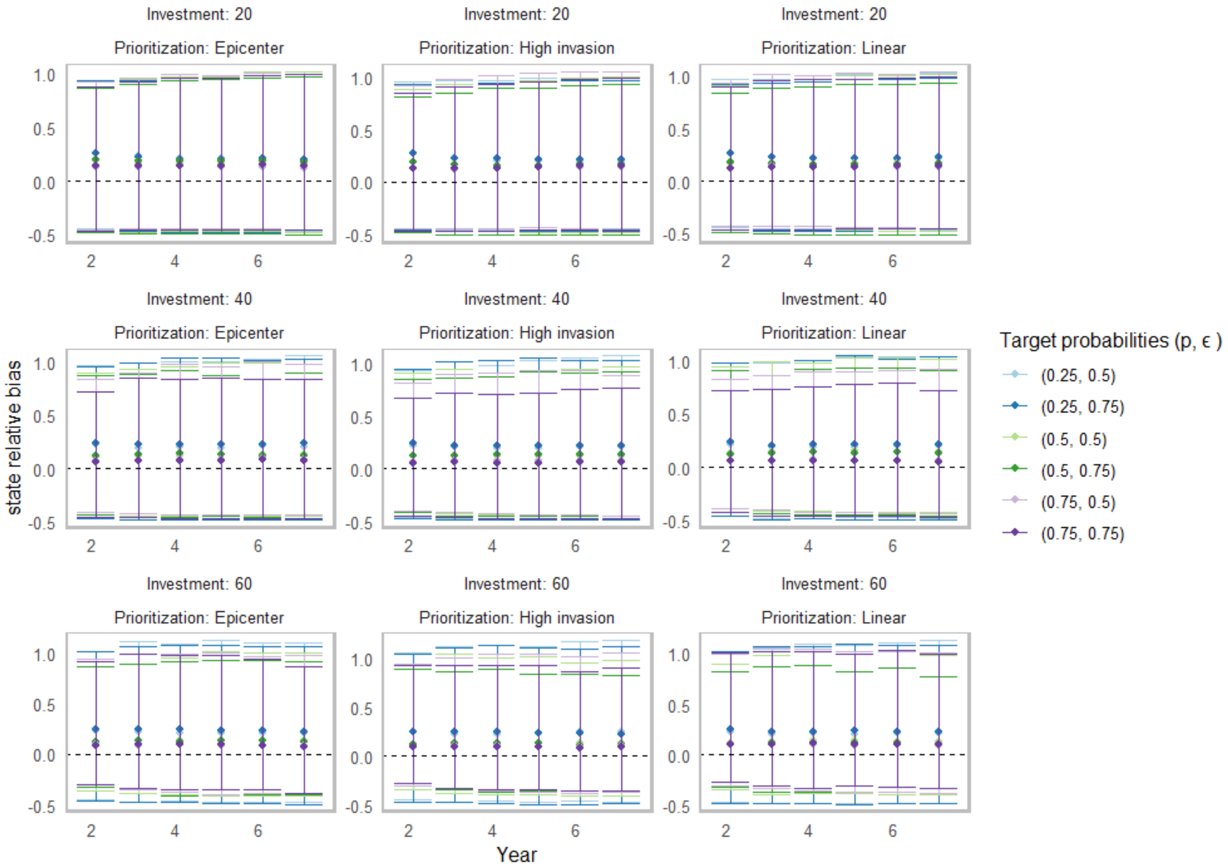


Figure S4.6 Results of the change in state relative bias through time (not including the first three years in which the alternatives had the same outcomes) for condition 1.

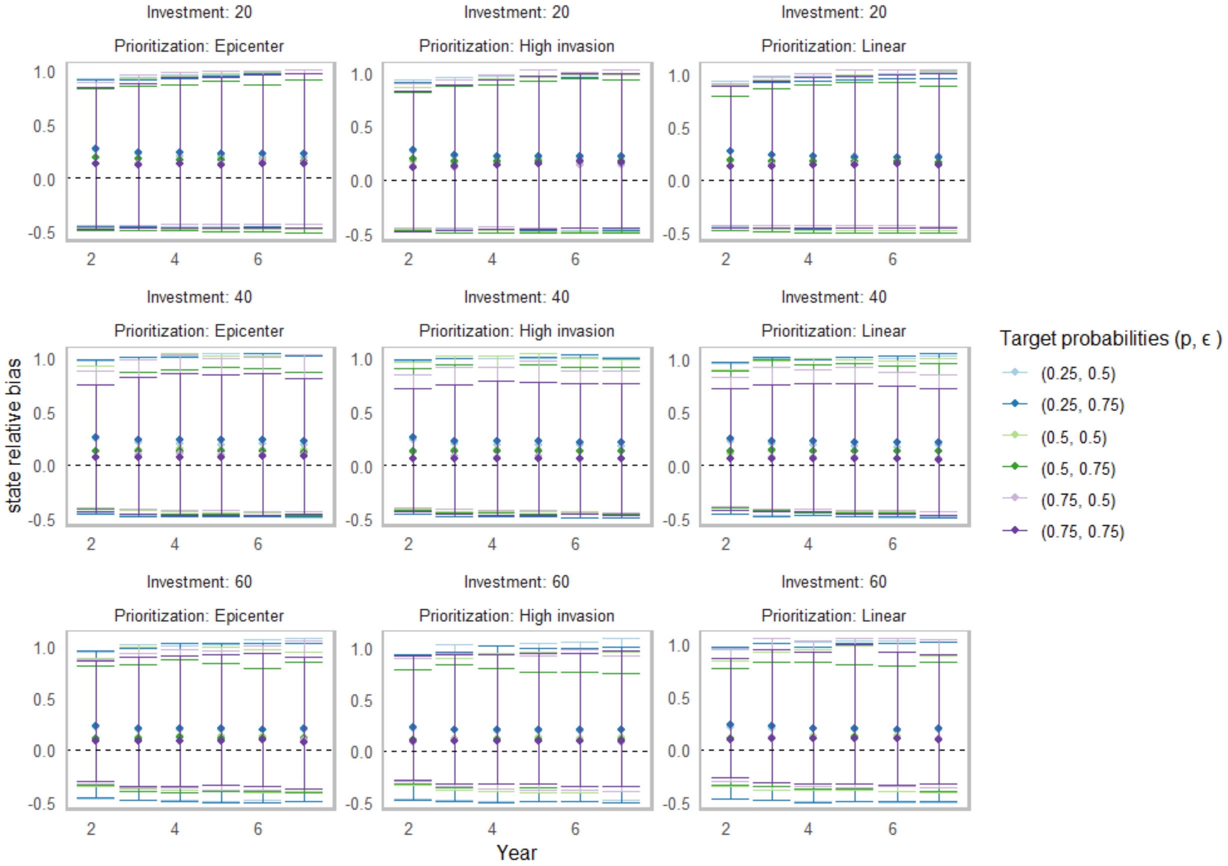


Figure S4.7 Results of the change in state relative bias through time (not including the first three years in which the alternatives had the same outcomes) for condition 2.

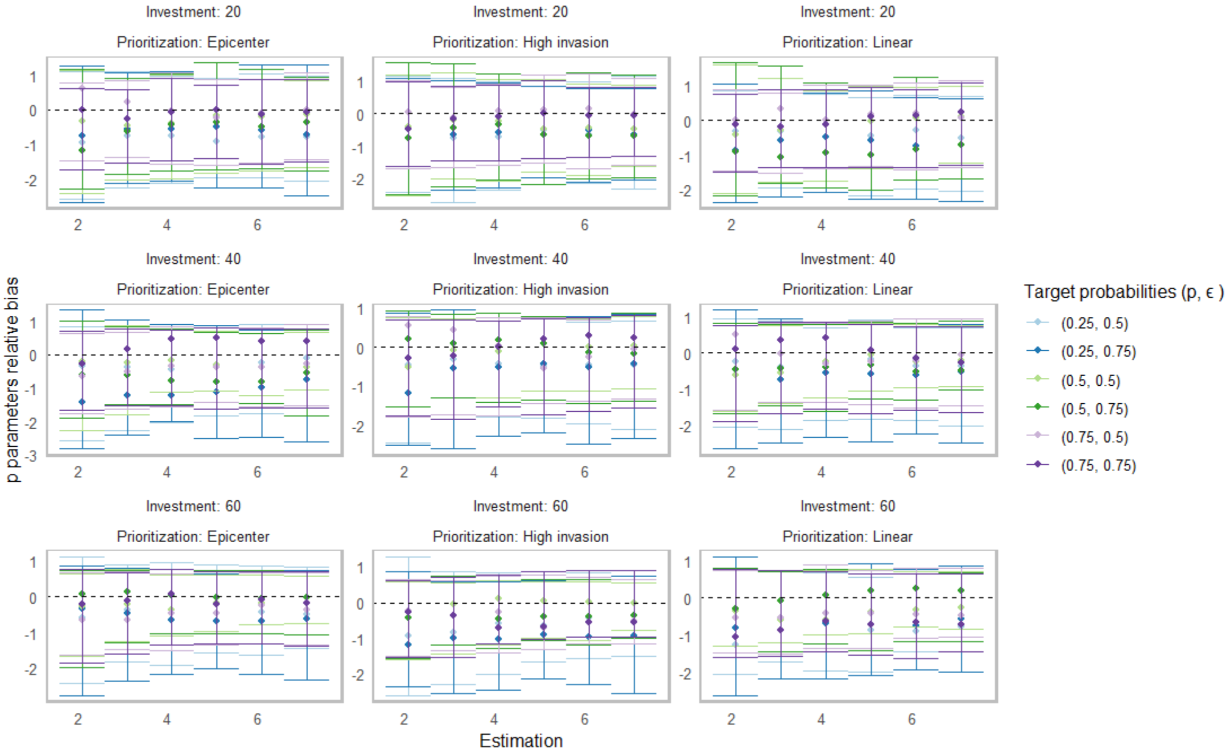


Figure S4.8 Results of the change in p parameters relative bias from the first year and final year the estimation model was run for each alternative (not including the first three years in which the alternatives had the same outcomes) for condition 1.

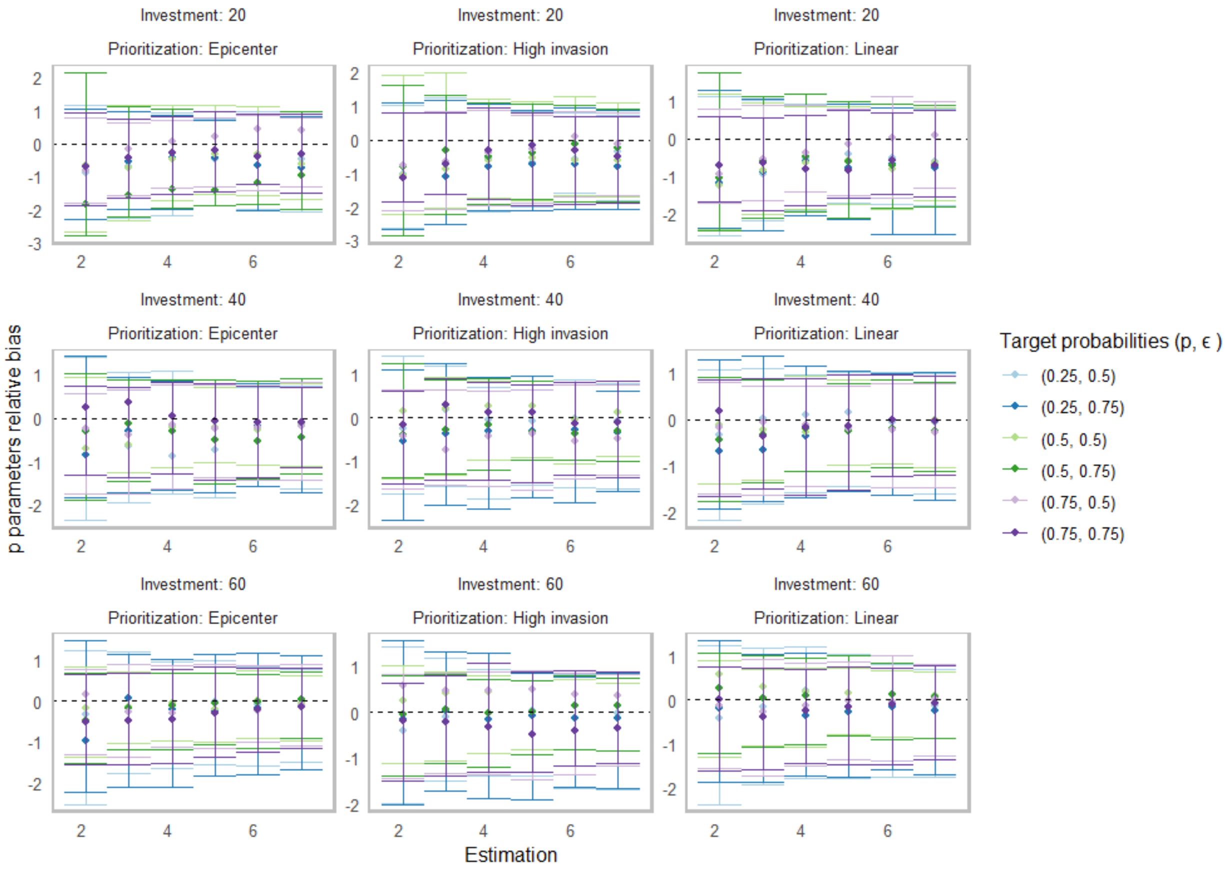


Figure S4.9 Results of the change in p parameters relative bias from the first year and final year the estimation model was run for each alternative (not including the first three years in which the alternatives had the same outcomes) for condition 2.

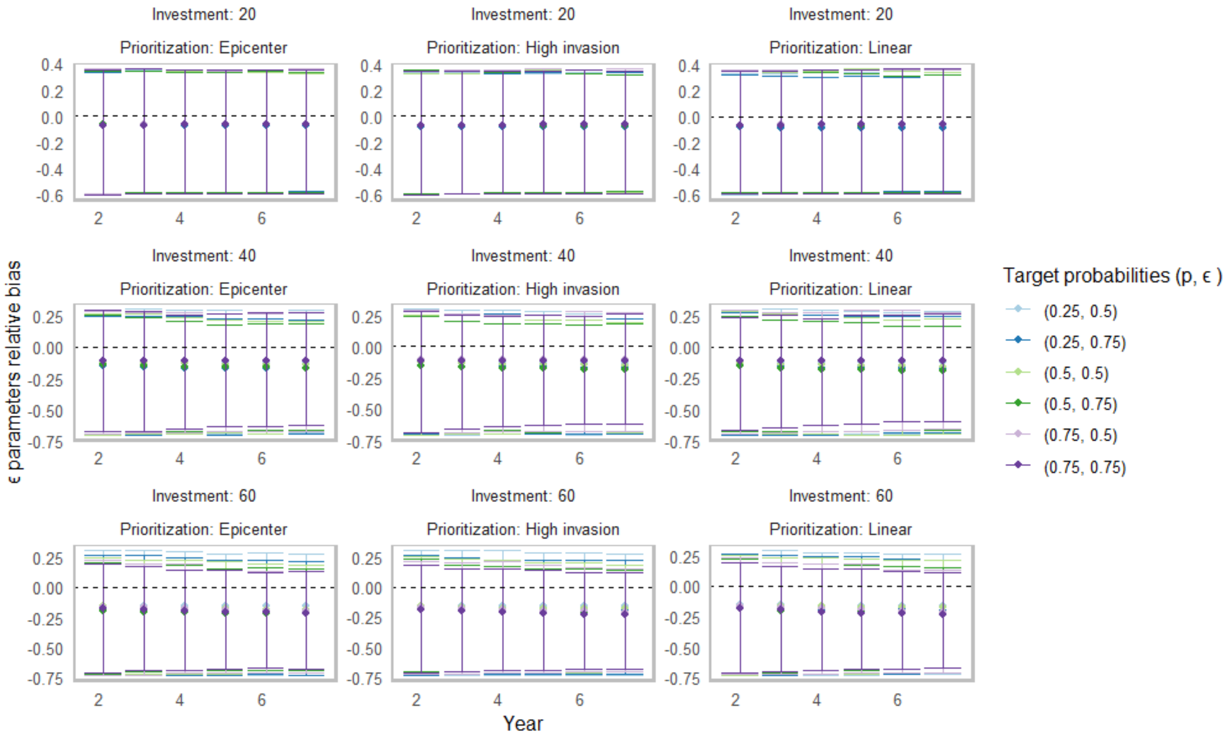


Figure S4.10 Results of the change in ϵ parameters relative bias from the first year and final year the estimation model was run for each alternative (not including the first three years in which the alternatives had the same outcomes) for condition 1.

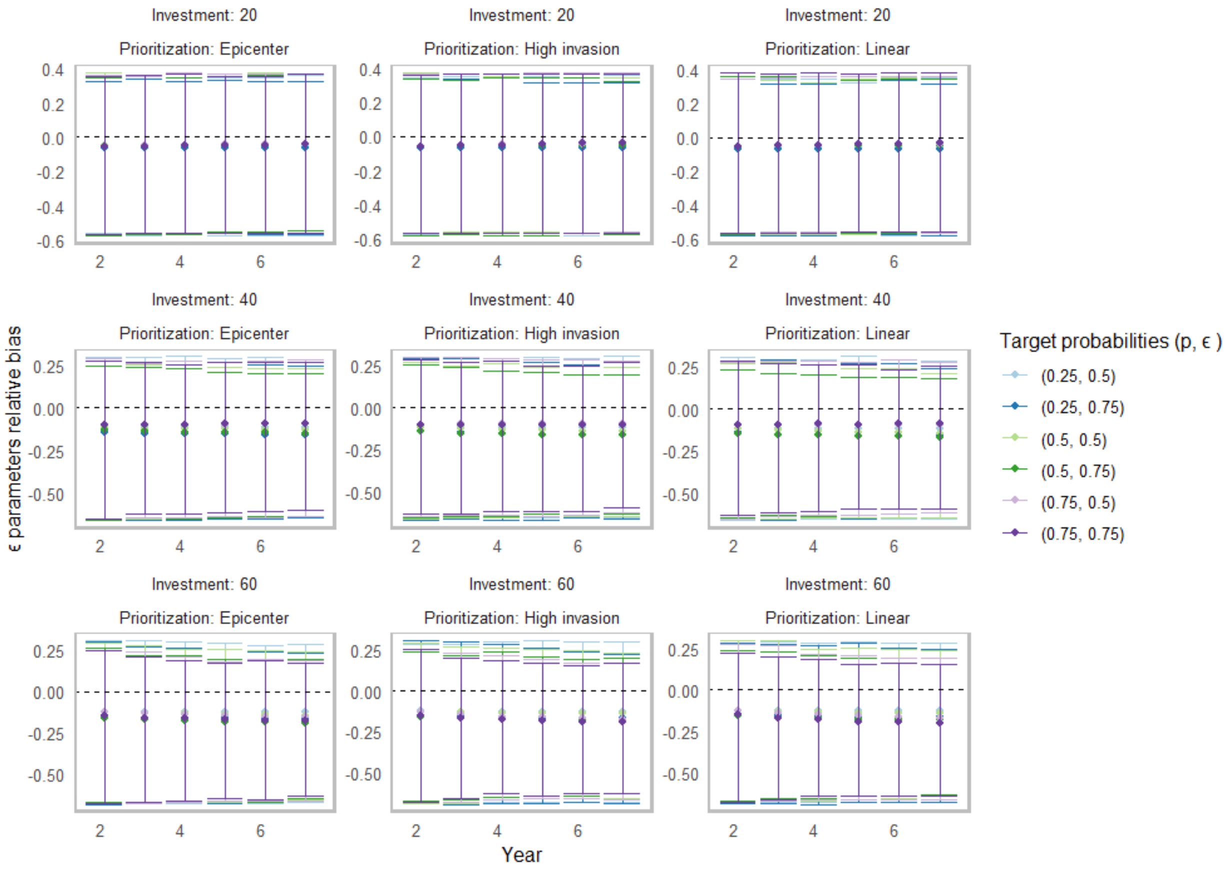


Figure S4.11 Results of the change in ϵ parameters relative bias from the first year and final year the estimation model was run for each alternative (not including the first three years in which the alternatives had the same outcomes) for condition 2.

CHAPTER 5. TWO CAN PLAY AT THAT GAME: CONTRASTING MULTI-CRITERIA DECISION ANALYSIS AND GAME THEORY FOR INFORMING INVASIVE SPECIES MANAGEMENT

Publication history: This study was co-authored with Julian D. Olden, Sarah J. Converse, and Christopher M. Anderson. At the time this dissertation was published, this chapter was not in review with a journal.

5.1 ABSTRACT

Two common challenges in conservation decision making include multiple objective and multiple decision maker problems. A common decision-analytic tool to address multiple objective problems is multi-criteria decision analysis (MCDA), which helps identify preferred actions in situations involving tradeoffs between objectives, such as cost and conservation outcomes. In contrast, a common economic method to deal with multiple decision maker problems is game theory, which identifies optimal actions of each decision maker when they consider the behaviors of each other. MCDA and game theory have independently been applied in a variety of conservation contexts. Here, we provide a comparison of both approaches in their ability to guide optimal invasive species harvest decisions involving a natural resource manager and a neighboring landowner. We considered three potential types of neighboring landowners: an environmentalist, who like the manager is concerned with cost and the invasive species population, a hobbyist who enjoys harvesting the invasive species, and a profiteer who receives profit from invasive species harvest. We identified management actions using MCDA expected utility for each decision maker and solved for game theory solutions including Nash equilibrium and Pareto optimality. We showed that by not accounting for the other decision maker's behavior, sometimes the MCDA solution failed to reveal optimal harvest actions compared to game theory. This occurred when the decision makers had different preferences, for example,

when the manager valued favorable invasion outcomes over cost and when the neighboring landowner was more concerned with cost over other objectives. However, MCDA does provide insight into the preferred actions of each player when the behavior of others is treated as a source of uncertainty, which is a key initial metric to identify in multi-decision maker settings. Hence, both game theory and MCDA can be used together to aid in decision making in settings involving multiple decision makers.

5.2 INTRODUCTION

For thousands of years, alongside worldwide human dispersal, various plants, animals, and other organisms have been introduced and established in new areas (DiCastri 1990; Seddon et al. 2012). Such introductions have occurred either intentionally because the species provides food, recreation, or aesthetic values, or unintentionally, for instance, from boat hull fouling or escape from captivity (Hulme et al. 2008; Essl et al. 2015). It was not until the 20th Century that scientists began to acknowledge that some introduced organisms, or invasive species, threaten the environment (Lacey Act 1900; Elton 1958; Richardson and Pyšek 2008). With the development of invasion biology as a scientific discipline, there has been a growing awareness of the threats that invasive species pose to biodiversity, economies, and human health (Doherty et al. 2016; Diagne et al., 2020; Mazza et al. 2014). Harmful introductions are projected to increase as globalization and environmental change continues (Meyerson and Mooney 2007; Rahel and Olden; 2008; Hulme 2009).

Although the ecological, economic, and social harms of invasive species are well established, perceptions of invasive species and their impacts vary among cultures and communities (Estévez et al. 2015; Crowley et al. 2017; Sax et al., 2022). Some invasive species are believed to have both advantages and disadvantages, inspiring terms such as “mixed-blessing invaders” and “double-edge” or “Janus syndrome” species (Kourantidou et al. 2022; Gozlan 2015). For example, invasive Nile perch (*Lates niloticus*) in Lake Victoria have provided the region with economic benefits from commercial and recreational fishing while causing ecological and social harms by facilitating the extinction of insectivorous cichlids, resulting in outbreaks of mosquito-borne diseases (Kourantidou et al. 2022). Some invasive species may provide ecosystem services (Sladonja et al. 2018) and even ecological benefits (Schlaepfer et al. 2011) such as the medicinal use of Jimsonweed (*Datura stramonium*) in North America (Maema et al. 2016) and pollination of native plants by invasive warbling white-eyes (*Zosterops japonicus*) and Red-billed Leiothrix (*Leiothrix lutea*) in Hawaii (Foster and Robinson 2007). Invasive species also can provide a sense of place or important cultural symbolism, such as free-roaming horses for some Indigenous groups in western North America (Bhattacharyya & Larson 2014). Thus, both the costs and benefits of invasive species may factor into the management of invasive species (Beever et al. 2019; Crowley et al. 2017; Kourantidou et al. 2022), increasing the complexity of these management decisions.

Decision analysis, also known as structured decision making, brings both a philosophical approach and a variety of tools to assist decision makers faced with difficult decisions (Keeney 2004; Gregory et al. 2012; Hemming et al. 2022). Decision analysis emphasizes deconstructing decisions into a set of component parts to identify and overcome impediments to decision making (Runge et al. 2020). These components include a statement of the decision problem, objectives, alternatives, model(s) to predict the consequences of alternatives in terms of objectives, and a method for dealing with tradeoffs (PrOACT; Hammond et al. 2002). The objectives are the component that represents decision maker and stakeholder values, expressed in a manner that allows for comparisons across alternative management actions (Keeney 1996).

Multi-criteria decision analysis (MCDA) constitutes a broad set of approaches for facilitating decisions involving tradeoffs among objectives (Keeney and Raffia 1993; Converse 2020). One common MCDA approach, for example, the Simple Multi-Attribute Rating Technique, involves converting predicted outcomes on different objectives to a common scale and applying weights that represent the relative importance of those objectives to the decision maker; alternatives can then be evaluated based on the sum of the weighted and scaled performance values across objectives (Edwards 1977). Decision analysis has been applied to a wide array of natural resource decision problems (Runge et al., 2020), including endangered species management (Gregory and Long 2009), wildlife disease (Sells et all., 2016), native species reintroduction (Converse et al., 2013), and invasive species management (van Poorten and Beck 2021).

Decision-analytic processes assume either a single decision maker representing their own values or a collaborative decision-making body that can agree on a process for representing their collective values. When members of a decision-making body are in disagreement, facilitation approaches, joint fact finding, or conflict resolution can be used to preserve the collaboration (Karl et al. 2007; Runge et al. 2013). The decisions of decision makers external to the body can be treated as a source of uncertainty (or can inspire a reframing of the decision) in decision-analytic processes. Tools for dealing with decisions under uncertainty can be harnessed in these cases (Runge and Converse 2020). Ignoring other decision makers in a system can adversely affect outcomes (Madani and Lund 2011). For example, in the United Kingdom, lethal control of invasive parakeets (*Psittacula krameri*) was thwarted, and ruddy duck (*Oxyura jamaicensis*) culling was delayed due to public attachment to the animals (Crowley et al. 2019; Cranswick & Hall 2010).

Game theory is a framework for explicitly considering the interactions of multiple decision makers through the analysis of strategic interactions, and optimal solutions are identified while considering the self-optimizing attitudes of each of the multiple decision makers (Luce and Raiffa 1957; Madani and Lund 2011). A game is composed of players (i.e., decision makers), their actions, strategies (i.e., combination of actions across players) and their payoffs (i.e., performance on objectives). The payoffs, often informed by a quantitative model, are a function of the choices made by each decision maker (Folmer and de Zeeuw 1999). In game theory, a variety of solution concepts, including Nash equilibria and Pareto optimality, are used to help identify solutions. Game theory solutions describe a prediction for how a game will end by identifying the strategy that will be executed assuming that each player wants to maximize their own outcomes given the probable actions of other players (Gibbons 1997). With roots in economics, game theory has been applied to a variety of natural resource decision problems (Frank and Sarkar 2010; Colyvan et al. 2011), such as fishery fleet operations (Jensen et al. 2015; Sumaila 1999), protected area planning (Sierra-Altamiranda et al. 2020), flood management (Machac et al., 2017), and invasive species management (Siriwardena et al. 2018; Yemshanov et al. 2022; Chen et al. 2023). A common critique of game theory, however, is that the payoffs are typically represented in monetary units. Although this is a reasonable approach for non-controversial species, it may not capture social concerns appropriately or explicitly (Kallis et al., 2013; Gomez-Baggethun and Barton 2013; Kenter et al., 2015).

Although MCDA and game theory have been used in a variety of natural resource management applications, the differences between the solution concepts from both fields have not been evaluated in conservation (but see Madini and Lund 2011 for an application in water resources management). On one hand, MCDA is used in situations where there is a single decision maker, and the actions of any external decision makers are treated as sources of uncertainty (Esmail and Geneletti 2017). On the other hand, game theory directly embeds the values of multiple decision makers in the analysis. In addition, game theory uses methods that can detect conflicts between players and identify opportunities for decision makers to cooperate, which could lead to better outcomes for both players (Frank and Sarkar 2010). Although game theory directly considers multiple decision makers, MCDA potentially provides more appropriate methods to elicit the values of each individual (Hammond et al. 2002). Given that these two fields of decision making have evolved separately, a direct comparison of both approaches can help identify the circumstances in which one approach is more effective at guiding decisions in multiple decision-maker environments.

Here, we evaluated and compared MCDA and game-theoretic solutions in an invasive species management context. We consider three applications, or “games,” each involving two players with individual values regarding invasive species, each of whom must make management decisions on their own property. These properties are adjacent, and a single population of an invasive species makes use of both. In all games, we assume that one player is a natural resource manager with two objectives: minimize invasive species abundance and minimize their own management costs. Given that landscapes consist of a “mosaic” of diverse types of individuals whose choices may impact invasive species management (Epanchin-Niell et al., 2010), the other player in the games is a neighbor whose objectives and preferences differ across games; we consider neighbors who are “environmentalists,” “hobbyists,” or “profiteers,” across the three games, each of which is representative of a real-world invasive species management problem. In each game, we assume that the manager and the neighbor have a choice between different harvest levels that they can implement on their own property. Then, we solve for the manager's MCDA solution, i.e., the optimal action of the manager if the manager were to treat the neighbor's decision as a source of uncertainty, and the neighbor's MCDA solution. We also evaluate game-theoretic solutions, e.g., Nash equilibria, and ask whether the manager could do better if they explicitly considered the perspective of their neighbor when making a decision. While we apply this analysis to invasive species management, our results revealed the value of game theory in environmental settings because it identifies the probable outcomes given strategic interactions between multiple decision makers who are acting on the system and who may have conflicting objectives. A variety of examples exist in natural resource management in which conflicts amongst decision makers are often a defining feature of the system, including wildlife disease management, predator management, and hunting or fishing regulation settings.

5.3 METHODS

Our goal is to contrast an MCDA approach with a game-theoretic approach to an invasive species management problem. From an MCDA perspective, we have just one decision to consider (in three different settings) for each player. From a game-theoretic perspective, we have three different games, and we identify strategies that consist of the combined actions of both decision makers. First, we present our methods initially from a game-theoretic perspective, providing the set up for the games, the decision makers (i.e., the players), the actions (i.e., the individual choices available to each player), and the strategies (i.e., the combined actions of both players relevant to the game-theoretic setting). Second, we describe the payoff functions (known in decision theory as multi-objective utility functions) for each player. Third, we describe the biological models and economic models that we use to predict outcomes. Fourth, we explain the solution concepts used to identify management actions for each player in the MCDA context or combined management strategies in the game-theoretic context.

5.3.1 GAME SETUP

In each game we assumed that an area was divided into two ownership parcels of equal size (hereafter, locations), both inhabited by the invasive species. In each game, the manager plays against a neighbor. We assumed in all games that the manager had two objectives: minimize invasive species abundance across the entire area (i.e., in both their own location and the neighbor's location) and minimize the management costs they incur.

In the first game, Manager vs Environmentalist, the neighbor is an environmentalist with objectives that are similar to those of the manager: minimize the abundance of the invasive species across the entire area and minimize the management costs they incur. There are many examples in which members of the public have aided in agency management efforts by removing invasive species (Table 5.1, Niemic et al., 2016; Bertolino et al., 2021). For example, landowners removing invasive barberry (*Berberis thunbergii*) from their property (Snyder et al. 2020); lakefront property owners removing invasive Eurasian milfoil (*Myriophyllum spicatum*, Olden & Tamayo 2014); and beachfront owners clearing toxic algae from beaches (Smith et al., 2004).

In the second game, Manager vs Hobbyist, the neighbor is a hobbyist with two objectives: maximize harvest of the invasive species, and minimize the costs they incur (e.g., due to costs such as gear and licenses). There are many examples of members of the public who engage with invasive species in this way (Table 5.1), including individuals who enjoy harvesting invasive plants for ornamental purposes (van Kleunen et al., 2018), individuals who hunt invasive pigs (*Sus scrofa*, Smith et al., 2023), recreational anglers who harvest invasive sportfish (e.g., smallmouth bass, *Micropterus dolomieu,* in Eastern states of the US, Seddon et al., 2012;

Long and Seguy 2024), and lionfish (*Pterois volitans*) spear fishers (Ulman et al., 2022). Hunters or anglers may even prefer to hunt or fish for invasive species because they are on average more aggressive or larger than native species (von Essen 2020; Shollenberger et al., 2019; Sbragaglia et al., 2022), increasing enjoyment of the sporting aspects of harvest.

In the third game, Manager vs Profiteer, the neighbor is a profiteer who obtains income from harvesting invasive species; their sole objective is to maximize profit. Many industries have received economic benefits from harvesting invasive species (Table 5.1, Geesing et al. 2004; Aloo et al., 2017; Pienkowski et al., 2015). For example, the honey industry in several U.S. southern US states has benefited from invasive honeybees (*Apis mellifera*; Carpenter and Harpur 2020), the aquaculture industry in South Africa has benefited from invasive tilapia (*Oreochromis niloticus*, Marr et al. 2017), and commercial fishers have gained economic benefits from the invasive red king crab fishery in Norway (*Paralithodes camtschaticus*, Kourantidou and Kaiser 2021).

In every game, we assumed that the manager and the neighbor (i.e., environmentalist, hobbyist, or profiteer) had three actions from which to choose, defined as three harvest rates they can apply in their own location. These include harvest rates of 1, 0.5, or 0 (or equivalently 100%, 50%, or 0% harvest rates) at each time step (year) over a 20-year time horizon. Combining the harvest action of the manager and the harvest action of the neighbor results in a “strategy;” thus, there are nine strategies that we denote as $(h_{M,s}, h_{N,s})$ for the harvest action of the manager, *M*, $h_{M,s}$ and the neighbor, *N*, $h_{N,s}$ for each strategy, *s* in strategy set $\boldsymbol{S}$. The nine possible strategies in strategy set $\boldsymbol{S}$ are:

$$\boldsymbol{S} = \left\{ \begin{array}{c} (h_{M,s=1}, h_{N,s=1}) = (1,1), \\ (h_{M,s=2}, h_{N,s=2}) = (1,0.5), \\ (h_{M,s=3}, h_{N,s=3}) = (1,0), \\ (h_{M,s=4}, h_{N,s=4}) = (0.5,1), \\ (h_{M,s=5}, h_{N,s=5}) = (0.5,0.5), \\ (h_{M,s=6}, h_{N,s=6}) = (0.5,1), \\ (h_{M,s=7}, h_{N,s=7}) = (0,1), \\ (h_{M,s=8}, h_{N,s=8}) = (0,0.5), \\ (h_{M,s=9}, h_{N,s=9}) = (0,0) \end{array} \right\} \quad .(1)$$

5.3.2 PAYOFF FUNCTIONS

Next, we quantitatively express the preferences of each player. Common to both MCDA and game theory is utility theory, which provides approaches for transforming outcomes to a number that represents utility, or perceived satisfaction with an outcome given the risk tolerance of the decision maker (Reichert et al., 2013; Leyton-Brown and Shoham 2022). For example, utility functions can be used to quantify the manager's satisfaction associated with the final total invasive population in the environment at the end of the management time horizon, given their risk attitude. An attribute is a measure of performance on objectives; for example, dollars are an attribute for the objective of minimizing costs. We assumed the utility function,

$$\mathrm{U}(x) = \ln(x + 1), \text{ for any attribute } x \quad , (2)$$

(see Table 5.2 for attribute descriptions). This utility structure indicates that the marginal utility, U(x) - U(x-1), declines as x increases. This implies, for example, that the hobbyist realizes greater happiness from the first fish they harvest than from the hundredth, and for a harvest cost attribute, the utility structure reflects diminishing marginal utility of cost. We summarize the attributes for the manager and all neighbors in Table 5.2.

Using the attributes (Table 5.2) and the utility function (Eq 2), we create a set of new functions, known as "payoff functions," also known as multi-attribute utility functions in the decision-analysis literature (Von Winterfeldt and Fischer 1975). A payoff function describes the relative level of satisfaction given a strategy and the utilities of each attribute weighted by how much the decision maker values that attribute. The weights on each attribute for the manager (*i* = *M*) or neighbor (*i* = *N*) are denoted as α_i for the first attribute (final population or cumulative harvest, Table 5.2), and β_i for the second attribute (cumulative cost). We assume the profiteer has a weight of 1 for their cumulative profit attribute because they are only concerned with that single attribute (see 5.3.3 *model descriptions* for calculations for each attribute).

We expressed the managers payoff function for strategy $s \in \boldsymbol{S}$ as a function of attributes: total invasive population (${X_s}^{\text{total}}$) and cumulative cost (${C^{\text{total}}}_{M,s}$):

$$f_{M,s} = \left(\alpha_M \times -\ln\left({X_s}^{\text{total}} + 1\right)\right) + \left(\beta_M \times -\ln\left({C^{\text{total}}}_{M,s} + 1\right)\right) \qquad .(3)$$

The negative terms indicate that a high invasive population and high cost results in a lower, less desirable, payoff. The environmentalist’s payoff was expressed similarly as:

$$f_{N_E,s} = \left(\alpha_M \times -\ln\left({X_N}^{\text{total}} + 1\right)\right) + \left(\beta_N \times -\ln\left({C^{\text{total}}}_{N,s} + 1\right)\right) \qquad . (4)$$

The payoff function for the hobbyist, for strategy $s \in \boldsymbol{S}$ was a function of cumulative harvest (${H^{\text{total}}}_{N,s}$) minus cumulative cost:

$$f_{N_H,a} = \alpha_N \ln\left({H^{\text{total}}}_{N,s} + 1\right) + \left(\beta_N \times -\ln\left({C^{\text{total}}}_{N,s} + 1\right)\right) \qquad , (5)$$

and the payoff function for the profiteer was a function of cumulative profit (${P^{total}}_{N,s}$):

$$f_{N_P,a} = \ln\left({P^{total}}_{N,s} + 1\right) \qquad , (6)$$

where profit was calculated as cumulative income minus cumulative cost (see 5.3.3 *model descriptions*). Since the profiteer has only one objective, weights are not needed.

There are various tools in MCDA that can be used to elicit weights from decision makers (Marsh et al., 2017). However, here we created nine sets of weights to evaluate a range of possibilties, where for each player *i* (either Manager, *M*, or neighbor, *N*), the weighting scheme consisted of either $\alpha_i = \beta_i$, $\alpha_i > \beta_i$, or $\alpha_i < \beta_i$ (Table 5.3). This means that the value placed on a unit of the attribute associated with a decision-maker's first objective (e.g., total population size, ${X_s}^{total}$, for the manager or environmentalist or total harvest, ${H_{N,s}}^{total}$, for the hobbyist) is either equal to, greater than, or less than the value placed on a unit of the attribute associated with the second objective (e.g., cumulative cost) (Table 5.2). Since the cost of management (attribute 2) was high in comparison to the invasive population, we needed to create weights that allowed us to compare these two attributes without cost always being the factor that drove the solutions (Table 5.3; Figure S5.1).

5.3.3 MODEL DESCRIPTIONS

We now describe the models that we used to calculate the terms expressed in the payoff functions. We developed both population and economic models, and these models were consistent across the games. In the model descriptions, we index players by *i*, harvest strategies by *s* ($s \epsilon \boldsymbol{S}$) (Eq. 1), and years by *t* (*t* = 1,2, …, 20).

The population model is a simple, discrete-time logistic population model where, in a given time step, removals occur first, followed by logistic growth and dispersal. The abundance of the invasive species at player *i*'s location, given strategy *s,* in year *t* after removals occur but before population growth and dispersal occur, is modeled as:

$$\widehat{X_{i,s,t}} = X_{i,s,t} - h_{i,s}X_{i,s,t} \tag{7}$$

where $h_{i,s}$ is the harvest rate of player *i* under harvest strategy *s* (Eq 1), and $X_{i,s,t}$ is the population at player *i*'s location under harvest strategy *s* at time *t* just prior to removals. Then, we model the abundance after the logistic growth and dispersal process, $X_{i,s,t+1}$, as:

$$X_{i,s,t+1} = \widehat{X_{i,s,t}} + r\widehat{X_{i,s,t}}\left(1 - \frac{\widehat{X_{i,s,t}}}{K}\right) + b\widehat{X_{j,s,t}} - b\widehat{X_{i,s,t}} \tag{8}$$

where the first term is the population size just after removals; the second term represents logistic growth where *r* is the population growth rate and *K* is the carrying capacity (equal across both locations); and the third and fourth terms capture the dispersal process, where *b* is the dispersal rate from one location to the other, such that the population entering player i's location from player j's location is $b\widehat{X_{J,s,t}}$, and the population leaving player i's location to enter player *j's* location is $b\widehat{X_{i,s,t}}$ (Kroetz and Sanchirico 2015). We set the initial population to 150 individuals in each of the two locations. We let *r* = 1, *K* = 600, and *b* = 0.3, representing an invasive species with moderate population growth and spread.

We modeled the cost of invasive species removal or harvest, $C_{i,s,t}$, as

$$C_{i,s,t} \ = \ c_h e^{-\gamma t} h_{i,s} X_{i,s,t} \tag{9}$$

where c_h is the per-unit cost of removal and γ is an annual discount rate of 5% (Hastings et al., 2006). We assumed c_h was $10 per invasive species harvested. We expressed cumulative cost, ${C_{i,s}}^{\text{total}}$, for each player as

$${C_{i,s}}^{\text{total}} = \ \sum_{t\,=\,1}^{T} C_{i,s,t} \tag{10}$$

We similarly modeled the revenue from removals, $R_{i,s,t}$, as:

$$R_{i,s,t} \ = \ c_r e^{-\gamma t} h_{i,s} X_{i,s,t} \tag{11}$$

where c_r = $200 was the revenue gained per unit harvested. We calculated cumulative revenue, ${R_{i,s}}^{\text{total}}$, as

$${R_{i,s}}^{\text{total}} = \sum_{t\,=\,1}^{T} R_{N,s,t} \qquad .(12)$$

and cumulative payoff, ${P_{i,s}}^{\text{total}}$, was calculated as total revenue minus total cost:

$${P_{i,s}}^{\text{total}} = {C_{i,s}}^{\text{total}} - {R_{i,s}}^{\text{total}} \qquad .(13)$$

We modeled cumulative harvest, which was captured in the Manager vs Hobbyist game and calculated only for the hobbyist, as:

$$H_{N,s}{}^{total} = \sum_{t=1}^{T} h_{s,t} X_{N,s,t} \qquad .(14)$$

5.3.4 SOLUTION CONCEPTS

After the payoff functions and respective models are created, the solutions are then identified. We solved for the following solution concepts, conditioned by the weight set, using MCDA and game theory. The specific solutions that are identified in MCDA and game theory differ. That is, in MCDA, the solution is the action that is prescribed by the MCDA process, with the action of the other decision maker treated as a source of uncertainty. In game theory, the solution is the strategy (i.e., the pairing of both player's actions) that is considered "stable" in that it maximizes each player's outcome given the preferred action of the other player. After we assess the MCDA solution for each player, we then compare it against the game theory solution.

To create a common notation structure between MCDA and game theory, we use a matrix, a game-theoretic approach, to organize each player's payoffs (Luce and Rasiffa 1957). The matrix represents the general format of each game where N, the neighbor, can be replaced with N_E , N_H , and N_P for each game (Figure 5.1). Each cell represents the combination of the manager (i = M) and neighbor's (i = N) payoff across each strategy s_1, …, $s_9 \epsilon \boldsymbol{S}$ for any given weight set w, $f^{w}{}_{i,s}$. For each multi-player interaction, or "game," we expressed the following solutions using concepts from MCDA and game theory.

First, we calculated an MCDA solution, by identifying the action with the highest expected utility for the manager, given uncertainty associated with the action of the neighbor. For expected utility, we need to calculate the performance of each action for each player. For example, using notation from Figure 5.1, the manager's expected utility for doing action 1, denoted as $\text{EU}(M, \text{action} = 1)$, would be:

$$\text{EU}(M, \text{action} = 1) = p_{N,\text{action}=1} \times f_{M,s=1} + p_{N,\text{action}=0.5} \times f_{M,s=2} + p_{N,\text{action}=0} \times f_{M,s=3} \quad (15)$$

where $p_{N,\text{action}=1}$, $p_{N,\text{action}=0.5}$, $p_{N,\text{action}=0}$ are the probabilities that the neighbor will take action 1, 0.5, or 0, respectively. Under maximum uncertainty, these probabilities are each 1/3, which is what we assumed in this analysis. We then compare $\text{EU}(M, \text{action} = 1)$, $\text{EU}(M, \text{action} = 0.5)$, and $\text{EU}(M, \text{action} = 0)$, and identify the optimal action for the manager as the action that maximizes EU. We also solved for the expected utility solution for the neighbor using the same method described above and assuming the manager had equal probability of doing any action, hence $p_{M,\text{action}=1}$, $p_{M,\text{action}=0.5}$, $p_{M,\text{action}=0}$ = 1/3.

Within games, solutions may be a Nash equilibrium, may be Pareto optimal, or may be both of these (Luce and Raiffa 1989). A Nash equilibrium occurs if no player would unilaterally change their action from this solution (Nash 1950). In other words, assuming the actions of the players are fixed, if no player wants to change their action to achieve a better outcome, then this strategy (i.e., this pair of actions) is a Nash equilibrium. Second, a solution is Pareto optimal if and only if no player could be made better off without making the other worse off. In games, a Pareto-optimal Nash equilibrium is desirable because no player would want to change their outcome because their payoffs are maximized. Identifying conflicts, or solutions that are not Pareto-optimal Nash equilibria, could encourage cooperation and enable constructive action to achieve more optimal outcomes (Frank and Sarkar 2010).

We conducted a sensitivity analysis on parameter values including growth rate (r), dispersal rate (b), per unit cost of harvest (c_h), and per unit revenue (c_r). We generated values for each parameter (Table S5.1) and generated 5,760 parameter sets defining unique combinations of all parameter values. In addition, we expressed MCDA solutions for each player across a wider set of weights (Figure S5.1). In addition, although our solutions often depended on final population or cumulative harvest, cost, and profit, we also identified the trend in those outcomes through time for each player under the 9 strategies (Figure S5.4-Figure S5.7).

5.4 RESULTS

5.4.1 MANAGER VS ENVIRONMENTALIST

When the manager's weight on the final population (α_M) was equal to or less than the weight on cost (β_M), the MCDA preferred action was 0 (i.e., 0% harvest) per expected utility (Figure 5.2). Unsurprisingly, given that the environmentalist has the same objectives as the manager, the MCDA preferred action for the environmentalist was also 0 when $\alpha_N = \beta_N$ and $\alpha_N < \beta_N$, (henceforth denoted as $\alpha_N \leq \beta_N$ when combined). Under these weights, $\alpha_M \leq \beta_M$ and $\alpha_N \leq \beta_N$, the Nash equilibrium was always (0,0), meaning that both players prefer action 0 (for weight sets *w* = 1, 3, 7, 9; Figure 5.2). Hence, under these weights, the cost of management drove the decision (Figure S5.4).

When the manager's weight on the final population was greater than the weight on cost ($\alpha_M > \beta_M$), the manager preferred action 1 (i.e., 100% harvest) according to MCDA (Figure 5.2). The environmentalist also preferred this action under a similar weight condition ($\alpha_N > \beta_N$). The Nash equilibrium when $\alpha_M > \beta_M$ and $\alpha_N > \beta_N$ was strategy (1,1), and they would both choose action 1 (*w* = 5, Figure 5.2).

When the weights of the attributes differed between players (i.e., when one player valued cost more and the other valued final population more) the Nash equilibrium was (0,0), meaning they should both do action 0 (*w* = 2, 4, 6, 8, Figure 5.2). This outcome reveals that the MCDA action may identify suboptimal solutions when they do not consider the preferences of another decision maker. For example, when α_M > β_M and α_N < β_N, the manager preferred action 1 per MCDA, yet the Nash equilibrium solution identified that the manager would receive a better payoff if they took action 0 (*w* = 8, Figure 5.2).

5.4.2 MANAGER VS HOBBYIST

When the hobbyist's weight on cumulative harvest was equal to or less than the weight on cost ($\alpha_N \leq \beta_N$), the hobbyist preferred action 0 according to MCDA (Figure 5.3). Since the manager's outcome does not change depending on the player, the manager's MCDA solution did not change with each game (Figure 5.2-Figure 5.4). Similar to the Manager vs Environmentalist game, when $\alpha_M \leq \beta_M$ and $\alpha_N \leq \beta_N$ the Nash equilibrium was always (0,0) (*w* = 1, 3, 7, 9 Figure 5.3).

For the hobbyist, when the weight on cumulative harvest was greater than the weight on cost (i.e., α_N > β_N), action 0.5 (i.e., 50% harvest) was preferred according to MCDA (Figure 5.3). Like the previous game, the manager's MCDA preferred action was action 1 when α_M > β_M (Figure 5.2-Figure 5.3). The Nash equilibrium when α_M > β_M and α_N > β_N was strategy (1, 0.5), where the manager would prefer action 1 and the hobbyist would prefer action 0.5 (*w* = 5, Figure 5.3).

When the manager weighted final population above cost (α_M > β_M) and the hobbyist had a low weight on cumulative harvest ($\alpha_N \leq \beta_N$) the Nash equilibrium was (0,0) (*w* = 2, 8, Figure 5.3). Like the previous game, this outcome suggests that MCDA actions may fail to identify optimal actions when dealing with multiple decision makers. Here, when α_M > β_M, the manager preferred action 1 according to MCDA, however the Nash equilibrium solution suggests that the manager should prefer action 0 (*w* = 2, 8 Figure 5.3).

If instead, the manager had a lower weight on final population ($\alpha_M \leq \beta_M$) while the hobbyist weighted harvest over cost ($\alpha_N > \beta_N$), the Nash equilibrium was (0, 0.5) (*w* = 4, 6, Figure 5.3).

5.4.2 MANAGER VS PROFITEER

The profiteer's MCDA preferred action was always 0.5 (i.e., 50% harvest) (Figure 5.4). Again, since the manager's outcome does not change depending on the player, the manager's MCDA solution did not differ in this game (Figure 5.2-Figure 5.4). When the manager weighted final population less than or equal to cost ($\alpha_M \leq \beta_M$) the Nash equilibrium solution was (0, 0.5). However, when the manager weighted final population more than cost ($\alpha_M > \beta_M$) the Nash equilibrium was (1, 0.5) (Figure 5.4).

5.4.3 SENSITIVITY ANALYSIS

We found that MCDA and game-theoretic solutions did not significantly change from the results shown above given the sensitivity analysis for all parameter sets (Figure S5.2, Figure S5.3). In addition, across various weight sets we found similar trends in the weight set sensitivity analysis as shown above. In general, an action of 0 was preferred based on expected utility (i.e., MCDA) when the weights of α (e.g., final population for the manager) were less than β (i.e., cumulative cost) for the manager, environmentalist, and hobbyist (Figure S5.1).

5.5 DISCUSSION

We compared solutions from MCDA and game theory for invasive species harvest decisions involving two decision makers: a natural resource manager and a neighboring landowner. We assumed the neighboring landowner was one of three distinct types: an environmentalist who had the same preferences as the manager, a hobbyist who enjoys harvesting the invasive species, and a profiteer who receives profit from invasive species harvest. We evaluated management outcomes using techniques of MCDA and game theory to show the differences between the outcomes that arise from both solution concepts. Overall, we have three main findings.

First, given that MCDA treats the behavior of another decision maker as a source of uncertainty, the preferred action from MCDA was occasionally suboptimal compared to the outcome from the action identified from game theory (i.e., worse payoffs for a decision maker; Figure 5.2-Figure 5.3). Specifically, MCDA methods fall short when the two decision makers have different preferences. For example, when the manager weighted final population over cost ($\alpha_M > \beta_M$) and the environmentalist weighted cost over final population ($\alpha_N < \beta_N$), MCDA identified that the manager should prefer action 1 (i.e., 100% harvest), while the neighbor should prefer action 0 (i.e., 0% harvest) (Figure 5.2). However, under these conditions, the Nash equilibrium suggested both players should prefer 0% harvest (w = 8, Figure 5.2). Hence, if the other decision maker prefers 0% harvest, the manager may also consider 0% harvest because the conservation benefits of just the manager conducting harvest are low compared to cost (w = 2, 8 Figure 5.2, Figure S5.4, Figure S5.5, also shown in w = 2, 8 Figure 5.3). Similar studies in water and energy resources management also recognized that by not considering the behavior of other players, MCDA may not correctly identify optimal solutions (Madini and Lund 2011; Motlaghzadeh et al 2020). In a study to inform offshore wind farm decision making, Golestani et al (2021) identified that MCDA methods alone are not suitable in multi-decision maker contexts because it ignores interactions and interdependence between decision makers, which could lead to worse outcomes.

Second, however, MCDA did provide useful insight into preferred actions when addressing tradeoffs between objectives for each individual player when the behavior of others is uncertain (Figure 5.2-Figure 5.4). For example, MCDA solutions for the manager and environmentalist were actions of 0% or 100% harvest, where 0% was preferred when cost was valued over invasive population outcomes (Figure 5.2). The hobbyist's MCDA solutions were 0% or 50% harvest, and 0% was preferred when cost was valued over cumulative harvest (Figure 5.3). The profiteer's MCDA solution was always 50% harvest (Figure 5.3). Hence, compared to game theory, MCDA identifies individual preferred actions, which is a key initial metric to identify in multi-decision maker settings (Motlaghzadeh et al 2020). For example, a study involving green building developments suggested that identifying and ranking preferred actions using MCDA could aid in initial natural resource management conversations involving multiple agents with conflicting interests (Bahadorestani et al., 2020).

Third, in every game, we found that all Nash equilibrium strategies were also Pareto optimal (Figure 5.2-Figure 5.4). This is an ideal outcome because a Pareto inefficient Nash equilibrium would suggest that the Nash equilibrium payoffs are not optimal, because both players could increase their payoffs if they switched their strategy. In conservation settings, a Pareto inefficient Nash equilibrium is found in the "tragedy of the commons," also referred to as a "prisoner's dilemma," wherein players will act in their own self-interest to degrade a natural resource (e.g., lumber) (Frank and Sarkar 2010; Carrozzo Magli et al., 2021). Our analysis did not demonstrate this phenomenon, though it could occur if the manager and neighbor were in direct conflict, for example, if the neighbor values the invasive population and does not obtain benefit from harvesting the population. This circumstance could certainly arise in invasive species management (Crowley et al., 2017). For example, some landowners in South Africa enjoy invasive cacti (*Cactaceae*) in their yard despite government agencies actively removing cacti from the environment (Kaplan et al., 2017). In another example, some citizens in Chicago enjoy seeing invasive Monk parakeets (*Myiopsitta monachus*) in the city as they represent a symbol of resilience during harsh winters, while natural resource agencies call for their removal from the city (Crowley et al., 2019). Hence, future studies involving extreme conflict should identify the status of whether Nash equilibrium solutions are Pareto optimal.

There are some limitations to the approach we provided in this study. For instance, we assumed a set of weights (Table 5.3) that were subjectively selected and not identified from real decision makers. There are a variety of methods that can be used to generate these weights from decision makers (see Hobbs and Meir 2000; Faccioli et al., 2019). For example, such methods involve asking the decision maker to make tradeoffs when given sets of potential alternatives of which vary in the attributes. Another limitation of our approach is that we assumed a single utility function across all attributes. Utility functions can be identified by asking decision makers to make choices between hypothetical gambles (Farquhar 1984; Runge and Converse 2020). This action helps identify the risk tolerance of the decision maker based on their choices between gambling options. However, there are some challenges with eliciting utility functions. For instance, a decision maker may not be consistent with their choices, which may result in an inaccurate function. In addition, a common MCDA practice is to re-standardize outcomes of attributes to a 0 to 1 scale to compare across different attributes (e.g., cost and invasive population). However, this practice is not performed in game theory because it violates axioms of game-theoretic utility theory (Yaroufakis 1993). Game theory assumes each player’s utility is assumed as given and thus prohibits transforming utilities to evaluate choices.

Further research in the space of MCDA and game-theoretic applications in conservation can extend upon the approach we provided. For instance, we assumed that individuals did not switch their harvest level throughout the entire 20-year span and individuals did not form an “alliance” to agree upon harvest levels. In game theory, this means we assumed we had a static non-cooperative game instead of a dynamic cooperative game, limiting the solution concepts that could be used. However, if decisions are identified iteratively through time, a dynamic game could be implemented. If alliances can be formed across players, a cooperative game could be used (see Büyüktahtakın et al., 2013 and Siriwardena et al. 2018 for examples of dynamic cooperative games in invasive species contexts). Also, one could consider more actions than the ones we described. For example, there could be an action where the neighbor illegally stocks invasive species into the environment (e.g., sportfish: Johnson et al., 2009; Fernández et al., 2019). In addition, other potential neighbors could be modeled. For example, one might consider the case that a manager and a "bounty hunter" are both removing invasive species in an area and game theory might be useful to examine conflict between these two players. In addition, we assumed that only two equal decision makers were involved in invasive species management. Future studies could consider an unequal management domain of the players and even multiplayer games could be explored in which all players interact with each other simultaneously (e.g., Manager vs Environmentalist vs Hobbyist vs Profiteer game; *N*-player games, Frank and Sarkar 2010). Also, approaches to hybridize methods from MCDA and game theory could be explored in conservation applications. In fact, a variety of other disciplines have developed approaches to hybridize these two fields by merging MCDA's various ranking techniques within a game context (Chhipi-Shrestha et al. 2019; Collins and Kumral 2020; Motlaghzadeh et al., 2023). In a recent review of hybrid MCDA and game-theory approaches, Ibrahim et al. (2021) described applications in a variety of fields including politics (Atashbar et al., 2009), supply chain management (Lau et al., 2020), and wastewater management (Liu and Ren 2022). Future studies could attempt to merge MCDA and game theory concepts in conservation applications.

In general, since natural resource management involves a variety of decision makers, managers can benefit by incorporating the potential preferences and actions of other decision makers into their decision analyses. We showed that MCDA solutions sometimes failed to reveal potential optimal actions for the manager because the Nash equilibrium solutions pointed to a different action, yielding a better outcome for the manager, compared to MCDA. However, MCDA does provide insight into the preferred actions of each decision maker when the behavior of others is not considered, which is a key initial metric to identify in multi-decision maker settings. We suggest that both game theory and MCDA analysis can be used alongside each other to aid in decision making involving multiple decision makers.

5.6 ACKNOWLEDGEMENT

This research was funded through support of B.K. Thompson by the Washington Cooperative Fish and Wildlife Research Unit, the College of the Environment, University of Washington, and the School of Aquatic and Fishery Sciences, University of Washington. We would like to thank Christopher Anderson for his guidance in the game theoretic components of this study. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

5.7 TABLES & FIGURES

Table 5.1 We assumed three multi-decision maker applications for invasive species management involving a natural resource manager and a neighboring landowner, the "neighbor." We assumed the manager has preferences to have low final invasive population and low management costs. The neighbor is either one of three potential neighbors: an environmentalist (same preferences as the manager), a hobbyist (enjoys harvesting the invasive species and prefers low harvest cost), or a profiteer (enjoys high profits, calculated as income minus cost). For each type of neighbor, we provide examples in terrestrial, freshwater, and marine applications. In MCDA the actions of the other decision maker are a source of uncertainty (e.g., the manager treats the actions of a profiteer neighbor as uncertain). In game theory, the actions and outcomes of both decision makers are evaluated simultaneously (e.g., the outcomes of the manager and the profiteer neighbor are evaluated together). Photographs: Licensed under Creative Commons

Neighbor	**Terrestrial Example**	**Freshwater Example**	**Marine Example**
Environmentalist	Invasive barberry landowner removal (Snyder et al. 2020) 	Invasive Eurasian milfoil lakefront property removal (Olden & Tamayo 2014)	Invasive algae removal in Hawaii (Smith et al. 2004)
Hobbyist	Invasive hog hunting (Smith et al. 2023)	Invasive bass recreational fishing (Long and Seguy 2024) 	Invasive lionfish spearfish hunting (Ulman et al. 2022)
Profiteer	Honey from invasive honeybees (Carpenter and Harpur 2020)	Invasive tilapia aquaculture (Marr et al. 2017)	Invasive red king crab fishery (Kourantidou and Kaiser 2021) 

Table 5.2 Objectives and associated attributes (i.e., units of measurement) for each player, including the manager (denoted as *M*) and each of the neighbors: environmentalist (N_E), hobbyist (N_H), and profiteer (N_P) including equations of the attributes. In the equations, index *M* references the manager, *N* references the neighbor, *s* describes the strategy, and *t* is years (from 1 to $T = 20$ years). The manager's first objective is to minimize final population in both player's areas, and the attribute for this objective is expressed as ${X_s}^{total}$ for strategy $s \in \boldsymbol{S}$ strategy set, where $X_{M,s,T}$ and $X_{N,s,T}$ are the final (year, $T = 20$) population in the manager and neighbor's location respectively for each strategy s . The manager's second objective is to minimize cumulative harvest, and the attribute is denoted as ${C_{M,s}}^{total}$, where $C_{M,s,t}$ is the manager's annual (t) harvest cost per strategy s. The environmentalist has similar objectives and attributes as the manager, except cumulative cost is in terms of the neighbor, ${C_{N,s}}^{total}$, where $C_{N,s,t}$ is the neighbor's annual harvest cost . The hobbyist' first objective is to maximize cumulative harvest, with an attribute denoted as ${H_{N,s}}^{total}$, summed across annual harvest, $h_{N,s}X_{N,s,t}$, where $h_{N,s}$ is the harvest rate per strategy s for the neighbor. The hobbyist's second objective is to minimize cumulative harvest cost, with an attribute denoted as ${C_{N,s}}^{total}$. The profiteer has one objective, to maximize cumulative profit, ${P_{N,s}}^{total}$, a function of cumulative revenue, denoted annually as $R_{N,s,t}$, minus annual harvest cost.

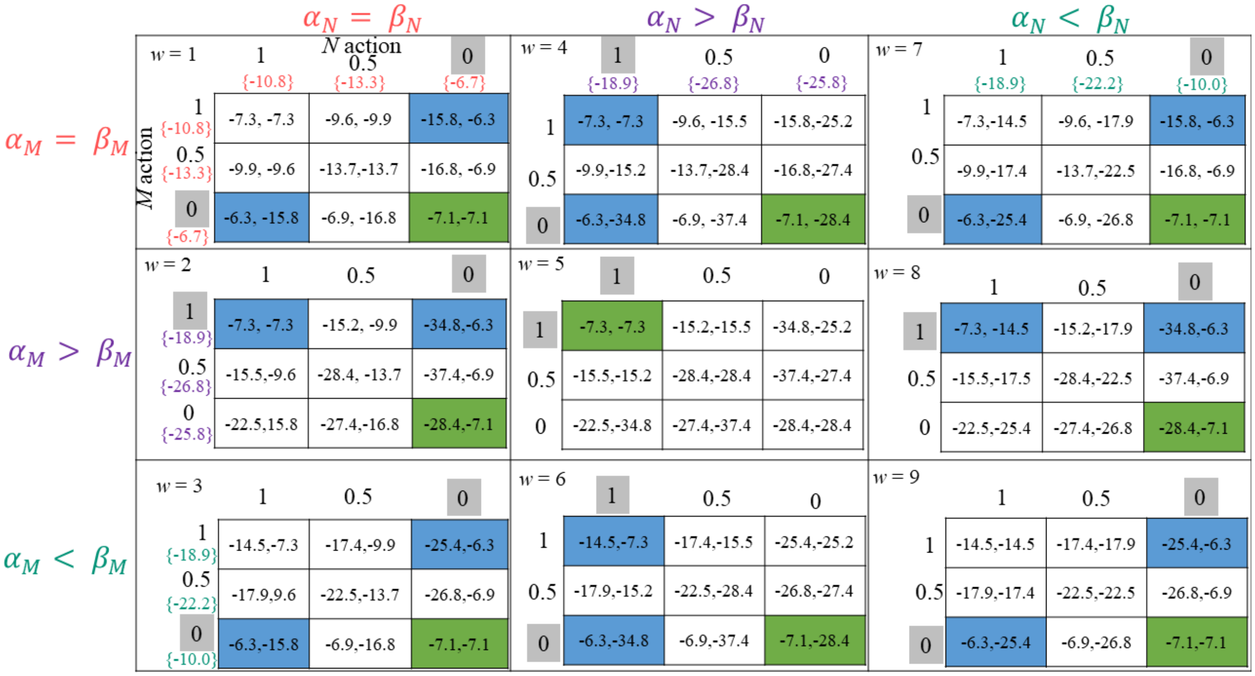
Player	Objective 1, Attribute	Objective 2, Attribute
Manager, *M*	Minimize final population in both player's areas, ${X_s}^{total} = X_{M,s,T} + X_{N,s,T}$	Minimize cumulative cost of harvest: ${C_{M,s}}^{total} = \sum_{t=1}^{T} C_{M,s,t}$
Environmentalist, N_E	Minimize final population in both player's areas, ${X_s}^{total} = X_{M,s,T} + X_{N,s,T}$	Minimize cumulative cost, ${C_{N,s}}^{total} = \sum_{t=1}^{T} C_{N,s,t}$
Hobbyist, N_H	Maximize cumulative harvest, ${H_{N,s}}^{total} = \sum_{t=1}^{T} h_{N,s}X_{N,s,t}$	Minimize cumulative cost, ${C_{N,s}}^{total} = \sum_{t=1}^{T} C_{N,s,t}$
Profiteer, N_P	Maximize cumulative profit (total Revenue – total Cost), ${P_{N,s}}^{total} = \sum_{t=1}^{T} R_{N,s,t} - \sum_{t=1}^{T} C_{N,s,t} =$ ${R_{N,s}}^{total} - {C_{N,s}}^{total}$	None

Table 5.3 Description of the nine weighting schemes we used in this study, where the weighting scheme was a function of the weights placed on attributes by both the manager and the neighbor players. α_i are the weights respectively for the attribute of Objective 1, for the manager when *i* = *M* and neighbor when *i* = *N*. β_i are the weights respectively for the attribute of Objective 2, for the manager when *i* = *M* and neighbor when *i* = *N*. For each player *i*, the weighting scheme consists of either $\alpha_i = \beta_i$, $\alpha_i > \beta_i$, or $\alpha_i < \beta_i$. This means that the attitude towards Objective 1's attribute is either equal to, greater than, or less than Objective 2's attribute, regardless of the unit comparison between attributes (e.g., invasive population and dollar amount).

Weight set	Manager weights	Neighbor's weights
1	$\alpha_M = \beta_M = 1$	$\alpha_N = \beta_N = 1$
2	$\alpha_M > \beta_M$: $\alpha_M = 4$, $\beta_M = 1$	$\alpha_N = \beta_N = 1$
3	$\alpha_M < \beta_M$: $\alpha_M = 1$, $\beta_M = 2$	$\alpha_N = \beta_N = 1$
4	$\alpha_M = \beta_M = 1$	$\alpha_N > \beta_N$: $\alpha_N = 4$, $\beta_N = 1$
5	$\alpha_M > \beta_M$: $\alpha_M = 4$, $\beta_M = 1$	$\alpha_N > \beta_N$: $\alpha_N = 4$, $\beta_N = 1$
6	$\alpha_M < \beta_M$: $\alpha_M = 1$, $\beta_M = 2$	$\alpha_N > \beta_N$: $\alpha_N = 4$, $\beta_N = 1$
7	$\alpha_M = \beta_M = 1$	$\alpha_N < \beta_N$: $\alpha_N = 1$, $\beta_N = 2$
8	$\alpha_M > \beta_M$: $\alpha_M = 4$, $\beta_M = 1$	$\alpha_N < \beta_N$: $\alpha_N = 1$, $\beta_N = 2$
9	$\alpha_M < \beta_M$: $\alpha_M = 1$, $\beta_M = 2$	$\alpha_N < \beta_N$: $\alpha_N = 1$, $\beta_N = 2$

		Neighbor, *N*, action		
		1	0.5	0
Manager, *M*, action	1	$f^w_{M,s=1}, f^w_{N,s=1}$	$f^w_{M,s=2}, f^w_{N,s=2}$	$f^w_{M,s=3}, f^w_{N,s=3}$
	0.5	$f^w_{M,s=4}, f^w_{N,s=4}$	$f^w_{M,s=5}, f^w_{N,s=5}$	$f^w_{M,s=6}, f^w_{N,s=6}$
	0	$f^w_{M,s=7}, f^w_{N,s=7}$	$f^w_{M,s=8}, f^w_{N,s=8}$	$f^w_{M,s=9}, f^w_{N,s=9}$

Figure 5.1 Graphical representation of a game in matrix form. Each cell represents the paired payoff of a manager ($f^{w}_{M,s}$, first payoff) and a neighbor ($f^{w}_{N,s}$, second payoff), for each strategy s_1, …, $s_9 \epsilon$ **S,** which is the combination of the manager and neighbor's actions of 1, 0.5, or 0 harvest rates. The payoffs are evaluated for each weight set *w*.



$\alpha_N = \beta_N$ | $\alpha_N > \beta_N$ | $\alpha_N < \beta_N$

$\alpha_M = \beta_M$

$w = 1$ (M action \ N action)	1 {-10.8}	0.5 {-13.3}	0 {-6.7}
1 {-10.8}	-7.3, -7.3	-9.6, -9.9	-15.8, -6.3
0.5 {-13.3}	-9.9, -9.6	-13.7,-13.7	-16.8, -6.9
0 {-6.7}	-6.3, -15.8	-6.9, -16.8	-7.1,-7.1

$w = 4$	1 {-18.9}	0.5 {-26.8}	0 {-25.8}
1	-7.3, -7.3	-9.6, -15.5	-15.8,-25.2
0.5	-9.9,-15.2	-13.7,-28.4	-16.8,-27.4
0	-6.3,-34.8	-6.9, -37.4	-7.1, -28.4

$w = 7$	1 {-18.9}	0.5 {-22.2}	0 {-10.0}
1	-7.3,-14.5	-9.6, -17.9	-15.8, -6.3
0.5	-9.9,-17.4	-13.7,-22.5	-16.8, -6.9
0	-6.3,-25.4	-6.9, -26.8	-7.1, -7.1

$\alpha_M > \beta_M$

$w = 2$	1	0.5	0
1 {-18.9}	-7.3, -7.3	-15.2, -9.9	-34.8,-6.3
0.5 {-26.8}	-15.5,-9.6	-28.4, -13.7	-37.4,-6.9
0 {-25.8}	-22.5,15.8	-27.4,-16.8	-28.4,-7.1

$w = 5$	1	0.5	0
1	-7.3, -7.3	-15.2,-15.5	-34.8,-25.2
0.5	-15.5,-15.2	-28.4,-28.4	-37.4,-27.4
0	-22.5,-34.8	-27.4,-37.4	-28.4,-28.4

$w = 8$	1	0.5	0
1	-7.3, -14.5	-15.2,-17.9	-34.8,-6.3
0.5	-15.5,-17.5	-28.4,-22.5	-37.4,-6.9
0	-22.5,-25.4	-27.4,-26.8	-28.4,-7.1

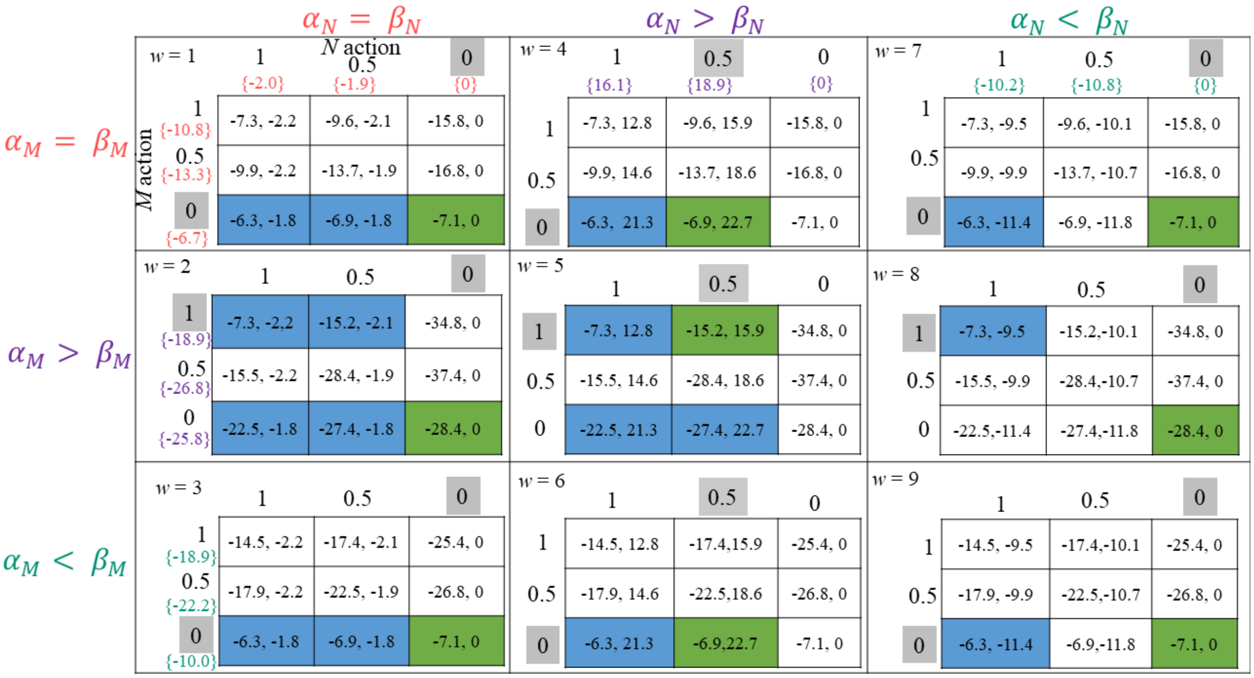
$\alpha_M < \beta_M$

$w = 3$	1	0.5	0
1 {-18.9}	-14.5,-7.3	-17.4,-9.9	-25.4,-6.3
0.5 {-22.2}	-17.9,9.6	-22.5,-13.7	-26.8,-6.9
0 {-10.0}	-6.3,-15.8	-6.9,-16.8	-7.1,-7.1

$w = 6$	1	0.5	0
1	-14.5,-7.3	-17.4,-15.5	-25.4,-25.2
0.5	-17.9,-15.2	-22.5,-28.4	-26.8,-27.4
0	-6.3,-34.8	-6.9,-37.4	-7.1,-28.4

$w = 9$	1	0.5	0
1	-14.5,-14.5	-17.4,-17.9	-25.4,-6.3
0.5	-17.9,-17.4	-22.5,-22.5	-26.8,-6.9
0	-6.3,-25.4	-6.9,-26.8	-7.1,-7.1

Figure 5.2 Matrix representation of the Manager vs Environmentalist game for each of the 9 sets of weights, indicated by α and β (the weight on attribute 1 and 2 for each player), the w symbol on the top left corner also represents the weight set. Each matrix has 9 cells, the first value represents the payoff of the manager's action, and the second value represents the payoff of the environmentalist's action. The actions of both players (harvest rates 1, 0.5, or 0) are identified outside of the matrix. The MCDA for expected utility action is shown with a grey box for each player. Each player's expected utility for each action is indicated in the colored bracket. The game theory solutions are shown with blue for Pareto optimal, and green for both Pareto optimal and Nash equilibrium.



$\alpha_N = \beta_N$

$\alpha_M = \beta_M$

w = 1	N action 1 {-2.0}	0.5 {-1.9}	0 {0}
M action 1 {-10.8}	-7.3, -2.2	-9.6, -2.1	-15.8, 0
0.5 {-13.3}	-9.9, -2.2	-13.7, -1.9	-16.8, 0
0 {-6.7}	-6.3, -1.8	-6.9, -1.8	-7.1, 0

$\alpha_M > \beta_M$

w = 2	1	0.5	0
1 {-18.9}	-7.3, -2,2	-15.2, -2.1	-34.8, 0
0.5 {-26.8}	-15.5, -2.2	-28.4, -1.9	-37.4, 0
0 {-25.8}	-22.5, -1.8	-27.4, -1.8	-28.4, 0

$\alpha_M < \beta_M$

w = 3	1	0.5	0
1 {-18.9}	-14.5, -2.2	-17.4, -2.1	-25.4, 0
0.5 {-22.2}	-17.9, -2.2	-22.5, -1.9	-26.8, 0
0 {-10.0}	-6.3, -1.8	-6.9, -1.8	-7.1, 0

$\alpha_N > \beta_N$

w = 4	1 {16.1}	0.5 {18.9}	0 {0}
1	-7.3, 12.8	-9.6, 15.9	-15.8, 0
0.5	-9.9, 14.6	-13.7, 18.6	-16.8, 0
0	-6.3, 21.3	-6.9, 22.7	-7.1, 0

w = 5	1	0.5	0
1	-7.3, 12.8	-15.2, 15.9	-34.8, 0
0.5	-15.5, 14.6	-28.4, 18.6	-37.4, 0
0	-22.5, 21.3	-27.4, 22.7	-28.4, 0

w = 6	1	0.5	0
1	-14.5, 12.8	-17.4,15.9	-25.4, 0
0.5	-17.9, 14.6	-22.5,18.6	-26.8, 0
0	-6.3, 21.3	-6.9,22.7	-7.1, 0

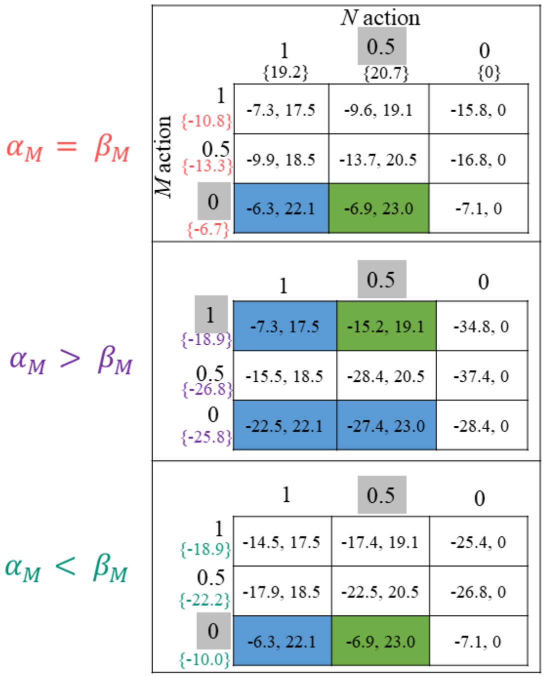
$\alpha_N < \beta_N$

w = 7	1 {-10.2}	0.5 {-10.8}	0 {0}
1	-7.3, -9.5	-9.6, -10.1	-15.8, 0
0.5	-9.9, -9.9	-13.7, -10.7	-16.8, 0
0	-6.3, -11.4	-6.9, -11.8	-7.1, 0

w = 8	1	0.5	0
1	-7.3, -9.5	-15.2,-10.1	-34.8, 0
0.5	-15.5, -9.9	-28.4,-10.7	-37.4, 0
0	-22.5,-11.4	-27.4,-11.8	-28.4, 0

w = 9	1	0.5	0
1	-14.5, -9.5	-17.4,-10.1	-25.4, 0
0.5	-17.9, -9.9	-22.5,-10.7	-26.8, 0
0	-6.3, -11.4	-6.9,-11.8	-7.1, 0

Figure 5.3 Representation of the Manager vs Hobbyist game for each of the 9 sets of weights. indicated by α and β (the weight on attribute 1 and 2 for each player), the w symbol on the top left corner also represents the weight set. Each matrix has 9 cells, the first value represents the payoff of the manager's action, and the second value represents the payoff of the environmentalist's action. The actions of both players (harvest rates 1, 0.5, or 0) are identified outside of the matrix. The MCDA for expected utility action is shown with a grey box for each player. Each player's expected utility for each action is indicated in the colored bracket. The game theory solutions are shown with blue for Pareto optimal, and green for both Pareto optimal and Nash equilibrium.



	1 {19.2}	0.5 {20.7}	0 {0}
1 {-10.8}	-7.3, 17.5	-9.6, 19.1	-15.8, 0
0.5 {-13.3}	-9.9, 18.5	-13.7, 20.5	-16.8, 0
0 {-6.7}	-6.3, 22.1	-6.9, 23.0	-7.1, 0

	1	0.5	0
1 {-18.9}	-7.3, 17.5	-15.2, 19.1	-34.8, 0
0.5 {-26.8}	-15.5, 18.5	-28.4, 20.5	-37.4, 0
0 {-25.8}	-22.5, 22.1	-27.4, 23.0	-28.4, 0

	1	0.5	0
1 {-18.9}	-14.5, 17.5	-17.4, 19.1	-25.4, 0
0.5 {-22.2}	-17.9, 18.5	-22.5, 20.5	-26.8, 0
0 {-10.0}	-6.3, 22.1	-6.9, 23.0	-7.1, 0

Figure 5.4 Representation of the Manager vs Hobbyist game for the three unique manager weights. Each matrix has 9 cells, the first value represents the payoff of the manager's action, and the second value represents the payoff of the environmentalist's action. The actions of both players (harvest rates 1, 0.5, or 0) are identified outside of the matrix. The MCDA for expected utility action is shown with a grey box for each player. Each player's expected utility for each action is indicated in the colored bracket. The game theory solutions are shown with blue for Pareto optimal, and green for both Pareto optimal and Nash equilibrium.

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5.9 APPENDIX 5

Sensitivity Analysis: Weights

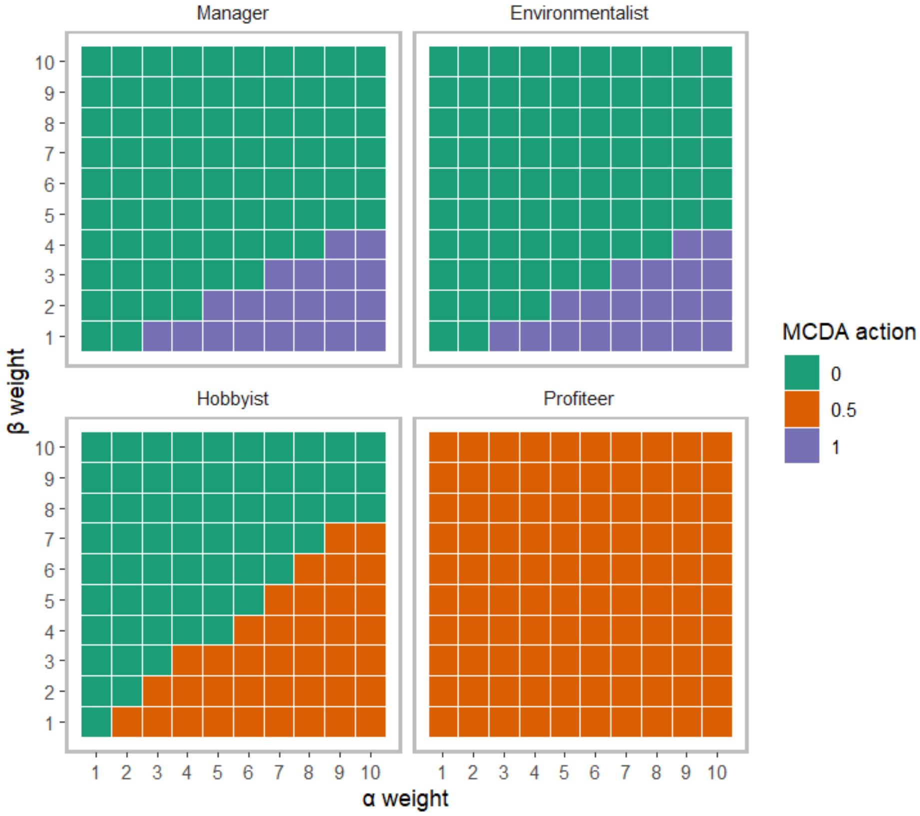

Figure S5.1 MCDA action for each player against different preference weights. For each player, (Manager, Environmentalist, Hobbyist, and Profiteer), the MCDA expected utility action (either 0, 0.5, or 1 harvest values, depicted with the colors) against different values of α (attribute 1) and β (attribute 2) is identified. The profiteer has no attribute weights, hence their MCDA action is always 0.5.

Sensitivity Analysis: Parameters

We provided a sensitivity analysis for parameter values in the biological and economic models. First, we generated 5,760 parameter sets describing unique combinations of the parameter values (Table S5.1). Then we compared results from the base model (Figure S5.2) and across all parameter sets (Figure S5.3). The sensitivity analysis revealed that parameter deviations did not change the most frequent action (for MCDA solutions) or strategy (for game theory) from those identified in this analysis (Table S5.1, Figure S5.2). Under some parameter values and weight sets, additional actions and strategies were identified. For example, when growth rates were less than 1, hobbyist and profiteer neighbors would do action 1.

Table S5.1 Description of parameter sensitivity analysis we performed on each parameter, growth rate (r), dispersal rate (b), per unit cost of harvest (c_h), and per unit revenue (c_r). Together, we generated 5,760 parameter sets that defined the unique combinations of all parameters given the perturbations. The second column represents the base value used in the results in the main text.

Parameter (notation)	**Base value**	**Parameter perturbation (sequence of values)**
Growth rate (r)	1	Sequence from 0.1 to 2 by 0.1
Dispersal rate (b)	0.3	Sequence from 0.1 to 0.9 by 0.1
Per unit cost of removal (c_h)	10	Sequence from 5 to 20 by 5
Per unit income (c_g)	200	Sequence from 10 to 400 by 50

In addition to expected value (in our case, expected utility), we also assessed maxi-max and maxi-min solutions for MCDA. The maxi-min criterion, which is used for risk-averse decision makers, identifies the action with an outcome that minimizes maximum payoff loss (i.e., the "best-worst" strategy, Savage 1951). To calculate this expression (using notation from Figure 5.1), we first find the minimum value across each action. For example, for the manager we would find the minimum value across action 1 as: $\min(\mathrm{M}, \mathrm{action} = 1) = \min\{f_{M,s=1}, f_{M,s=2}, f_{M,s=3}\}$, the minimum value across action 0.5 as $\min(\mathrm{M}, \mathrm{action} = 0.5) = \min\{f_{M,s=4}, f_{M,s=5}, f_{M,s=6}\}$, and the minimum across action 0 as $\min(\mathrm{M}, \mathrm{action} = 0) = \min\{f_{M,s=7}, f_{M,s=8}, f_{M,s=9}\}$. Then we would select the maxi-min solution as the action (either action 1, 0.5, or 0) that resulted in the maximum value when comparing $\mathrm{Min}(\mathrm{M}, \mathrm{action} = 1), \mathrm{Min}(\mathrm{M}, \mathrm{action} = 0.5)$, and $\mathrm{Min}(\mathrm{M}, \mathrm{action} = 0)$. We calculated this criterion for the Neighbor similarly.

The maxi-max criterion, used for risk-seeking decision makers, identifies an outcome that maximizes the maximum payoff. To calculate this expression, we first find the maximum value across each action. For example, for the manager we would find the maximum value across action 1 as: $\max(\mathrm{M}, \mathrm{action} = 1) = \max\{f_{M,s=1}, f_{M,s=2}, f_{M,s=3}\}$, the maximum value across action 0.5 as $\max(\mathrm{M}, \mathrm{action} = 0.5) = \max\{f_{M,s=4}, f_{M,s=5}, f_{M,s=6}\}$, and the maximum across action 0 as $\max(\mathrm{M}, \mathrm{action} = 0) = \max\{f_{M,s=7}, f_{M,s=8}, f_{M,s=9}\}$. Then we would select the maxi-max solution as the action (either action 1, 0.5, or 0) that resulted in the maximum value when comparing $\mathrm{Max}(\mathrm{M}, \mathrm{action} = 1), \mathrm{Max}(\mathrm{M}, \mathrm{action} = 0.5)$, and $\mathrm{Min}(\mathrm{M}, \mathrm{action} = 0)$. We calculated this criterion for the Neighbor similarly. Across the weight sets, we found the relative frequency of each action in being the expected value, maxi-min, and maxi-maxi solution for each player.

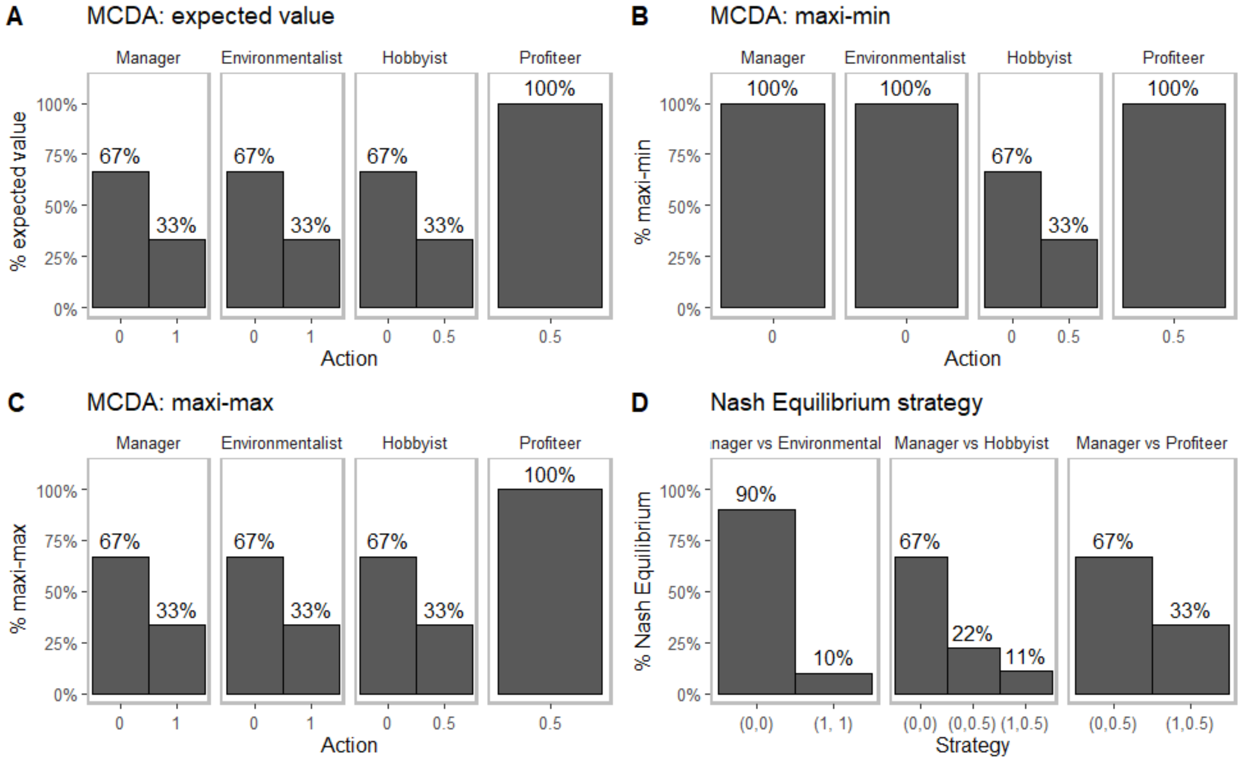

Figure S5.2 Relative frequency of MCDA for each player and game theory outcomes for each game across the parameter values used in the main analysis. A. Frequency of an action in being the expected utility solution for each player. B. Frequency of an action in being the maxi-min solution for each player. C. Frequency of an action in being the maxi-max solution for each player. D. The Nash equilibrium strategy for each game.

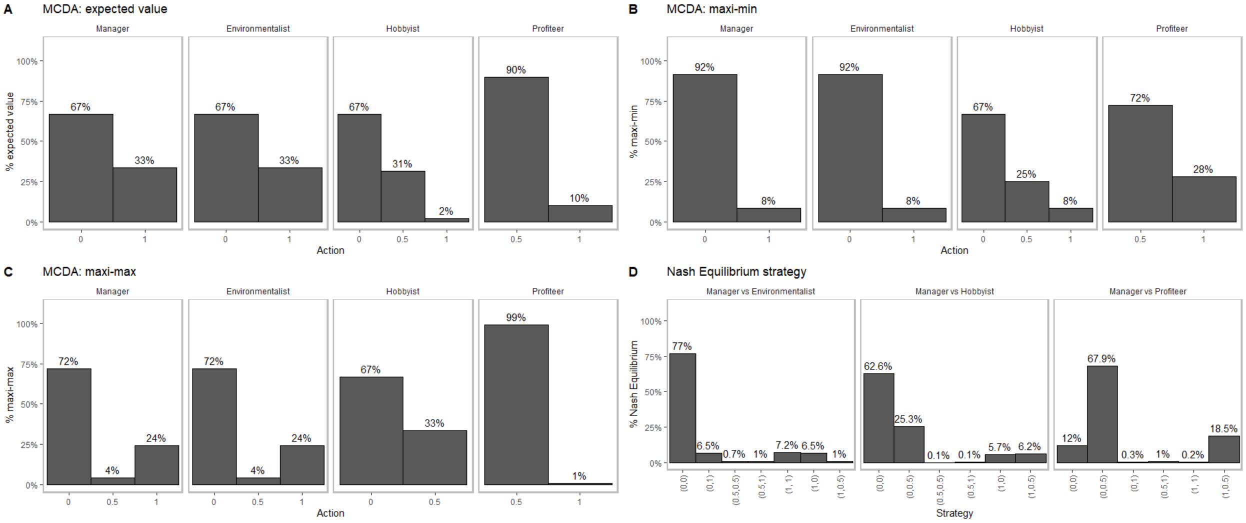

Figure S5.3 Relative frequency of MCDA for each player and game theory outcomes for each game across the parameter values used in the main analysis. A. Frequency of an action in being the expected utility solution for each player. B. Frequency of an action in being the maxi-min solution for each player. C. Frequency of an action in being the maxi-max solution for each player. D. The Nash equilibrium strategy for each game.

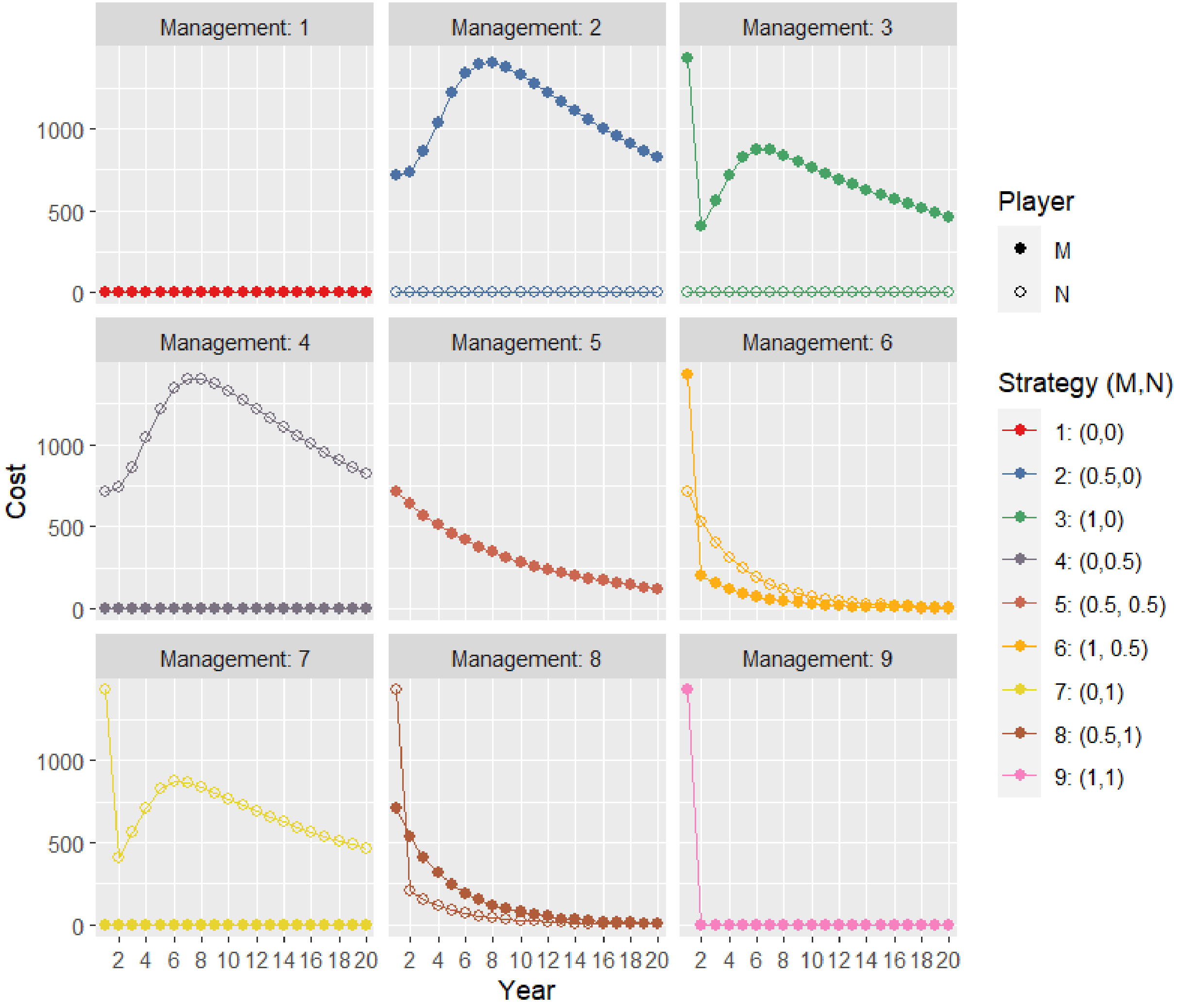

Figure S5.4 Harvest cost through time for the manager (M, denoted with closed circles), and neighbor (N, denoted with open circles) for each of the 9 potential strategies, (indicated with the facet plots and the color of the points).

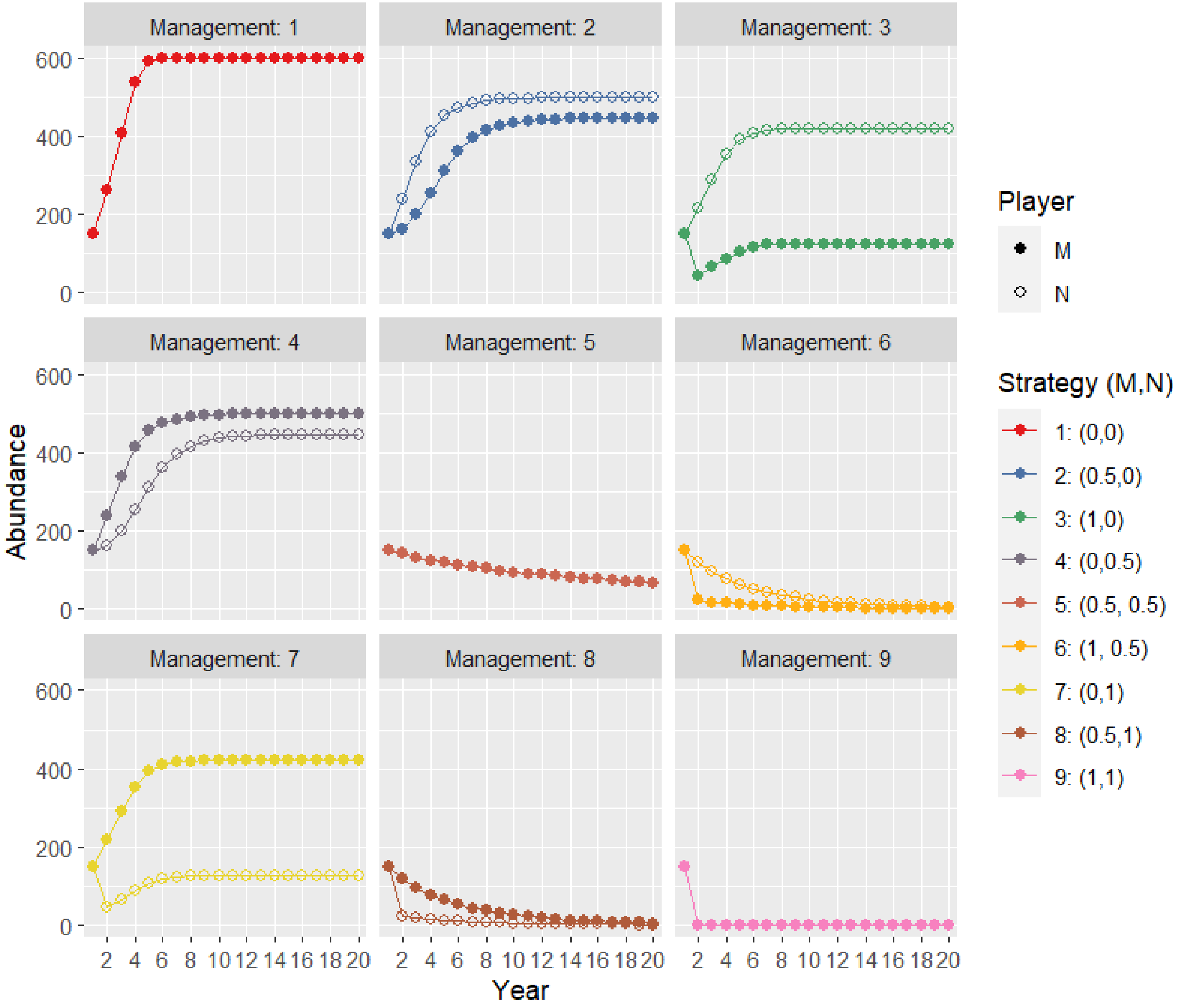

Figure S5.5 Invasive population abundance through time for the manager (M, denoted with closed circles), and neighbor (N, denoted with open circles) for each of the 9 potential strategies, (indicated with the facet plots and the color of the points).

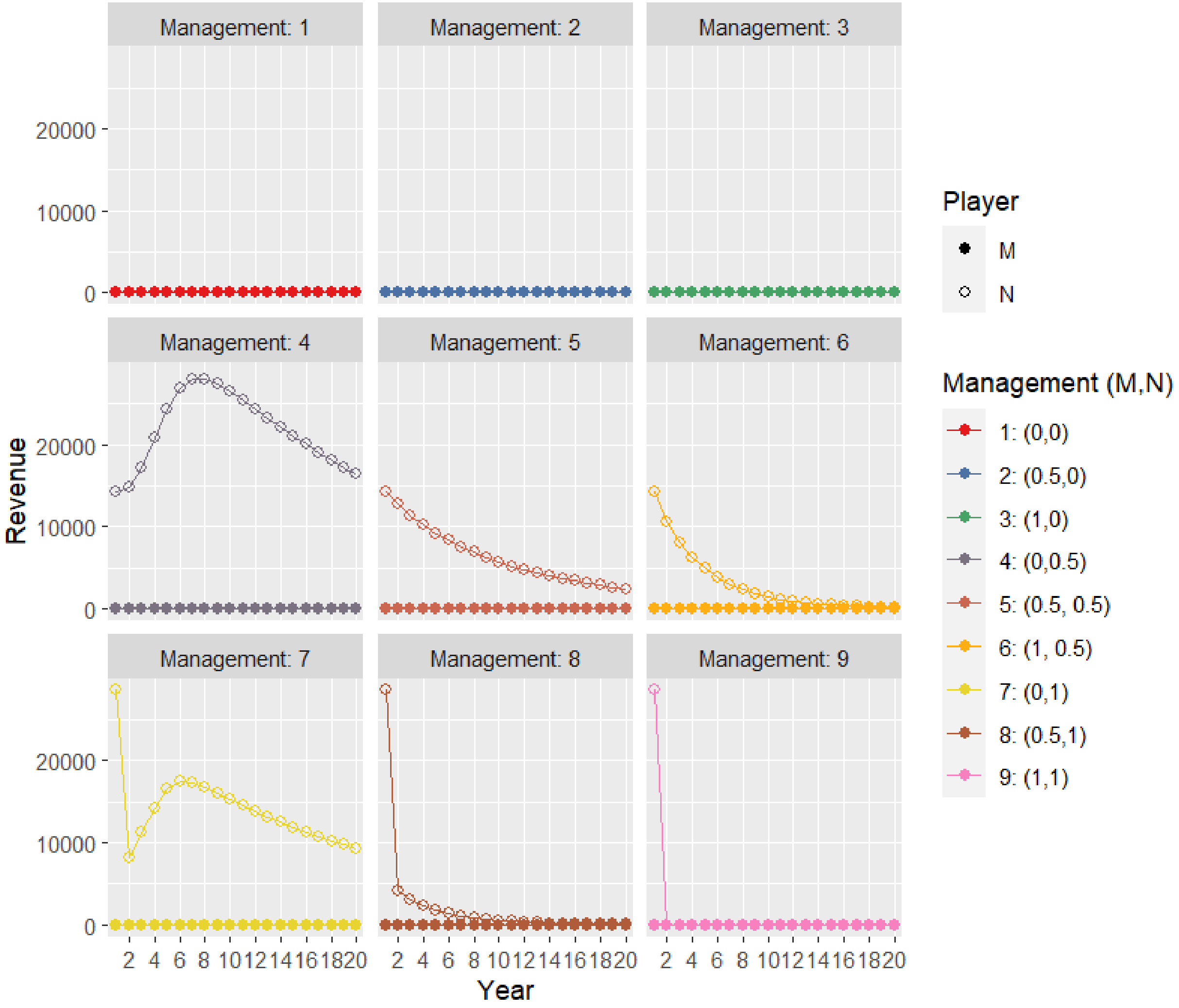

Figure S5.6 Harvest through time for the manager (M, denoted with closed circles), and neighbor (N, denoted with open circles) for each of the 9 potential strategies, (indicated with the facet plots and the color of the points).

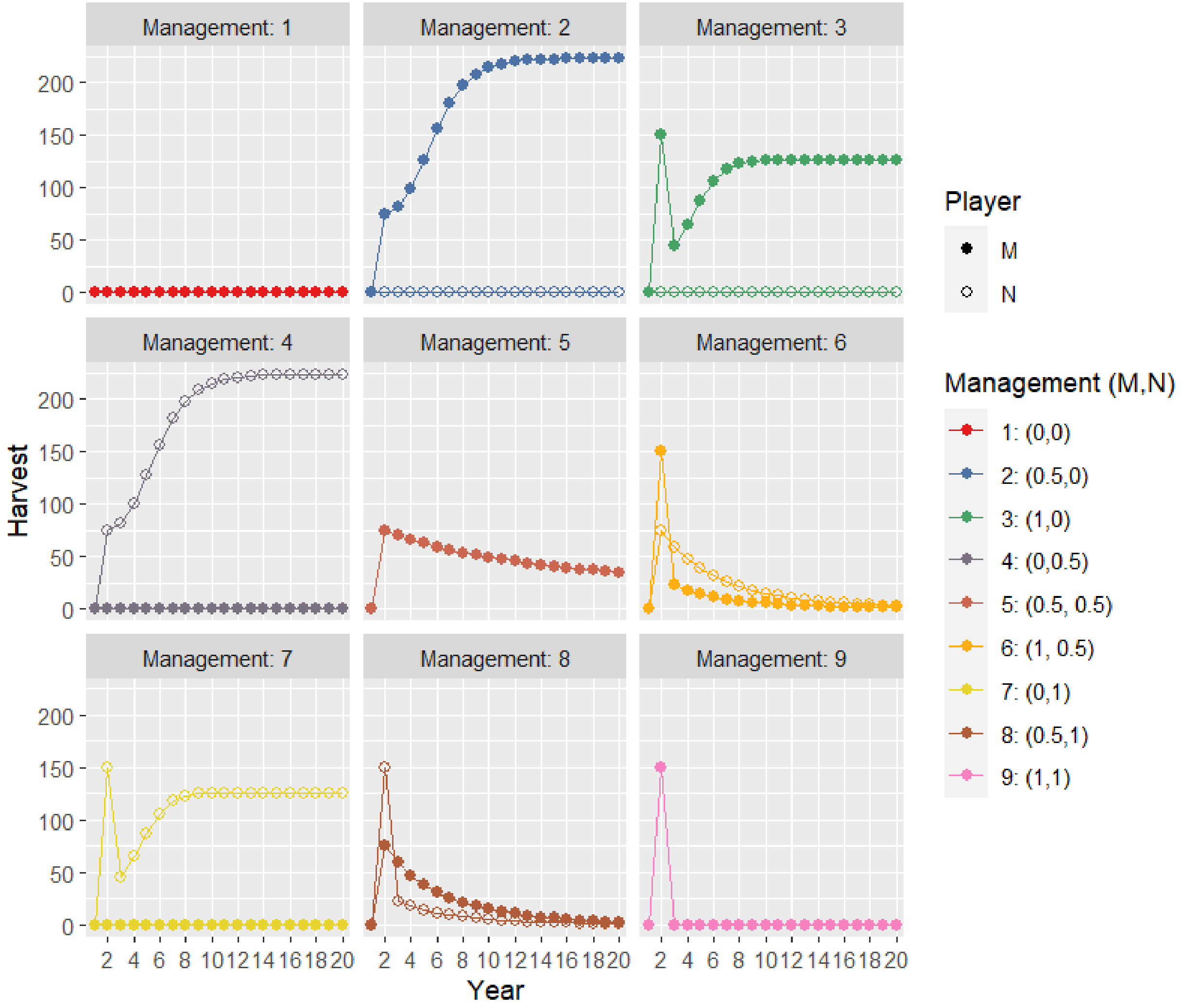

Figure S5.7 Revenue through time for the manager (M, denoted with closed circles), which was always 0, and neighbor (N, denoted with open circles) for each of the 9 potential strategies, (indicated with the facet plots and the color of the points).