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ARTICLE



Optimizing management of invasions in an uncertain world using dynamic spatial models

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Abstract

Dispersal drives invasion dynamics of nonnative species and pathogens. Applying knowledge of dispersal to optimize the management of invasions can mean the difference between a failed and a successful control program and dramatically improve the return on investment of control efforts. A common approach to identifying optimal management solutions for invasions is to optimize dynamic spatial models that incorporate dispersal. Optimizing these spatial models can be very challenging because the interaction of time, space, and uncertainty rapidly amplifies the number of dimensions being considered. Addressing such problems requires advances in and the integration of techniques from multiple fields, including ecology, decision analysis, bioeconomics, natural resource management, and optimization. By synthesizing recent advances from these diverse fields, we provide a workflow for applying ecological theory to advance optimal management science and highlight priorities for optimizing the control of invasions. One of the striking gaps we identify is the extremely limited consideration of dispersal uncertainty in optimal management frameworks, even though dispersal estimates are highly uncertain and greatly influence invasion outcomes. In addition, optimization

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frameworks rarely consider multiple types of uncertainty (we describe five major types) and their interrelationships. Thus, feedbacks from management or other sources that could magnify uncertainty in dispersal are rarely considered. Incorporating uncertainty is crucial for improving transparency in decision risks and identifying optimal management strategies. We discuss gaps and solutions to the challenges of optimization using dynamic spatial models to increase the practical application of these important tools and improve the consistency and robustness of management recommendations for invasions.

KEYWORDS

alien species, bioeconomic, decision analysis, disease, dispersal, invasion, invasive species, management, optimal control, resource allocation, spatial, uncertainty

INTRODUCTION

Globally, invasions of pest species and pathogens (invaders) impose devastating costs on economic sectors, natural ecosystems, and human health (Diagne et al., 2021; Early et al., 2016). Once an invader becomes established, its elimination or even containment can be extremely costly and difficult to achieve (Leung et al., 2002). Thus, answering the question of how resources should be allotted over time and space to optimize the management of invasions is crucial for control activities to proceed costeffectively (Baker, 2017; Chadès et al., 2011; Travis & Park, 2004) and may determine success or failure (Moody & Mack, 1988). Optimization with dynamic spatial models of established invasions can serve this question well (Baker, 2017, Chadès et al., 2011; Travis & Park, 2004) but also introduces novel methodological and conceptual challenges. The addition of space to dynamic optimization increases the computational complexity dramatically relative to optimization problems that only consider time. In addition, invasions are governed by dispersal (rates and directions that individuals move throughout landscapes), which is often poorly understood and difficult to measure (Cayuela et al., 2018), leading to high uncertainty in spatial predictions. Optimizing dynamic spatial models informed by dispersal introduces the need to account for additional sources of uncertainty, adding both conceptual complexity and data requirements.

Numerous studies have demonstrated the benefits of using dynamic spatial models to optimize resource allocation in the management of invasions (Chadès et al., 2011; Glen et al., 2013; Haydon et al., 2006; Pepin, Smyser, et al., 2020; Travis & Park, 2004), but recommendations for managers have been context-specific and lack generalized management recommendations across studies (Büyüktahtakın & Haight, 2018; Appendix S1: Table S1). Some illustrative examples of the variety of different recommendations include the following: "target the most highly connected local populations" when examining a network of spatially segregated local populations (Perry et al., 2017) or "target the source" when modeling individuals as dispersing continuously in space (Baker, 2017). Using network approaches, Epanchin-Niell and Wilen (2012) recommended preventing or delaying spread in directions of high potential for invasion damage. In a different network analysis, Chadès et al. (2011) recommended prioritizing the management of (1) upstream local populations in directional networks, (2) any local population and then its nearest neighbors in ring structured networks, and (3) endpoints in networks with bidirectional or linear dispersal. Even more nuanced recommendations can emerge under other conditions (Caplat et al., 2014; Chadès et al., 2011; Travis & Park, 2004). This wide variety of recommendations for managing invasions demonstrates a lack of ability to recommend consistent optimal management strategies for invasions based on specific system features (e.g., dispersal direction), making it challenging to predict optimal management strategies in new contexts or invasions.

The lack of consistent recommendations also reflects the context-specific nature of some management problems and the fact that applications of dynamic spatial models to invasion management are not yet sufficiently widespread to allow generalizations of model results. Furthermore, because optimal management problems are interdisciplinary, even similar systems are often solved using different modeling assumptions and optimization techniques, depending on the quantitative expertise at hand (Appendix S1: Table S1). This diversity in approaching management optimization problems means that existing applications of dynamic spatial models are rarely comprehensive and often fail to consider important spatial processes and their potential feedback loops (Appendix S1: Table S1).

The purpose of this article is to make optimal management methods more accessible to both modelers and managers dealing with invasion management. We address this aim through the following multistep approach: (1) describing current gaps, considerations, and challenges for landscape-level optimization using dynamic spatial models, (2) providing a workflow (i.e., simple guidelines) for optimizing landscape-level management of invasions, and (3) providing guidance for choosing the appropriate components and methodologies to apply in the workflow. We focus on spatial processes, especially movement and dispersal, that determine the dynamics and optimal management of invasions. We begin by describing dispersal. We then describe components of the workflow, including articulating the decision context and translating it into a biological or bioeconomic model, choosing the appropriate optimization technique, and incorporating the relevant sources of uncertainty and their interactions. Our target audience is newcomers to management optimization problems and those who have worked on these problems but have less experience with integrating dynamic spatial models.

DISPERSAL: THE DRIVER OF INVASION SPREAD

The spatiotemporal dynamics of any given population arise from three main ecological processes: birth, death, and dispersal (including immigration and emigration). Birth and death rates dictate the number of individuals that can spread via dispersal. Dispersal is thus the lynchpin that enables colonization of new areas, even if the population might ultimately go extinct in its current location. Birth and death processes are well studied, both empirically and theoretically. Dispersal is more poorly understood (Beckman et al., 2019; Bullock et al., 2006; Cayuela et al., 2018) and represents a considerable source of uncertainty that hampers the identification of optimal management strategies (Pepin, Smyser, et al., 2020; Shea et al., 2014; White et al., 2019).

Dispersal is often modeled using continuous functions (Bullock et al., 2017; Jongejans et al., 2008; Nathan et al., 2012; Okubo & Levin, 2001; Skellam, 1951). Much of this work assumes a species-specific dispersal kernel or so-called dispersal syndromes (Cayuela et al., 2018; Ronce & Clobert, 2012) represented by a stochastic distribution. However, in addition to stochasticity, within-species variation due to sex and age (Truvé & Lemel, 2003), phenotypic plasticity (Johnson et al., 2019), individual-level variation (Cayuela et al., 2018; Clobert et al., 2009; Schupp et al., 2019), or multiple dispersal processes acting on different scales (Rogers et al., 2019; Shigesada &

Kawasaki, 1997) might also be significant in determining dispersal outcomes.

It may be common, and perhaps universal, that dispersal kernels for invasive species consist of multiple natural and human-assisted processes (Rogers et al., 2019), associated level of uncertainty each with an (Nathan, 2007). These processes may operate at different spatial scales (Pauchard & Shea, 2006), which have been called stratified dispersal (Shigesada & Kawasaki, 1997) or total dispersal kernel (Nathan, 2007), that describe multiple dispersal pathways for a single species (Nathan, 2007; Rogers et al., 2019). For example, the invasive forest-defoliating moth Lymantria dispar spreads locally when wind-dispersed caterpillars are transported from tree to tree on silk threads but also accomplishes long-distance dispersal when egg masses are transported by humans (Liebhold et al., 1992). Humans may persistently contribute to the intentional or unintentional expansion of invasive species, including species with very different biological traits, such as Agrilus planipennis (Emerald ash borer) (Muirhead et al., 2006; Evans, 2016), Dreissena polymorpha (zebra mussels) (Chivers et al., 2017), and Sus scrofa (wild pigs) (Tabak et al., 2017). For example, humans intentionally relocate wild pigs over long distances (Hernandez et al., 2018; Tabak et al., 2017) to establish new hunting opportunities (Bevins et al., 2014). The same holds for many weeds that are wind-dispersed locally but moved long distances as unintentional contaminants in agricultural seed or via the horticulture trade (e.g., Ambrosia artemisiifolia, common ragweed) (van Boheemen et al., 2017).

Dispersal is also affected by landscape heterogeneity or by changing habitats or environments (Nesslage et al., 2007; Neupane & Powell, 2015; Soons et al., 2004). Such situations are often modeled by applying the metapopulation concept (Hanski, 1998), where a landscape is partitioned into suitable and unsuitable patches and dispersal is quantified as the demographic connectivity among subpopulations. Connectivity is also an important concept for describing dispersal in populations that are more spatially homogeneous (Baker, 2017). In what follows, we outline a workflow and special considerations for optimizing the management of invasions using dynamic spatial models that incorporate dispersal or connectivity.

WORKFLOW FOR OPTIMIZING INVASION MANAGEMENT IN AN UNCERTAIN WORLD

There are many challenges associated with solving natural resource management optimization problems in practice (Büyüktahtakın & Haight, 2018), making the process difficult to navigate. First, multiple stakeholders with different resources and objectives can make problem framing difficult. Second, the choice of models and optimization techniques often are not ideal for the problem but instead are chosen based on the available technical expertise, sometimes with insufficient input from practitioners and system experts. Finally, several sources of uncertainty about the system and our inability to observe it without error can impose multiple dimensions to the problem that are difficult to capture using optimization techniques because of the high number of potential conditions to explore. We describe a general workflow for optimizing invasion management (Figure 1) that seeks to assist teams of researchers and practitioners in navigating these challenges. The general workflow is a seven-step process: (1) frame the problem (elicit management objectives, translate objectives into an objective function, and specify possible management actions); (2) develop a bioeconomic model of the invader, including ecological, economic, and management processes; (3) use the model to understand the impacts of uncertainty on identifying the optimal strategy and the value of reducing specific uncertainties; (4) optimize the objective function based on the bioeconomic model to identify the best management strategy(ies); (5) implement the optimal strategy; (6) prioritize monitoring based on uncertainty analyses; and (7) update the bioeconomic model based on current stakeholder input, new monitoring data, and the most recent management outcomes.

These steps are relevant to both spatial and nonspatial situations.

The special feature of spatial problems is the need to include movement or dispersal processes (hereafter referred to as dispersal for simplicity). We therefore highlight key components of our proposed workflow that are especially relevant for optimizing spatial problems: characterizing dispersal processes, quantifying uncertainties in dispersal and their interactions with other uncertainties, and understanding the value of reduced uncertainty in dispersal and other factors or processes that may feed back on dispersal (Figure 2).

DECISION THEORY: ARTICULATING THE MANAGEMENT PROBLEM FRAMING

Identify and consult stakeholders and identify their management objectives

The first step in our workflow for determining optimal management strategies (Figure 1) is to identify the appropriate group of stakeholders for consultation. These discussions should be structured with the goal of eliciting and formulating management objectives (framing the problem), which involves understanding the desired management outcomes, constraints, and alternative

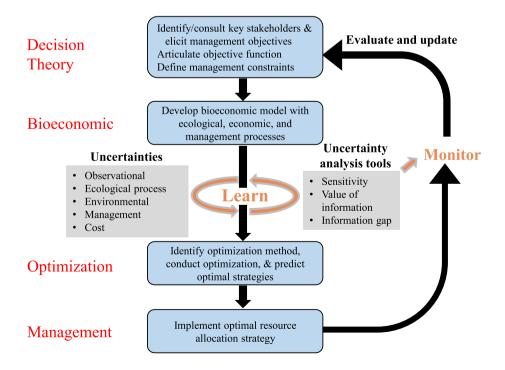


FIGURE1 General workflow for determining optimal resource allocation strategies highlighting key considerations broken down into six steps

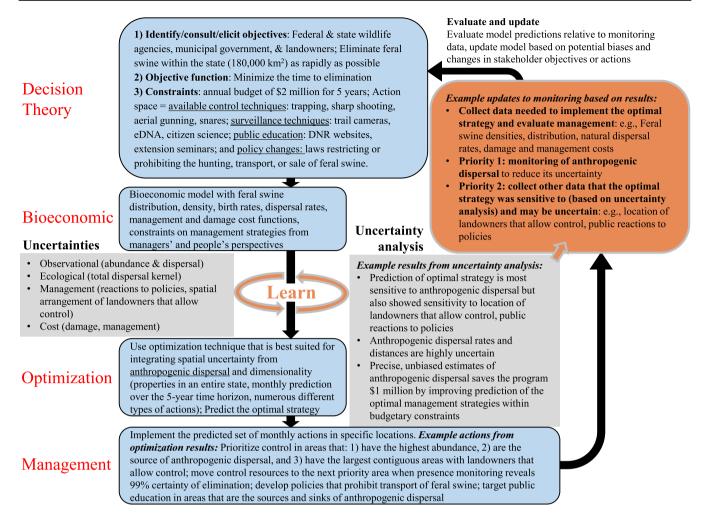


FIGURE 2 Workflow in Figure 1 applied to a management problem (statewide elimination of invasive wild pigs in United States) using fictitious details

actions so that they can be specified mathematically. The field of decision analysis provides valuable methodology for engaging stakeholders to specify management objectives (Gregory et al., 2012). Framing the problem correctly is essential for developing an appropriate bioeconomic model and conducting optimization in a way that addresses stakeholder objectives effectively because optimal strategies may differ depending on the management objectives (Probert et al., 2016; Shea et al., 2010).

Translate management objectives into an objective function

Next, stakeholder objectives should be translated into an objective function. This function will guide choosing the components of the bioeconomic model and will form the criterion that is optimized in subsequent steps of the workflow. The objective function should deliver the outcomes desired by stakeholders that are affected by

invasion management. Especially in spatial contexts, there may be multiple desired management outcomes that are measured on different scales, necessitating optimization methods that can accommodate multiple objectives (Baker, 2017; Salinas et al., 2005). A useful approach to many multiobjective problems is to express them with a scalar (one-dimensional) objective function, thereby simplifying the specification of the bioeconomic model and its optimization. Specific examples of scalar objective functions might include minimizing the total costs of both control and damage from the invader (Carrasco et al., 2010; Eiswerth & Johnson, 2002; Epanchin-Niell & Wilen, 2012; Olson & Roy, 2002; Runge et al., 2017), minimizing damage caused by invaders over a specified time period using a fixed annual budget for control costs (Blackwood et al., 2010), and minimizing the total number of patches containing the invasive species for a given total budget for control effort (Giljohann et al., 2011). The difference between these objective functions is that the last two are constrained by available funding over

time, whereas the first is not. These can produce different optimal management strategies (Giljohann et al., 2011; Moore & Runge, 2012; Pepin, Smyser, et al., 2020).

In natural resource optimization problems, be they spatial or nonspatial, there are numerous ways that multiple objectives can be expressed as a scalar function for optimization. For example, a multicriteria objective function can be formulated as a weighted function of multiple objectives through a process such as multicriteria decision analysis (MCDA). This approach allows all of the objectives to be expressed on their natural scales (Keeney, 1992) and integrated into a single outcome by taking a weighted sum reflecting stakeholders' preferences (Jit, 2018). A second approach is to include either the nonmonetary benefits or costs as the objective function criterion, which is then optimized subject to the constraint of the other (costs or benefits). This allows benefits and costs to be measured in different metrics (Boyd et al., 2015; Dodd et al., 2017). For example, benefits could be measured as the area of uninvaded landscape, while costs could be in dollars per square kilometer of invasion treated. A third approach is to translate all costs and benefits into common, usually monetary, units (Hanley & Roberts, 2019; Welsh et al., 2021). The objective function can then be specified as net benefits, for example, dollars saved in damages minus those spent on control. With each of these approaches, when considering spatial management of invasions, the various costs and benefits need to be summed across time and space. This gives rise to another important consideration: how the future state is valued (Moore et al., 2008; Polasky, 2010). High discounting rates on future benefits place lower value on future benefits and costs, which can result in less intensive control strategies and discourage active learning (Moore et al., 2008).

Define the action space

Another important step in framing the invasion management problem is identifying feasible spatial and temporal scales of management (Williams & Brown, 2016) and defining the set of possible management actions that can be conducted (the action space from which the optimal solution can be identified) (Hammond et al., 2002; Williams et al., 2009). Defining the action space is not an evaluation step. Rather, it is the articulation of the set of management conditions (e.g., tools, scale of action, resources) over which evaluation will take place when seeking to optimize the objective function. The action space arises, first and foremost, from the authority of the decision maker-What is the range of actions over which the decision maker has jurisdiction? Second, the action space arises out of existing methods and technology-What sorts of actions can be taken that are thought to affect the system of

interest? Third, the action space may be constrained by limitations on equipment, personnel, expertise, budget, and time. The definition of the action space can be a creative process that envisions new strategies that might be effective but need to engage decision makers to ensure that the optimal strategy is feasible within management constraints. The set of actions might be a simple discrete set of fundamentally different action options (e.g., do nothing vs. monitoring vs. treatment vs. monitoring and treatment) (e.g., Haight & Polasky, 2010). Or the action space might be a continuous set of alternatives for a single type of intervention, such as the density of toxic bait application (Pepin, Snow, et al., 2020). But most often, the action space consists of complex portfolios of action. In a spatial prioritization problem, for example, each alternative might be a set of sites at which to implement eradication (Caplat et al., 2014; Perry et al., 2017); here the action space is all the myriad ways of selecting a subset of the available sites and specific types of actions (e.g., culling, fertility control, monitoring, movement restrictions, public education). In dynamic spatial models, the action space generally requires specifying the location or spatial area over which each action is implemented, which can dramatically increase the number of possible management strategies for optimization.

SPECIFYING BIOECONOMIC MODELS

Once the objective function and action space are determined, spatial bioeconomic models can be developed and used to forecast how invasion management activitiesincluding prevention, early detection and management, and control of established populations-affect costs and damage over time (Epanchin-Niell, 2017). For bioeconomic models, the basic components include ecological (demographic dynamics, including dispersal), management (surveillance and control actions), and economic (cost and benefits) processes. In spatial problems, dispersal can be a key consideration in both the ecological and management components. The model is specified to predict the impact of management on the ecological and economic components that determine the objective function, which may be optimized with an appropriate optimization algorithm (described in the "Optimization methods" section).

Bioeconomic models that are developed by ecologists tend to focus on the details of demographic processes and their variation while simplifying cost functions, for example (Caplat et al., 2014; Shea et al., 2010, 2014), whereas economists tend to emphasize social context and more complex valuation of economic components while simplifying ecological processes (Albers et al., 2010; Cacho et al., 2008; Epanchin-Niell & Wilen, 2012; Hall et al., 2018). However, for a decision analyst, the important consideration is that the bioeconomic model is structured around the decision context, with the alternative management actions as inputs, the objective function shaped by stakeholder objectives, and an inner structure that reflects the best available understanding of the system. Given that all models are necessarily simplified representations of systems, it is important that represented details of ecological, economic, and management processes be selected to effectively inform the management objectives (Büyüktahtakın & Haight, 2018). Otherwise, the predicted optimal control strategies could be misleading because these processes interact to affect management outcomes (Bevins et al., 2014; Davis, Leland, et al., 2018; Regan et al., 2011; Rout et al., 2014; Yokomizo et al., 2009). It may also be important to specify several different bioeconomic models initially and use subsequently obtained monitoring data to identify the best model or subset of models (see the "Tools for reducing uncertainty" section for guidance on how this can be done) for predicting the optimal management strategies. In a spatial context, for example, considering several different specifications for the dispersal kernel could be important (Shea et al., 2014).

OPTIMIZATION METHODS

Optimization of the objective function identifies the spatiotemporal management strategy that best achieves the specified objective, subject to the constraints, dynamics, and uncertainty (described in the section "Sources of uncertainty") expressed in the bioeconomic model. Optimization algorithms select among potential actions to identify the set of actions (across time and space) that best achieve the optimization criteria (i.e., balance among objectives as specified by the objective function), accounting for temporal tradeoffs and spatial interactions specified in the model.

Choosing the appropriate optimization approach requires consideration of each approach's ability to handle problem dimensionality and key forms of uncertainty. In addition, the ease of translating model output into practical recommendations also varies across approaches. A common theme of spatial optimization approaches is the need to simplify representation of the space-time processes and uncertainties so that optimization will be tractable. Studies have simplified systems in different ways. Some incorporate a variety of cost functions but use a simple ecological model (Blackwood et al., 2010; Epanchin-Niell et al., 2012), whereas others consider complex ecological models with a limited cost model (Baker, 2017; Caplat et al., 2014). Another approach is to

concurrently consider a broader set of the important ecological and economic processes and uncertainties but simpler models of each component, including reduced dimensionality of space or time (e.g., Chadès et al., 2011). Each approach can facilitate understanding of how specific factors might affect optimal control strategies but may not provide practical guidance if complexity or interactions among the processes that critically affect optimal control strategies are ignored. Ultimately, selection of model complexity depends on the management, ecological, economic, or uncertainty processes that are most important for capturing the decision context in a particular system and that can be feasibly incorporated. A useful approach is to start by including all the processes and interactions that are anticipated to be important based on expert opinion and scientific evidence. Then sensitivity analyses can be conducted to identify components that can be dropped (i.e., those that do not have substantial effects on optimal strategies) and the model pared down to the minimally sufficient set of features that drive differences in optimal management strategies. Alternatively, one can start with simple models and add complexities through a similar testing process.

Common optimization approaches (Table 1) typically involve some tradeoff between the model complexity that can be accommodated and the optimality of the solution. Deterministic optimal control problems using partial differential equations (e.g., Baker, 2017) accommodate high dimensionality for spatial processes, but spread is modeled as a diffusion process, making it challenging to examine management strategies that target spatially distinct, separated patches or allow for long-distance spread. Furthermore, these methods can only accommodate uncertainty through sensitivity analysis (i.e., running the optimization on different values of the fixed parameters or different functional forms and evaluating effects on the optimal strategies). They do not provide a means to deal with stochasticity or uncertainty in the observation of state variables through time. In contrast, stochastic models, such as Markov decision process (MDP) models, solved by stochastic dynamic programming (SDP) allow the incorporation of stochasticity and management actions in discrete patches (e.g., Walker et al., 2015), however, they also do not allow uncertainty in the observation of state variables through time. Unfortunately, the dimensionality (i.e., number of patches) that can be considered with these approaches is limited (Chadès et al., 2011), and they are not suitable to account for imperfect observation of system states (Regan et al., 2011).

Alternatively, SDP with a partially observable Markov decision process (POMDP) provides a powerful tool for decision-making under multiple types of uncertainty, especially imperfect observation of system states.

TABLE 1 Common techniques to optimize allocation of resources in bioeconomic models

	Strengths	Weaknesses			Examples	
Method			Spatial	Uncertainty	Method	Example
Optimal control theory applied to partial differential equations	Solves for a large number of spatial coordinates well beyond the current capabilities of stochastic dynamic programming (SDP)	Movement is modeled as a diffusion process—not amenable to incorporating explicit uncertainty (besides sensitivity analysis) or examining management strategies that divide resources among spatially distinct patches	++	No (except through sensitivity analysis)	Kamien & Schwartz (2012)	Baker (2017)
Markov decision process (MDP) solved using SDP	Allows for modeling management in separated (discrete) patches; can account for random variation in ecological or management processes	Computationally prohibitive as the number of patches and parameters increases; cannot be used to address observational uncertainty of state variables through time	+	Stochastic growth and spread	Marescot et al. (2013)	Walker et al. (2015)
Partially observable Markov decision process (POMDP) analyzed using SDP	Can address observational uncertainty because observed states are described as probabilities of true state given what is observed; can account for uncertainty in extent of invasion or impact of control	Computationally prohibitive with more than one patch (typically only a single patch is modeled) and as number of different uncertainties increases; exact solutions are usually intractable (solutions are approximated)		Stochastic, management, or observational uncertainty	Williams (2009)	Regan et al. (2011), Rout et al. (2014) (implemented with only one patch)
Factored partially observable Markov decision process (FPOMDP)	Builds on POMDP to handle more patches and account for spatial relationships between patches by representing patch structure using networks (which reduces dimensionality by condensing patch information)	Modeling of spatial relationships is coarse (network motifs—does not handle large networks), remains the same over time, and assumes spatial relationships are perfectly known; exact solutions are usually intractable (solutions are approximated)	+	Stochastic, management, or observational uncertainty	Poupart (2005)	Chadès et al. (2011), Nicol et al. (2015)

(Continues)

TABLE1 (Continued)

					Examples	
Method	Strengths	Weaknesses	Spatial	Uncertainty	Method	Example
Scenario optimization (forward simulation with stochastic models and identifying strategies that best meet management objectives)	Highly flexible for addressing spatial processes and a variety of uncertainties at any desired spatial or temporal scale; particularly well suited for problems where practical constraints only allow a limited number of management actions	Does not guarantee true optimality because only a predefined set of possibilities is examined (i.e., does not fully explore all theoretical possibilities)	++	Any type of uncertainty		Higgins et al. (2000), Wadsworth et al. (2000), Grevstad (2005), Pepin, Smyser, et al. (2020)

Note: The *spatial* column indicates the ability of the method to handle large spatial extents (++, can handle large spatial areas or numbers of patches; +, can handle small numbers of spatially distinct patches; -, does not represent space explicitly or handle large numbers of spatial patches). Note that here we contrast optimization methods that are commonly applied to spatial optimization problems. The uncertainty column highlights the types of uncertainty that can be accommodated within the optimization methods (i.e., aside from sensitivity analysis of functional forms or fixed parameters). For a more comprehensive review of optimization methods in general with more nuanced methodological explanations, see Chadès et al. (2017).

However, it is computationally prohibitive to examine many patches because, for each patch, the method stores information about all other states of all other patches at each time step, regardless of spatial relationships. Thus, typically it has been applied to make inference about single patches when imperfect observation of ecological states is an important consideration (Fackler & Haight, 2014; Haight & Polasky, 2010; Regan et al., 2011; Rout et al., 2014), but in doing so, Rout et al. (2014) gained insight about recommendations for spatially structured management actions. Also, the method becomes computationally prohibitive as the number of different uncertainties increases, and the representation of states and control actions are necessarily coarse because they can only take a discrete set of specified values (e.g., presence/absence). Factored POMDP (FPOMDP) can address issues of imperfect detection in multiple patches (e.g., Chadès et al., 2011; Nicol et al., 2015) while also accounting for spatial relationships among patches by representing relationships among patches as network motifs. FPOMDP and POMDP approaches are typically too complex to solve exactly, and approximation methods may also be required to translate the optimal solutions into practical management recommendations (Dujardin et al., 2017; Ferrer-Mestres et al., 2021; Poupart et al., 2011). Another recent method is linear integer programming (LIP) with hidden Markov random field (HMRF) (Bonneau et al., 2019). This approach is more amenable to optimizing the spatial allocation of control actions in systems with noisy

observations, heterogeneous costs, and a large number of patches. But in this example, the population is only modeled as presence/absence, the set of actions is discrete, the number of dimensions, including both patches and types of uncertainty, that can be incorporated concurrently is limited, and the method requires substantial expertise to implement.

Methods that are designed to handle the high dimensionality of dynamic spatial models have, until now, mostly been used in engineering and finance contexts. One example is approximate dynamic programming (ADP)-a modeling framework that offers strategies for tackling the problems of dimensionality in large, multiperiod, stochastic optimization problems (Powell et al., 2012). Its essence is to replace the true value function that is maximized in SDP or the policy function with a statistical approximation (Powell, 2011). Another promising approach is artificial intelligence (AI), which has enabled the exploration of simplified methods, such as surrogate-based optimization (Queipo et al., 2005; Simpson et al., 2008), and replaces computationally intensive functional evaluations with less intensive ones. The approximation models can be built for the objective and state function(s) by randomly sampling data from the design space. One can then optimize the much simpler surrogate models, and a Monte Carlo approach can be used to quantify uncertainty and obtain output statistics (Rumpfkeil, 2013). As with ADP, surrogatebased optimization techniques have been used mostly in

engineering. They offer a promising approach to dealing with the space, time, and uncertainty dimensions that are common in invasive species management.

Simulation-based methods provide additional options. For example, the dimensionality of dynamic spatial models of management can be reduced by predefining the set of conditions of interest and analyzing simulation output (e.g., scenario optimization) (Table 1). Another approach that addresses dimensionality reduction while conducting optimization is to treat the simulation of the ecological processes and optimization of management actions separately and sequentially, rather than together (Onal et al., 2020). Simulationbased methods can be especially useful in systems where the scope of management strategies is heavily constrained.

RECOMMENDING PRACTICAL MANAGEMENT ACTIONS

Optimization of the bioeconomic model provides recommendations for management. However, optimization approaches can provide extremely nuanced recommendations based on the spatial and temporal resolution, for example, "apply a control effort of 33% in Week 1 in Patch X, then 45% in Week 2 in Patch Y." These types of answers are usually impractical for managers because management techniques may be constrained to applications over coarser spatial and temporal scales, it may not be possible to be sufficiently precise with effort allocation, or the infrastructure may not allow frequent shifts in resources. In other words, the true optimal control strategy may not be achievable in practice. This practical constraint can be addressed by (1) constraining the bioeconomic model and optimization approach to only consider feasible management actions that were defined by managers during the problem forming phase (see our "Decision theory" section) or (2) conducting optimization with more flexible management constraints but followed by a post hoc summary of optimization results that delivers recommendations on a scale that matches the management constraints (e.g., Chadès et al., 2011; Moore et al., 2017). It can be useful to take the latter approach when there is potential for management constraints to change over time.

MONITORING AND EVALUATION

An important step to conduct in concert with management is monitoring of both the management actions that were implemented and of the state of the system that informs the success of the management objectives. In spatial optimization, it is crucial that monitoring include not just overall population abundance but a measure of where individuals occur in space (i.e., distribution or movement). Moreover, the spatial design of monitoring the state of the system over time needs to be compatible for evaluating the spatial optimal management strategies predicted by the bioeconomic model and management objectives (Nichols et al., 2021). For managers, monitoring can be a tough sell because it requires resources that could be used on control (Bogich et al., 2008; Epanchin-Niell et al., 2012). Thus, it is important to establish the value of monitoring to the management objectives, which can be accomplished using uncertainty analysis and evaluating the optimization criteria under different levels of uncertainty. A complementary approach is to develop monitoring techniques that impose little burden on managers (e.g., Davis, Leland, et al., 2018; Davis et al., 2022; Moore et al., 2017). As an example, controlling gray sallow invasion into alpine bogs in Australia demonstrated the importance of investing time in developing less burdensome monitoring techniques-in this case moving from paper-based data recording to automated GPS tracking-to decrease the costs of monitoring and improve the quality of the monitoring data for model evaluation and analysis (Moore et al., 2017). Uncertainty analysis (described in what follows) is useful to guide the monitoring design, especially when optimization shows that reduction of key uncertainties leads to better management solutions based on the optimization function. When using dynamic spatial models in optimization, this sensitivity analysis approach can be used to determine the benefit of expending monitoring resources on reducing uncertainty in dispersal and for identifying where and how much sampling could reveal the most informative data on species abundance/distribution/dispersal for the management objectives.

SOURCES OF UNCERTAINTY AND WHY WE NEED TO ACCOUNT FOR THEM

Failing to consider uncertainties can result in suboptimal or even detrimental control strategies (Pepin, Smyser, et al., 2020; Regan et al., 2011) and obscure decision risk. Building on Williams et al. (2009), we describe five different types of uncertainty that are likely to influence optimal spatial management strategies and show how their effects are not independent (Figure 2). Uncertainty can be reducible, by coupling the previously described techniques with model-guided data collection, or irreducible, due to stochastic variation. Although irreducible, stochastic variation should be incorporated into analysis where possible because it embeds risk analysis into the optimization and provides for more robust and transparent predictions of the optimal strategy.

In what follows, we focus on uncertainties that are especially important for managing invasions and that can be reduced using our workflow. Specifically, we consider uncertainties that (1) are critically important for identifying optimal management solutions correctly in management applications, (2) are generally neglected in invasion management, and (3) may magnify uncertainty in dispersal, the fundamental process of invasions. We describe why these uncertainties are important, tools for reducing them, and how they can be incorporated into the workflow to optimize management of invasions (Figure 1).

UNCERTAINTY THAT IS KNOWN TO BE IMPORTANT

Observational uncertainty of distribution or abundance

If management is to be optimized based on the current status of species distribution or abundance, accurate estimates of these parameters are needed (Rout et al., 2017). For established invasions it may be more important to quantify abundance or distribution for the evaluation of management objectives (Davis, McCreary, et al., 2018), whereas when a population is near elimination, the critical population metric is the probability of absence given no detections (Anderson et al., 2013). Uncertainty in our ability to observe system states and processes accurately can reduce the efficiency of control and monitoring strategies (Bonneau et al., 2019; Kendall & Moore, 2012) by misrepresenting the true state of the system, leading to incorrect predictions of population viability (Meir & Fagan, 2000), ineffective management actions (Harwood & Stokes, 2003), or unnecessary economic costs (Mastin et al., 2019).

Hauser et al. (2016) demonstrated a method for optimizing the discovery of infestations beyond the known population boundary to improve prioritization decisions for resource allocation toward control in *Hieracium praealtum* (King Devil Hawkweed). Limited resources were allocated optimally by focusing control on areas where presence was more certain and conducting surveillance in areas where presence was less certain. The importance of accounting for observational uncertainty in presence/abundance for determining optimal management strategies accurately (Rout et al., 2017) emphasizes that this source of uncertainty should be included in workflows for spatial optimization as well. Observational uncertainties vary depending on the sampling design, population metric used, and the true underlying abundance, affecting accuracy or precision of estimates. Guidance for choosing among population metrics and their potential implications on accuracy and precision are described in Appendix S1: Section S1 and Appendix S1: Table S2.

UNCERTAINTY THAT IS GENERALLY NEGLECTED

Though some types of uncertainty are relatively well understood and accounted for in optimal management frameworks, others that are also likely important have been generally neglected (Figure 3) (Büyüktahtakın & Haight, 2018) and present priorities for investigation in optimal management applications.

Uncertainty in dispersal

Observational uncertainty in dispersal has been largely neglected to date, partly because dispersal is challenging to measure, but recent advances in estimating dispersal provide an opportunity to improve management optimization using dispersal estimates and dynamic spatial models. However, even state-of-the-art methods can produce highly uncertain dispersal metrics (Baguette et al., 2012; Cayuela et al., 2018; Lowe & Allendorf, 2010), and these uncertainties need to be considered alongside other uncertainties relevant to the system and objective function. Most methods of measuring dispersal directly either track individuals (Lagrangian methods) or document the density of individuals in space (Eulerian approaches), and they may produce different estimates (Skarpaas et al., 2011) and, thus, optimal management strategies. Another approach is to estimate demographic connectivity among patches or subpopulations (Baguette et al., 2012) using methods that link individual movement data to landscape features, for example, least-cost path (Etherington & Perry, 2016) or circuit theory (McRae et al., 2008). These inference approaches are clearly useful for modeling dispersal in different landscapes, but their accuracy for inferring realized connectivity remains unclear and is, thus, an important topic for improving optimal management strategies that rely on accurate measures of connectivity.

The use of genetic tools to infer patterns of dispersal throughout landscapes has emerged as a complement or, in some cases, alternative (e.g., Browett et al., 2020; Carroll et al., 2014) to more direct measures of connectivity. By sampling across a landscape, genetic patterns can be used to infer both patterns and rates of connectivity among populations. However, unique genetic processes

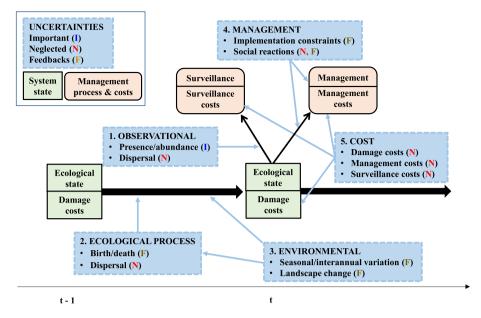


FIGURE 3 Schematic illustrating how interrelating sources of uncertainty affect knowledge of system states (light green rectangles) through management processes (light orange rounded rectangles). The relationships for just a single time point are shown but would be similar for each point in time *t*. Five major sources of uncertainty are numbered and given in light blue rectangles. Light blue arrows show where each uncertainty affects the system. We highlight uncertainties that are most commonly important (blue text), those that are generally neglected (red text), and those that are likely to feed back on uncertainty in dispersal (bronze text). Definitions of the five sources of uncertainty are (1) observational (occurrence/abundance or dispersal): imperfect observation of true state of ecological system; (2) ecological process (birth/death or dispersal): limitations in knowledge about true ecological processes; (4) management: (a) when implementation of management differs from planned actions or (b) when consequences of a management policy are different from expectation (social reactions); (5) cost: limitations in knowledge of costs/benefits of management and damage, including relationship between costs and invader abundance

that accompany an invasion can also make such inferences challenging. For example, estimates of genetic connectivity derived from pairwise estimates of genetic distances for populations assumed to be in migrationdrift equilibrium are often not applicable to populations along an invasion front (Faubet et al., 2007; Fitzpatrick et al., 2012; Lowe & Allendorf, 2010; Meirmans, 2014). Similarly, founder effects may serve to reduce genetic diversity in invasive species, reducing genetic differentiation between populations and making it difficult to identify movement among populations (Tsutsui et al., 2000). Nonetheless, even with high genetic similarities among invasive populations, the increasing availability of highresolution molecular tools (ranging from RADseq to whole-genome resequencing) are providing sufficient power to identify movement between closely related populations across small spatial scales (see Appendix S1: Section S2 for strategies to improve genetic-based estimates of dispersal). As these genomic-scale approaches replace more traditional data streams and their associated uncertainties are reduced, decision makers may have an opportunity to use these population genomic estimates of dispersal more easily in the near future.

Uncertainty about dispersal can also be structural. We refer to a lack of knowledge of the form of the dispersal kernel as uncertainty in the ecological process in Figure 3. When the spread of invaders is determined by multiple modes of movement, each of the underlying dispersal processes must be identified and adequately described for optimal management. Incorrect or incomplete representation of this *total dispersal kernel* can lead to biased predictions about spatial spreading rates and directions across landscapes. Shea et al. (2014) demonstrated the benefit of considering multiple evidence-based dispersal kernels that predict different spread rates and outbreak sizes for foot-and-mouth disease virus, thereby improving predictions of optimal control strategies by incorporating uncertainty in the disease dispersal kernel.

Uncertainty in management due to social processes

Uncertainty in management may occur when decision makers rely on the public to implement a control measure (e.g., mask wearing to control COVID-19 or the need to conduct control on private lands). For example, wild pigs are widespread across public and private lands. While some landowners welcome lethal control of wild pigs, others value their presence and prevent access of managers to their land (Carlisle et al., 2020), which could prevent achieving planned management actions. Additionally, the consequences of management actions can be uncertain, despite strong knowledge of ecological processes because systems act differently in the presence of perturbations from management (e.g., behavioral responses in humans during the COVID-19 pandemic under evolving public health recommendations and perceived infection risk). Reducing management uncertainty can be especially important when control budgets are tight (Li et al., 2019) and may be achieved through sociological studies that determine where and what proportion of the public support control. When optimizing management using spatial models, accounting for spatial variation in management uncertainty is important because optimal strategies could vary substantially from location to location (e.g., the optimal amount of resources spent on control vs. public education or treatment incentives may vary spatially depending on spatial differences in management uncertainty).

Cost uncertainty

The objective function for the optimization of control strategies often involves minimizing damage and control costs based on constraints. Each damage or control cost is defined as the cost per unit of density, abundance, or presence of invaders (Olson & Roy, 2008). Uncertainty in the occupancy or abundance of the target species can compound uncertainty in these costs (Welsh et al., 2021). The typical management cost function assumes that it becomes increasingly costly to locate and remove the remaining individuals as density/abundance decreases (Fischer et al., 2020; Olson & Roy, 2008). Parameters of this relationship can have substantial impacts on predicting the outcome of control strategies and identifying the optimal control strategy (Pepin, Smyser, et al., 2020), although uncertainty in cost functions is rarely considered in optimization applications (both spatial and nonspatial). In spatial contexts, there may be additional considerations for the parameterization of management cost functions. For example, Pepin, Snow, et al. (2020) considered the case where control was conducted using bait sites. In such cases, it is more costly to conduct baiting at sites that are farther apart relative to conducting baiting at the same number of bait sites placed closer together because of the driving time between sites. Thus, it can be important to invoke a more

complex cost function that varies based on the spatial arrangement of the intervention being conducted.

Characterizing damage costs is challenging because some types of damage are difficult to value (e.g., damage to natural resources) (Pejchar & Mooney, 2009; Bagstad et al., 2013), but lack of information about the shape of the damage function can generate large uncertainty in the optimal management strategy (Davis, Leland, et al., 2018; Hornberg, 2001; Jackson et al., 2015; Yokomizo et al., 2009). Management will typically be too little, too late for invaders that cause high impact at low density, whereas ignorance of the density-impact curve can lead to overinvestment in management with little reduction in impact for species that are only problematic at high density (Davis, Leland, et al., 2018; Hornberg, 2001; Jackson et al., 2015; Yokomizo et al., 2009). A consideration for spatial contexts is that both the type and amount of damage can vary regionally such that it is often important to allow the damage function to vary accordingly (although data to parameterize any damage function is rare and represents a major knowledge gap).

UNCERTAINTY IN DISPERSAL IS MAGNIFIED BY OTHER UNCERTAINTIES

Several of the uncertainties listed in Figure 3 could affect dispersal, potentially amplifying its uncertainty. Because dispersal rates are typically driven by new births, interor intraspecific interactions, and environmental conditions, uncertainty in both the ecological processes and environmental conditions (Figure 3) can increase variation in dispersal, potentially affecting the optimal control strategy. If, for example, the relationship between dispersal and environmental variation is poorly understood, spatial predictions of invader presence or abundance could fail under some environmental conditions, biasing predictions of optimal resource allocation strategies. Similarly, management uncertainty has been shown to feed back on dispersal uncertainty when the management action changes the characteristics of dispersal. One example is boat inspection stations for reducing the spread of invasive zebra mussels among lakes. If boat inspection stations charge a fee, then boaters may shift behavior by recreating at uncontrolled water bodies to avoid the inspection cost (Chivers et al., 2017), which can lead to the unanticipated contamination of other lakes (altered dispersal). Similarly, the introduction of hunting reward (bounty) programs in Tennessee and California as a policy for controlling wild pigs was accompanied by the illegal transport and release of wild pigs to new areas to create locally accessible hunting opportunities (Bevins et al., 2014). These examples illustrate how social and

fiscal reactions to management policies (management uncertainty) can have unintended, but predictable, feedbacks on dispersal uncertainty, including a dramatic expansion and establishment of new populations rather than local population reduction. These knowledge gaps could be reduced through sociological studies to understand predictors of behavioral responses to interventions and ecological studies that estimate management effects on dispersal, allowing for more accurate recommendations of optimal control strategies.

Reducing management uncertainty in spatial optimization applications also requires understanding the spatial context of social reactions relative to the dispersal kernel of the species (Coutts et al., 2013). If the benefits of invasive species control far outweigh the costs, multiple adjacent landowners may work cooperatively to achieve socially desirable control (Coutts et al., 2013; Epanchin-Niell & Wilen, 2015). However, when there is substantial long-distance dispersal of the invasive species, even a small number of recalcitrant landowners can allow invasive species to persist at a broad spatial scale despite the success of cooperative localized control (Coutts et al., 2013). Reducing this type of management uncertainty requires understanding the incentive basis of specific landowners and how the arrangement of their lands might influence dispersal and the effectiveness of different management strategies. This understanding provides a platform for investigating strategies that include social pressure on those landowners who may have the severest consequences on the control or dispersal of the invader.

TOOLS FOR REDUCING UNCERTAINTY

Though the first step is to recognize and understand the sources of uncertainty that have the largest potential impact on optimal management of spatially structured populations, the next is to reduce the most influential sources of uncertainty (using the workflow described in Figure 1). Uncertainty analysis tools facilitate the identification of components of uncertainty that are most valuable to reduce (Li et al., 2019; Runge et al., 2011; Shea et al., 2014) and can be applied to any model structure or optimization approach. Tools such as sensitivity analysis and value-of-information analysis provide systematic approaches for evaluating the consequences of different sources of uncertainty on decisions (Moore & Runge, 2012).

Sensitivity analysis examines uncertainty in parameter values or functions and how ranges on these components affect uncertainty in the output variables (Moore & Runge, 2012). Components that have the greatest impact on

management objectives are the factors to which the system is most "sensitive"-that is, uncertainties whose reduction would most improve the robustness of prediction of the optimal management strategies. Value-of-information analyses, in contrast, identify the uncertainties that most affect the choice of action (Runge et al., 2011) by calculating the difference between the expected value of an optimal decision when information is perfect and the expected value of the optimal decision in the presence of the current level of uncertainty. Thus, value-of-information analyses provide guidance on which types of research or monitoring data might best improve the outcome of management decisions. Under extreme uncertainties, techniques such as minimax and information-gap theory (reviewed in Epanchin-Niell, 2017) can evaluate worst-case scenarios that could arise from different types of uncertainty. Similarly, robust optimization techniques (Yemshanov et al., 2017) can be used to optimize surveillance and management at the outset in a system where very little is known. The utility of valueof-information analysis (and similar techniques) to identify the most important information gaps has been applied in conservation only recently (Canessa et al., 2015; Nicol et al., 2019) and remains underutilized in invasive species management (Moore & Runge, 2012).

The following example illustrates steps for reducing uncertainty in a real-world management context to improve the robustness of optimal management recommendations. Moore and Runge (2012) worked with managers to define the management objectives and evaluation metrics of interest for control of Salix cinerea (invasive willow) populations. They then specified an appropriate demographic model for prediction using expert knowledge and field data to define ranges for parameter values that captured their uncertainty about the values. They represented parameters as distributions and used sensitivity analyses to identify which parameters had the largest influence on management outcomes and value-of-information analysis to determine the effect of uncertainty on decisions. This allowed them to identify robust long-term strategies for managing willow invasions while accounting for parametric uncertainty. Their work demonstrates a transparent framework for explicitly including parametric uncertainty in decision-making and avoiding the pitfalls of ignoring it (Milner-Gulland & Shea, 2017). These strategies can be applied similarly to reduce uncertainty in dispersal estimates (Shea et al., 2014) and other uncertainties that might affect those estimates.

Another approach to addressing ecological process uncertainty is to consider multiple models concurrently as a so-called ensemble and use model aggregation methods to combine predictions of different models to reduce prediction bias (Shea et al., 2020; Yamana et al., 2016) or to use bias and convergence weighting to evaluate management strategies in a structured decisionmaking framework (Webb et al., 2017). The choice of models to include in the ensemble will affect prediction, and it may be useful to consider a suite of models that are balanced with respect to differences in predicted outcomes. Value-of-information analyses applied to a balanced set of models can help reveal which approach (starting ensemble vs. a single or smaller set of models) is best for identifying the optimal control strategy (Li et al., 2019). Dispersal processes can also have some stochastic uncertainty that is irreducible but important to consider for accurate assessments of decision risks.

KEY PRIORITIES IN SCIENCE AND PRACTICE OF OPTIMIZING INVASION MANAGEMENT

We have synthesized persistent knowledge gaps and challenges in using dynamic spatial models to optimize the management of invasions and described approaches that would bridge current gaps. Our synthesis of system uncertainties highlights the following priorities for improving invasion management.

Addressing uncertainty in dispersal/ connectivity

Dispersal estimates can have substantial uncertainty in rates, direction, and functional form. Sometimes only a single value of the mean dispersal distance is all the information available for an entire species at the outset of management optimization. A critical gap is failing to consider variation and uncertainty in dispersal-both in terms of the factors that drive dispersal and the quantification of dispersal kernels. For example, if the optimal solution is to control the source (Baker, 2017), uncertainty in identifying the real source and rates of dispersal from it is needed to determine the optimal solution and provide transparency in decision risk for managers. Dispersal has been challenging to measure, but advances in both measurement and estimation have made it possible to estimate dispersal rates more accurately and better quantify its uncertainty.

Evaluating processes that influence dispersal and its uncertainty

Dispersal can be influenced by ecological, management, or environmental processes. These feedback loops can magnify uncertainty in dispersal, thereby demanding attention in planning the optimal management of invasions. A

common challenge is that there may be very little information to account for feedback of important processes on dispersal. Sensitivity and value-of-information analyses spanning realistic parameter values from the management system would be a useful first step in identifying and understanding the most important uncertainties affecting dispersal and associated optimal management solution. Eliciting expert opinion or using values from previous studies is a useful starting point for parameterizing these analyses, which in turn help guide which data are most important to collect to better understand potential feedbacks of uncertainties on dispersal (Buckley et al., 2005). This kind of holistic approach to understanding dispersal drivers and uncertainties is an important direction for optimizing the management of invasions because it reduces the risk of focusing on local optimality outcomes that may fail in the longer term.

Understanding how the spatial aspects of management uncertainty affect outcomes

In all management optimization problems, management uncertainty, which arises from variation in human behavior, is less well studied than ecological or observational uncertainty. However, in managing invasions, the spatial heterogeneity and distribution of stakeholder attitudes and responses can matter more than overall attitudes. For example, if we estimate that 80% of landowners would allow control on their parcels but do not account for where those landowners are relative to the parcels that need control according to the optimal strategy, then the optimal strategy may well fail. Accounting for spatial heterogeneity in uncertainty in management responses across the management zone is a key consideration for optimizing the management of invasions.

Incorporating multiple sources of uncertainty

Incorporating multiple sources of uncertainty is technically challenging and has rarely been attempted in spatial or nonspatial management optimization problems of invasions. When uncertainty is incorporated, it has focused primarily on species presence or abundance uncertainty. Accounting for multiple uncertainties concurrently is a crucial gap because there are usually multiple types of uncertainty that underlie predictions of optimal management strategies (Figure 3), and optimization approaches are limited to the parameter space given as inputs. As a result, approaches that neglect key uncertainties can wrongly identify globally optimal solutions and misrepresent the risk associated with different management decisions. For better transparency of decision risks and more accurate identification of optimal strategies, uncertainties need to be modeled *jointly* so their interaction can be accounted for and appropriate propagation of uncertainties can occur.

CONCLUSION

A key challenge with determining optimal management solutions using dynamic spatial models is their increased dimensionality relative to nonspatial problems. This explains why solutions for spatial resource allocation problems have lagged behind nonspatial approaches, including joint modeling of multiple sources of uncertainty. Utilizing tools from decision analysis to identify the uncertainties that have the most significant impact on correctly identifying spatial resource allocation strategies can help to focus on those dimensions that will most effectively inform optimal solutions. Advances in estimating dispersal processes provide a platform for improving the management guidance that can be gleaned from knowledge of dispersal and methods for including dispersal uncertainty in optimal management solutions. Optimization practitioners have recently developed promising new methods for handling high-dimensional problems, such as optimization under multiple sources of uncertainty, where many patches and sources of uncertainty can be considered concurrently, and feedback loops on sources of uncertainty and their effects on optimal solutions can be considered. These complex optimization techniques are attractive tools for tackling multidimensional ecological problems, but they require substantial expertise to implement, which can be achieved through increased investment by institutions in collaboration with specialists from optimization, ecology, economics, sociology, and decision theory.

AUTHOR CONTRIBUTIONS

All authors contributed to idea development, wrote sections of the first draft, and edited the final version. Kim M. Pepin led the collaboration, collated the sections, and refined the final version.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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