Mechanistic invasive species management models and their application in conservation

Brielle K. Thompson1,2 | Julian D. Olden2 | Sarah J. Converse3

1Quantitative Ecology and Resource Management Program, University of Washington, Seattle, Washington, USA
2School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA
3US Geological Survey Washington Cooperative Fish and Wildlife Research Unit, School of Environmental and Forest Sciences & School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA

Correspondence
Brielle K. Thompson, Ocean Teaching Building, Suite 300, Box 357941 Seattle, WA 98195, USA.
Email: bkwarta@uw.edu

Funding information
College of the Environment, University of Washington; Washington Cooperative Fish and Wildlife Research Unit; U.S. Geological Survey Invasive Species Program

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, nonspatial 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.

KEYWORDS
biological invasions, dispersal, invasive species management, mathematical models, spatial spread

INTRODUCTION

Invasive species are pervasive drivers of global change (Early et al., 2016; Pyšek & Richardson, 2010). They disrupt ecosystems, leading to loss of biodiversity and ecosystem function (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016), introduce diseases threatening human health (Mazza, Tricarico, Genovesi, & Gherardi, 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, Siilström, Asplund, & Vander Zanden, 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 & 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, 2021). 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, Thorbek, DeAngelis, & Grimm, 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 (Converse, 2020; Epanchin-Niell, 2017; 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, that is, by subtracting individuals from population abundance projections (Hastings, Hall, & Taylor, 2006; Link, Converse, Yackel Adams, & Hostetter, 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, Liebhold, & Roberts, 1998), or fecundity rates could be reduced if management actions alter reproductive capability, such as neutering mammals (e.g., Lohr, Cox, & Lepczyk, 2013) or destroying fish spawning sites (e.g., Loppnow, Vascotto, & Venturelli, 2013). Management-based adjustments to vital rates can be informed by empirical studies (e.g., Holmes et al., 2019).

Despite their potential to inform decision-making, a disconnect remains 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). Modelers are often not trained nor incentivized to translate models into terms nonmodelers can understand, therefore mathematical models are typically viewed as too complex or considered a “black box” (Lorscheid, Heine, & Meyer, 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, Williams, Mata, Thomas, & Bekessy, 2018). This can lead to better integration of scientific information into management decisions via decision-analytic processes (Runge, Converse, Lyons, & Smith, 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 (RADMs), integrodifference equations (IDEs), gravity models (GMs), particle transport models (PTMs), nonspatial and spatial discrete-time population growth models (PGMs, SPGMs), cellular automata (CA), and individual(agent)-based models (IBMs). 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; Baker & Bode, 2021; García-Díaz et al., 2019). 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 | INVASIVE SPECIES MANAGEMENT MODELS (ISMMs)

Our review explores several types of ISMMs, including RADMs, IDEs, GMs, PTMs, nonspatial and spatial discrete-time PGMs, CA, and IBMs. 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, offer example applications from the 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.

2.1 | Reaction–advection–diffusion models

RADMs provide a spatially explicit, continuous-time approach to predict invasive species population growth and spread (Figure 1, Table 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.

| 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. | \[
\frac{\partial N}{\partial t} = -D\nabla^2 N - \gamma(x) N
\]
where \(N\) = density of organisms at \(x, y\), and time \(t\); \(D\) = diffusion coefficient; \(\gamma(x)\) = advection coefficient; \(\phi\) = population growth function | Baker 2017 |
| 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. | \[N_{t+1}(x) = \int f(x-y)N_t(y)\,dy\]
where \(N_t(x)\) = population growth at time \(t, x\), \(y\) = current location, \(f(x-y)\) = dispersal kernel, \(\phi(x, y)\) = population growth function | Caplat et al. 2012 |
| 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. | \[N_j = \frac{Q_j}{d^a}\]
where \(N_j\) = number of individuals moving from location \(i\) at \(j\), \(Q_j\) = scalar that ensures all individuals at \(i\) reaches a destination, \(d_i\) = individuals at \(i\), \(d_j\) = distance from \(i\) to \(j\), \(a\) = distance coefficient. | Bossenbroek et al. 2001 |
| 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. | \[\frac{\partial C}{\partial t} + \mathbf{v} \cdot \nabla C = \nabla \cdot \mathbf{D}\]
where \(C\) = concentration of the population in 3-D, \(\mathbf{v}\) = velocity vector, \(K\) = diffusivity tensor in 3-D, \(Q\) = locations of sources and sinks | Belovsky et al. 2017 |
| 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/size structure of a population. | \[N_{t+1} = LN_t\]
where \(N_t\) = population abundance at time \(t, L\) = matrix describing population vital rates of ages or stages of a population | Goffinjukku et al. 2005 |
| 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. | \[N_{t+1} = L N_t\]
where \(N_t\) = population abundance at time \(t, L\) = matrix describing population vital rates at each cell | Blackwood et al. 2010 |
| 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. | \[X_{t+1}(x) = f(X_t, S)\]
where \(X_t\) = state of the cell \(t\) at time \(t\) (from a finite set of states), \(f\) = transition function, \(S\) = state of neighboring cells | Azebi et al. 2006 |
| 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. | \[f_j(x) = \text{transition function for each individual } x_j \text{ to be updated to a new state } S_{x_j+1}\]
where \(f_j\) = probability space that \(f_j\) is selected | Carraresi et al. 2012 |

**FIGURE 1** Types of invasive species management models (reaction–advection–diffusion models, integrodifference equations, gravity models, particle transport models, nonspatial 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 a generalized mathematical formula and respective parameters, and examples from the literature where the model was used to study invasive species dynamics and/or management.
**TABLE 1** Classification of each invasive species management model (reaction–advection–diffusion models, integrodifference equations, gravity models, particle transport models, nonspatial and spatial discrete-time population growth models, cellular automata, and individual-based models) regarding various temporal, spatial, and demographic attributes, indicated by checkmarks.

| Model                                | Temporal attributes | Spatial attributes | Demographic attributes |
|--------------------------------------|---------------------|--------------------|------------------------|
|                                      | Temporally         | Spatially          | Models heterogeneous   |
|                                      | explicit           | explicit           | environments           |
|                                      | Continuous          | Continuous          | Includes growth        |
|                                      | in time             | in space            | terms                  |
|                                      | Dynamic             | Stochastic          | Simulated individuals  |
|                                      | environment         | spread              | follow rules           |
|                                      |                     |                    | Simulated              |
|                                      |                     |                    | individuals            |
|                                      |                     |                    | follow complex         |
|                                      |                     |                    | rules                  |
| Reaction–advection–diffusion models  | ✓                   | ✓                  | ✓                      |
| Integrodifference equations          | ✓                   | ✓                  | ✓                      |
| Gravity models                       | ✓                   | ✓                  | ✓                      |
| Particle transport models            | ✓                   | ✓                  | ✓                      |
| Nonspatial discrete-time population  | ✓                   | ✓                  | ✓                      |
| growth models                        |                     |                    |                        |
| Spatial discrete-time population     | ✓                   | ✓                  | ✓                      |
| growth models                        |                     |                    |                        |
| Cellular automata                    | ✓                   | ✓                  | ✓                      |
| Individual-based models              | ✓ ✓*                | ✓                  | ✓ ✓*                   |

Note: Model attributes were assigned based on typical representation in the 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.
three-dimensions (i.e., 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:

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

(1)

where \(N\) is the density of organisms at spatial coordinates \(x, y\), and time \(t\) (Baker, 2017; Holmes, Lewis, Banks, & Veit, 1994). The first term on the right-hand side represents diffusion, where \(D\) is a diffusion coefficient (in units of distance\(^2\) time\(^{-1}\)) and \(\nabla\) represents change in three-dimensions (\(x, y, \) and time \(t\)). The second term represents advection, with advection coefficient \(v\), 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; Tobin, Berec, & Liebhold, 2011; Wang & Kot, 2001). 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, Diele, Lacitignola, Marangi, & Martiradonna, 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, United States, 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, Baker, MacLeod, Knight, & Mumford, 2010; Epanchin-Niell & Liebhold, 2015).

Although RADMs have provided insight into invasive species dynamics in heterogeneous environments, limitations of these models 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, a software tool requiring minimal coding experience that codes RADMs and allows for comparing management strategies (Beeton et al., 2015).

### 2.2 | Integrodifference equations

IDEs model invasive species spread and population growth across continuous space, but unlike RADMs, IDEs treat time in a discrete manner (Figure 1, Table 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, Kot, & Lewis, 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:

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

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, Kot, & Neubert, 2002). The kernel can describe broad or species-specific movement by allowing for accelerating movement rates and jump dispersal (Hudgins, Liebhold, & Leung, 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, Shea, Skarpaas, Kelly, & Ellner, 2011).

Conservation scientists have used IDEs to predict invasive species spread and population control efforts. In one example, Caplat, Nathan, and Buckley (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, Barbeau, Locke, Wang, and Watmough (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, Lenhart, & Gaff, 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., nondirectional). This is an unrealistic assumption for many animal species, but more reasonable for plant species, where IDEs have seen greater application (e.g., Caplat et al., 2012; Neubert & Caswell, 2000; Neubert & Parker, 2004). 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, Gaffney, Bullock, & White, 2014). However, IDEs can be expanded to incorporate various types of dispersal, dynamic environments, and environmental heterogeneity (Rodriguez, 2015).

### 2.3 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 (PTMs are the other; Figure 1, Table 1). Spread by jump dispersal can describe human-mediated extra-range dispersal of invasive species beyond the natural range of spread (Wilson, Dormontt, Prentis, Lowe, & Richardson, 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, Holway, & Case, 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:

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

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 $\alpha$ is a coefficient on distance (Bossenbroek, Kraft, & Nekola, 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, for example, by considering how management could modify parameters $W_j$ or $\alpha$. In perhaps the first application of GMs to invasive species, Bossenbroek et al. (2001) forecasted zebra mussel
(Dreissena polymorpha) spread in the upper midwestern United States 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, Borbely, Muirhead, & Graniero, 2004; Muirhead & MacIsaac, Muirhead & Macisaac, 2005; Leung & Mandrak, 2007). For example, Fischer, Beck, Herborg, and Lewis (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, United States. 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 is 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.

2.4 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 1, Table 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:

\[
\frac{\partial c}{\partial t} = \nabla K \nabla c - \nabla v c + Q
\]

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 are \( -\nabla vc \), where \( v \) represents velocity. The sources and sinks, \( Q \), of the population are incorporated as an additive term for population concentration. The symbol \( \nabla \) represents changes in three dimensions, where \( v, K, \) 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 (Lymnoperma 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, Dittel, Miller, and Epifanio (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 United States. 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 \( v \). Direct removals could also be represented in Equation (4). One way to include this is to subtract \( hc \) from the right-hand side of Equation (4), 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, for example, wind or water current data, to inform dispersal; aerial and aquatic
2.5 Nonspatial discrete-time population growth models

Nonspatial discrete-time 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 1, Table 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:

\[ N_{t+1} = rN_t \]  

(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, Ellner, & Dixon, 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:

\[ N_{t+1} = LN_t \]  

(6)

where \( L \) is a matrix defining vital rates of each subset of the population, and the dimension of \( L \) is defined by the number of ages or stages. Consider an invasive population consisting of newborns, 1-year-olds, and adults (2-years 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-year old, \( s_2 = \) survival from 1-year old to 2-years old, \( s_3 = \) survival of individuals 2-years old and older, and \( f = \) fecundity of individuals (number of female offspring per female) 2-years old and older, the population abundance vector at time \( t+1 \) is calculated as:

\[
\begin{bmatrix}
  n_1 \\
  n_2 \\
  n_3
\end{bmatrix}_{t+1} =
\begin{bmatrix}
  0 & sf & sf \\
  s_1 & 0 & 0 \\
  0 & s_2 & s_3
\end{bmatrix}
\begin{bmatrix}
  n_1 \\
  n_2 \\
  n_3
\end{bmatrix}_t
\]  

(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, for example, 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, United States, 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, Altwegg, and Anholt (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, Robinson, & Lambin, 2015), and terrestrial (e.g., Shyu, Pardini, Knight, & Caswell, 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.

### 2.6 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 1, Table 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., behavioral model of animal vectors; Jongejans, Skarpaas, & Shea, 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 SPGM can be expressed as:

$$N_{t+1,s} = L_s N_{t,s}$$

where $N_{t,s}$ is a matrix describing population density at time $t$ for each of the $s$ spatial cells. $L_s$ is a transition matrix of size $s \times s$ that defines the demographic and dispersal processes that may vary across cells and stages. The matrix can be written as $L_{t,s}$ 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, Hastings, and Costello (2010) modeled spread and control of *S. alterniflora* on the coast of Washington State, United States, 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, United States. 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, Johnson, Hooten, Ver Hoef, & Morales, 2014). In addition, the explicit modeling of movement, births, and deaths within a SPGM can make these models data hungry.

### 2.7 Cellular automata

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 1, Table 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 and 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 Section 2.8) 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 CA 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, Hochmair, Scheffrahn, & DeAngelis, 2014).

CAs can be described as:

\[ X_{s,t+1} = f(X_{s,t}, S) \]  

where \( X_{s,t} \) is a finite set that represents the state of cell \( s \) at time step \( t \). 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, Zhang, Guan, & Wang, 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, Rebaudo, Silvain, and Dangles (2011) used a CA to describe natural and human-mediated spread of invasive potato tuber moths (\textit{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, Haight, Mercader, and McCullough (2014) used a CA to simulate an emerald ash borer population in Minnesota, United States 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., Arii & Parrott, 2006; Marco, Páez, & Cannas, 2002).

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.

2.8 Individual-based models

Individual- or agent-based models reproduce ecological events by simulating individuals that follow distinct rules (Figure 1, Table 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, James, Anderson, & Plank, 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, and humans) that are assigned different states, \( x_{i,t} \), based on characteristics such as age, sex, spatial location, and so forth, 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:

\[ f_{i,t} : S_t \rightarrow x_{i,t+1} \]

where \( f_{i,t} \) uses neighboring and current states denoted as \( S_t \), to determine the new state, \( x_{i,t+1} \) (Hinkelmann, Murrugarra, Jarra, & Laubenbacher, 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 (\textit{Diabrotica virgifera virgifera}) in the United Kingdom. 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., 2013).

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).

3 | 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 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 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 limitations of the models can help guide the user to 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, 2014) 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 Eigen analysis 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, for example, 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, Jeschke, & Garcia-Del-Lomas, 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, that is, the factors hindering 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, Likens, & Lindenmayer, 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, Robley, Forsyth, and Choquenot (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, Chadès, and Possingham (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, Landguth, Bearlin, Holden, and Whiteley (2018) built an IBM to describe the spread and population growth of eastern brook trout (Salvelinus fontinalis) in the Pacific Northwest, United States, 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, Martin, McDonald-Madden, & Walters, 2011), adaptive management has been used relatively infrequently to guide on-the-ground invasive species management (see Dietterich, Taleghan, & Crowley, 2013; Hooten & Wikle, 2008). 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, Converse, & Lyons, 2011). However, there is opportunity to apply adaptive management in invasive species applications as practitioners continue to grapple with uncertainty (Allen, Fontaine, Pope, & Garmestani, 2011; Runge, 2011; Williams & Brown, 2016).

Multiple-objective decision making

The key to any good decision is a clear articulation of management objectives, that is, 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 nontarget 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, United States, deployed a multi-objective approach with budget and labor constraints to identify strategies that minimized damage to native cactus, local buildings, and vegetation ( Büyüktahtakın, Feng, & Szidarovszky, 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, United States. 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, Liebhold, & Shea, 2008; Lampert, Hastings, Grosholz, Jardine, & Sanchirico, 2014; Liu, Sheppard, Kriticos, & Cook, 2011), 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.

4 | 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.

ACKNOWLEDGMENTS

We thank two anonymous reviewers whose comments greatly improved the article. Funding support for B. 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.

CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

AUTHOR CONTRIBUTIONS

Brielle K. Thompson, Julian D. Olden, and Sarah J. Converse conceived the study and wrote the manuscript.

DATA AVAILABILITY STATEMENT

Not applicable.

ETHICS STATEMENT

The authors are not aware of any ethical issues regarding this work.

ORCID

Brielle K. Thompson https://orcid.org/0000-0001-6440-4790
Julian D. Olden https://orcid.org/0000-0003-2143-1187
Sarah J. Converse https://orcid.org/0000-0002-3719-5441

REFERENCES

Addison, P. F. E., Rumpff, L., Bau, S. S., Carey, J. M., Chee, Y. E., Jarrad, F. C., ... Burgman, M. A. (2013). Practical solutions for making models indispensable in conservation decision-making. *Diversity and Distributions*, 19(5–6), 490–502. https://doi.org/10.1111/ddi.12054

Allen, C. R., Fontaine, J. J., Pope, K. L., & Garmestani, A. S. (2011). Adaptive management for a turbulent future. *Journal of Environmental Management*, 92(5), 1339–1345. https://doi.org/10.1016/j.jenvman.2010.11.019
Arii, K., & Parrott, L. (2006). Examining the colonization process of exotic species varying in competitive abilities using a cellular automaton model. *Ecological Modelling*, 199(3), 219–228. https://doi.org/10.1016/j.ecolmodel.2006.05.032

Bair, L. S., Yackulic, C. B., Springborn, M. R., Reimer, M. N., Bond, C. A., & Coggins, L. G. (2018). Identifying cost-effective invasive species control to enhance endangered species populations in the Grand canyon, U.S. *Biological Conservation*, 220(January), 12–20. https://doi.org/10.1016/j.biocon.2018.01.032

Baker, C. M. (2017). Target the source: Optimal spatiotemporal resource allocation for invasive species control. *Conservation Letters*, 10(1), 41–48. https://doi.org/10.1111/conl.12236

Baker, C. M., & Bode, M. (2013). Spatial control of invasive species in conservation landscapes. *Computational Management Science*, 10(4), 331–351. https://doi.org/10.1007/s10287-013-0196-0

Baker, C. M., & Bode, M. (2016). Placing invasive species management in a spatiotemporal context. *Ecological Applications*, 26(3), 712–725. https://doi.org/10.1890/15-0095

Baker, C. M., Bower, S., Tartaglia, E., Bode, M., Bower, H., & Pressley, R. L. (2018). Modelling the spread and control of cherry guava on Lord Howe Island. *Biological Conservation*, 227(December 2017), 252–258. https://doi.org/10.1016/j.biocon.2018.09.017

Baker, C. M., & Bode M. (2021). Recent advances of quantitative modeling to support invasive species eradication on islands. *Conservation Science and Practice*, 3(2). https://doi.org/10.1111/csp2.246

Baker, C. M., Diele, F., Lacitignola, D., Marangi, C., & Martiradonna, A. (2019). Optimal control of invasive species through a dynamical systems approach. *Nonlinear Analysis: Real World Applications*, 49, 45–70. https://doi.org/10.1016/j.nonwa.2019.02.007

Beeton, N. J., McMahon, C. R., Williamson, G. J., Potts, J., Bloomer, J., Bester, M. N., … Johnson, C. N. (2015). Using the spatial population abundance dynamics engine for conservation management. *Methods in Ecology and Evolution*, 6(12), 1407–1416. https://doi.org/10.1111/2041-210X.12434

Beletsky, D., Beletsky, R., Rutherford, E. S., Sieracki, J. L., Bossenbroek, J. M., Lindsay Chadderton, W., … Lodge, D. M. (2017). Predicting spread of aquatic invasive species by lake currents. *Journal of Great Lakes Research*, 43(3), 14–32. https://doi.org/10.1016/j.jglr.2017.02.001

Blackwood, J., Hastings, A., & Costello, C. (2010). Cost-effective management of invasive species using linear-quadratic control. *Ecological Economics*, 69(3), 519–527. https://doi.org/10.1016/j.ecolecon.2009.08.029

Bogich, T. L., Liebhold, A. M., & Shea, K. (2008). To sample or eradicate? A cost minimization model for monitoring and managing an invasive species. *Journal of Applied Ecology*, 45(4), 1134–1142. https://doi.org/10.1111/j.1365-2664.2008.01494.x

Bonneau, M., Johnson, F. A., Smith, B. J., Romagosa, C. M., Martin, J., & Mazzotti, F. J. (2017). Optimal control of an invasive species using a reaction–diffusion model and linear programming. *Ecosphere*, 8(10), e01979. https://doi.org/10.1002/ecs2.1979

Bossenbroek, J. M., Kraft, C. E., & Nekola, J. C. (2001). Prediction of long-distance dispersal using gravity models: Zebra mussel invasion of inland lakes. *Ecological Applications*, 11(6), 1778–1788. https://doi.org/10.1890/1051-0761(2001)011[1778:POLDDU]2.0.CO;2

Büyüktahtakıncı, İ. E., Feng, Z., & Szidarovszky, F. (2014). A multi-objective optimization approach for invasive species control. *Journal of the Operational Research Society*, 65(11), 1625–1635. https://doi.org/10.1057/jors.2013.104

Büyüktahtakıncı, I. E., & Haight, R. G. (2018). A review of operations research models in invasive species management: State of the art, challenges, and future directions. *Annals of Operations Research*, 271(2), 357–403. https://doi.org/10.1007/s10479-017-2670-5

Byers, J. E., & Pringle, J. M. (2006). Going against the flow: Retention, range limits and invasions in advective environments. *Marine Ecology Progress Series*, 313 (Müller 1982), 27–41. https://doi.org/10.3354/meps313027

Caplat, P., Nathan, R., & Buckley, Y. M. (2012). Seed terminal velocity, wind turbulence, and demography drive the spread of an invasive tree in an analytical model. *Ecology*, 93(2), 368–377. https://doi.org/10.1890/11-0820.1

Carrasco, L. R., Baker, R., MacLeod, A., Knight, J. D., & Mumford, J. D. (2010). Optimal and robust control of invasive alien species spreading in homogeneous landscapes. *Journal of the Royal Society Interface*, 7(44), 529–540. https://doi.org/10.1098/rsif.2009.0266

Carrasco, L. R., Cook, D., Baker, R., MacLeod, A., Knight, J. D., & Mumford, J. D. (2012). Towards the integration of spread and economic impacts of biological invasions in a landscape of learning and imitating agents. *Ecological Economics*, 76, 95–103. https://doi.org/10.1016/j.ecolecon.2012.02.009

Cartwright, S. J., Bowgen, K. M., Collop, C., Hyder, K., Nabe-Nielsen, J., Stafford, R., … Sibly, R. M. (2016). Communicating complex ecological models to non-scientist end users. *Ecological Modelling*, 338, 51–59. https://doi.org/10.1016/j.ecolmodel.2016.07.012

Caswell, H. (2001). *Matrix population models: Construction, analysis, and interpretation*. 2. Sunderland: Sinauer.

Caswell, H., & Etter, R. J. (1993). Ecological interactions in patch environments: From patch-occupancy models to cellular automata. In S. A. Levin, T. M. Powell, & J. W. Steele (Eds.), *Patch dynamics* (pp. 93–109). Berlin: Springer Science & Business Media.

Chadès, I., Nicol, S., Rout, T. M., Péron, M., Dujardin, Y., Pichoncacht, J. B., … Hauser, C. E. (2017). Optimization methods to solve adaptive management problems. *Theoretical Ecology*, 10(1), 1–20. https://doi.org/10.1007/s12080-016-0313-0

Cole, V., & Albrecht, J. (1999). Modelling the spread of invasive species—parameter estimation using cellular automata in GIS. *Proceedings Second International Workshop on Dynamic and Multi-Dimensional GIS (DMGIS’99).*

Converse, S. J. (2020). Introduction to multi-criteria decision analysis. In M. C. Runge, S. J. Converse, & J. E. Lyons (Eds.), *Situational decision making: Case studies in natural resource management* (pp. 51–61). Baltimore: Johns Hopkins University Press.

Crespo-Pérez, V., Rebaudo, F., Silvain, J. F., & Dangles, O. (2011). Modeling invasive species spread in complex landscapes: The Case of potato moth in Ecuador. *Landscape Ecology*, 26(10), 1447–1461. https://doi.org/10.1007/s10980-011-9649-4
Dana, E. D., Jeschke, J. M., & García-De-Lomas, J. (2014). Decision tools for managing biological invasions: Existing biases and future needs. *Oryx, 48*(1), 56–63. https://doi.org/10.1017/S0030605312001263

Day, C. C., Landguth, E. L., Bearlin, A., Holden, Z. A., & Whiteley, A. R. (2018). Using simulation modeling to inform management of invasive species: A Case study of eastern brook trout suppression and eradication. *Biological Conservation, 221*, 10–22. https://doi.org/10.1016/j.biocon.2018.01.017

DeAngelis, D. L., & Díaz, S. G. (2019). Decision-making in agent-based modeling: A current review and future prospectus. *Frontiers in Ecology and Evolution, 6*, 1–15. https://doi.org/10.3389/fevo.2018.00237

Diagne, C., Leroy, B., Gozlan, R. E., Vaissière, A. C., Assailly, C., Nuninger, L., ... Courchamp, F. (2020). InvacoSet, a public database of the economic costs of biological invasions worldwide. *Scientific Data, 7*(1), 1–12. https://doi.org/10.1038/s41597-020-00586-z

Dietterich, T. G., Taleghani, M. A., & Crowley, M. (2013). PAC optimal planning for invasive species management: Improved exploration for reinforcement learning from simulator-defined MDPs. *Proceedings of the 27th AAAI Conference on Artificial Intelligence, AAAI 2013, 1270–1276.*

Dimou, K. (1992). 3-D hybrid Eulerian–Lagrangian/particle tracking model for simulating mass transport in coastal water bodies. (Doctoral dissertation). Massachusetts Institute of Technology. 233.

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America, 113*(40), 11261–11265. https://doi.org/10.1073/pnas.1602480113

Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M., ... Tatem, A. J. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. *Nature Communications, 7*(1), 1–9. https://doi.org/10.1038/ncomms12485

Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology, 81*(3), 694–708.

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics, 40*, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Ellner, S. P., & Rees, M. (2006). Integral projection models for species with complex demography. *American Naturalist, 167*(3), 410–428. https://doi.org/10.1086/499438

Epanchin-Niell, R. S. (2017). Economics of invasive species policy and management. *Biological Invasions, 19*(11), 3333–3354. https://doi.org/10.1007/s10530-017-1406-4

Epanchin-Niell, R. S., & Liebhold, A. M. (2015). Benefits of invasion prevention: Effect of time lags, spread rates, and damage persistence. *Ecological Economics, 116*, 146–153. https://doi.org/10.1016/j.ecolecon.2015.04.014

Erickson, R. A., Eager, E. A., Kocovsky, P. M., Glover, D. C., Kallis, J. L., & Long, K. R. (2018). A spatially discrete, integral projection model and its application to invasive carp. *Ecological Modelling, 387*(September), 163–171. https://doi.org/10.1016/j.ecolmodel.2018.09.006

Fischer, S. M., Beck, M., Herborg, L. M., & Lewis, M. A. (2020). A hybrid gravity and route choice model to assess vector traffic in large-scale road networks. *Royal Society Open Science, 7*(5), e191858. https://doi.org/10.1098/rsos.191858

García-Díaz, P., Prowse, T. A. A., Anderson, D. P., Lurgi, M., Binny, R. N., & Cassey, P. (2019). A concise guide to developing and using quantitative models in conservation management. *Conservation Science and Practice, 1*(2), 1–12. https://doi.org/10.1111/csp2.11

Garrard, G. E., Williams, N. S. G., Mata, L., Thomas, J., & Bekessy, S. A. (2018). Biodiversity sensitive urban design. *Conservation Letters, 11*(2), 1–10. https://doi.org/10.1111/conl.12411

Gharouni, A., Barbeau, M. A., Locke, A., Wang, L., & Watmough, J. (2015). Sensitivity of invasion speed to dispersal and demography: An application of spreading speed theory to the green crab invasion on the Northwest Atlantic coast. *Marine Ecology Progress Series, 541*, 135–150. https://doi.org/10.3334/meps11508

Gilbert, M. A., Gaffney, E. A., Bullock, J. M., & White, S. M. (2014). Spreading speeds for plant populations in landscapes with low environmental variation. *Journal of Theoretical Biology, 363*, 436–452. https://doi.org/10.1016/j.jtbi.2014.08.022

Govinderajulu, P., Altweeg, R., & Anholt, B. R. (2005). Matrix model investigation of invasive species control: Bullfrogs on Vancouver Island. *Ecological Applications, 15*(6), 2161–2170. https://doi.org/10.1890/05-0486

Grechi, I., Chadès, I., Buckley, Y. M., Friedel, M. H., Grice, A. C., Possingham, H. P., ... Martin, T. G. (2014). A decision framework for management of conflicting production and biodiversity goals for a commercially valuable invasive species. *Agricultural Systems, 125*, 1–11. https://doi.org/10.1016/j.agsy.2013.11.005

Gregory, R., Failing, L., Harstone, M., Long, G., McDaniels, T., & Ohlson, D. (2012). Structured decision making: A practical guide to environmental management choices. Chichester: John Wiley & Sons.

Grimm, V., Augusiak, J., Focks, A., Frank, B. M., Gabsi, F., Johnston, A. S. A., ... Railsback, S. F. (2014). Towards better modelling and decision support: Documenting model development, testing, and analysis using TRACe. *Ecological Modelling, 280*, 129–139. https://doi.org/10.1016/j.ecolmodel.2014.01.018

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Gintot, V., Giske, J., ... DeAngelis, D. L. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling, 198*(1–2), 115–126. https://doi.org/10.1016/j.ecolmodel.2006.04.023

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., ... DeAngelis, D. L. (2005). Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science, 310*(5750), 987–991. https://doi.org/10.1126/science.1116681

Hastings, A., Cuddington, K., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A., ... Thomson, D. (2005). The spatial spread of invasions: New developments in theory and evidence. *Ecology Letters, 8*(1), 91–101. https://doi.org/10.1111/j.1461-0248.2004.00687.x

Hastings, A., Hall, R. J., & Taylor, C. M. (2006). A simple approach to optimal control of invasive species. *Theoretical Population Biology, 70*(4), 431–435. https://doi.org/10.1016/j.tpb.2006.05.003

Hauser, C. E., & McCarthy, M. A. (2009). Streamlining “search and destroy”: Cost-effective surveillance for invasive species.
management. *Ecology Letters*, 12(7), 683–692. https://doi.org/10.1111/j.1461-0248.2009.01323.x

Higgins, S. I., & Richardson, D. M. (1996). A review of models of alien plant spread. *Ecological Modelling*, 87(1–3), 249–265. https://doi.org/10.1016/0304-3800(95)00022-4

Hinkelmann, F., Murruugarra, D., Jarrah, A. S., & Laubenbacher, R. (2011). A mathematical framework for agent based models of complex biological networks. *Bulletin of Mathematical Biology*, 73(7), 1583–1602. https://doi.org/10.1007/s11538-010-9582-8

Holden, M. H., & Ellner, S. P. (2016). Human judgment vs. quantitative models for the management of ecological resources. *Ecological Applications*, 26(5), 1553–1565. https://doi.org/10.1890.15-1295

Holmes, E. E., Lewis, M. A., Banks, J. E., & Veit, R. R. (1994). Partial differential equations in ecology: Spatial interactions and population dynamics. *Ecology*, 75(1), 17–29. https://doi.org/10.2307/1939378

Holmes, N. D., Spatz, D. R., Oppel, S., Tershy, B., Croll, D. A., Keitt, B., ... Butchart, S. H. (2019). Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. *PLoS One*, 14(3), e0212128.

Hooten, M. B., & Wikle, C. K. (2008). A hierarchical Bayesian nonparametric spatio-temporal model for the spread of invasive species with application to the Eurasian collared-dove. *Environmental and Ecological Statistics*, 15(1), 59–70. https://doi.org/10.1007/s10651-007-0040-1

Huang, H. M., Zhang, L. Q., Guan, Y. J., & Wang, D. H. (2007). A probabilistic species risk assessments. *Bioscience*, 57(13), C19–C21. https://doi.org/10.1093/biosci/bim056

Huang, I. H., & Reid, K. J. (2011). A mathematical framework for agent based models of invasive species eradication and endangered species management. *Science*, 344(6187), 1028–1031. https://doi.org/10.1126/science.1250763

Lenhart, S., & Workman, J. T. (2007). *Optimal control applied to biological models*. 1. New York: CRC Press.

Leung, B., & Mandrak, N. E. (2007). The risk of establishment of aquatic invasive species: Joining invasibility and propagule pressure. *Proceedings of the Royal Society B: Biological Sciences*, 274(1625), 2603–2609. https://doi.org/10.1098/rspb.2007.0841

Link, W. A., Converse, S. J., Yackel Adams, A. A., & Hostetter, N. J. (2018). Analysis of population change and movement using robust design removal data. *Journal of Agricultural, Biological, and Environmental Statistics*, 23(4), 463–477. https://doi.org/10.1007/s13253-018-0335-8

Liu, S., Sheppard, A., Kriticos, D., & Cook, D. (2011). Incorporating uncertainty and social values in managing invasive alien species: A deliberative multi-criteria evaluation approach. *Biological Invasions*, 13(10), 2323–2337. https://doi.org/10.1007/s10530-011-0045-4

Lohr, C. A., Cox, L. J., & Lepczyk, C. A. (2013). Costs and benefits of trap-neuter-release and euthanasia for removal of urban cats in Oahu, Hawaii. *Conservation Biology*, 27(1), 64–73. https://doi.org/10.1111/j.1523-1739.2012.01935.x

Loppnow, G. L., Vascotto, K., & Venturelli, P. A. (2013). Invasive smallmouth bass (*Micropterus dolomieu*): History, impacts, and control. *Management of Biological Invasions*, 4(3), 191–206. https://doi.org/10.3391/mbi.2013.4.3.02

Lorscheid, I., Heine, B. O., & Meyer, M. (2012). Opening the black box of simulations: Increased transparency and effective communication through the systematic Design of Experiments. *Computational and Mathematical Organization Theory*, 18(1), 22–62. https://doi.org/10.1007/s10588-011-9097-3

Lustig, A., James, A., Anderson, D., & Plank, M. (2019). Pest control at a regional scale: Identifying key criteria using a spatially explicit, agent-based model. *Journal of Applied Ecology*, 56(7), 1515–1527. https://doi.org/10.1111/1365-2664.13387

MacIsaac, H. J., Borbely, J. V. M., Muirhead, J. R., & Graniero, P. A. (2004). Backcasting and forecasting biological invasions of inland lakes. *Ecological Applications*, 14(3), 773–783. https://doi.org/10.1890/02-5377

Marco, D. E., Páez, S. A., & Cannas, S. A. (2002). Species invasiveness in biological invasions: A modelling approach. *Biological Invasions*, 4(1–2), 193–205. https://doi.org/10.1023/A:1020518915320
Mazza, G., Tricarico, E., Genovesi, P., & Gherardi, F. (2014). Biological invasions are threats to human health: An overview. *Ethology Ecology & Evolution*, 26(2–3), 112–129. https://doi.org/10.1080/03949370.2013.863225

McCarthy, M. A., & Possingham, H. P. (2007). Active adaptive management for conservation. *Conservation Biology*, 21(4), 956–963. https://doi.org/10.1111/j.1523-1739.2007.00677.x

McClintock, B. T., Johnson, D. S., Hooten, M. B., Ver Hoef, J. M., & Morales, J. M. (2014). When to be discrete: The importance of time formulation in understanding animal movement. *Movement Ecology*, 2(1), 1–14. https://doi.org/10.1186/s40462-014-0021-6

Melero, Y., Robinson, E., & Lambin, X. (2015). Density- and age-dependent reproduction partially compensates culling efforts of invasive non-native American mink. *Biological Invasions*, 17(9), 2645–2657. https://doi.org/10.1007/s10530-015-0902-7

Messer, 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. https://doi.org/10.1111/ddi.12829

Michalak, A. M., Anderson, E. J., Beletsky, D., Boland, S., Bosch, N. S., Bridgeman, T. B., … Zagorski, M. A. (2013). Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. *Proceedings of the National Academy of Sciences, USA*, 110(16), 6448–6452. https://doi.org/10.1073/pnas.1216006110

Muirhead, J. R., & MacIsaac, H. J. (2005). Development of inland lakes as hubs in an invasion network. *Journal of Applied Ecology*, 42(1), 80–90. https://doi.org/10.1111/j.1365-2664.2004.00988.x

Murray, J. D. (2002). *Mathematical biology I: An introduction*. New York; London: Springer.

Murray, J. D. (2003). *Mathematical biology II: Spatial models and biomedical applications*. New York: Springer.

Neubert, M. G., & Caswell, H. (2000). Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, 81(6), 1613. https://doi.org/10.2307/177311

Neubert, M. G., Kot, M., & Lewis, M. A. (2000). Invasion speeds in fluctuating environments. *Proceedings of the Royal Society B: Biological Sciences*, 267(1453), 1603–1610. https://doi.org/10.1098/rspb.2000.1185

Neubert, M. G., & Parker, I. M. (2004). Projecting rates of spread for invasive species. *Risk Analysis*, 24(4), 817–831. https://doi.org/10.1111/j.0272-4332.2004.00481.x

Papes, M., Sillström, M., Asplund, T. R., & Vander Zanden, M. J. (2011). Invasive species research to meet the needs of resource management and planning. *Conservation Biology*, 25(5), 867–872. https://doi.org/10.1111/j.1523-1739.2011.01714.x

Parkes, J. P., Robley, A., Forsyth, D. M., & Choquenot, D. (2006). Adaptive management experiments in vertebrate Pest control in New Zealand and Australia. *Wildlife Society Bulletin*, 34(1), 229–236. https://doi.org/10.2193/0091-7648(2006)34[229:amev]2.0.co;2

Pejchar, L., & Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology and Evolution*, 24(9), 497–504. https://doi.org/10.1016/j.tree.2009.03.016

Pepin, K. M., Smyser, T. J., Davis, A. J., Miller, R. S., McKee, S., VerCauteren, K. C., … Slootmaker, C. (2020). Optimal spatial prioritization of control resources for elimination of invasive species under demographic uncertainty. *Ecological Applications*, 30, 1–15. https://doi.org/10.1002/eap.2126

Prasad, A. M., Iverson, L. R., Peters, M. P., Bossenbroek, J. M., Matthews, S. N., Sydor, T. D., & Schwartz, M. W. (2010). Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. *Landscape Ecology*, 25(3), 353–369. https://doi.org/10.1007/s10980-009-9434-9

Prato, C. G. (2009). Route choice modeling: Past, present and future research directions. *Journal of Choice Modelling*, 2(1), 65–100. https://doi.org/10.1016/S1755-5345(13)70005-8

Pyšek, P., & Richardson, D. M. (2010). Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources*, 35, 25–55. https://doi.org/10.1146/annurev-environ-033009-095548

Python Software Foundation. (2008). *Python programming language*. Hampton, New Hampshire: Python Software Foundation.

R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Rebaudo, F., & Dangles, O. (2013). An agent-based modeling framework for integrated pest management dissemination programs. *Environmental Modelling and Software*, 45, 141–149. https://doi.org/10.1016/j.envsoft.2012.06.014

Regan, T. J., Chades, I., & Possingham, H. P. (2011). Optimally managing under imperfect detection: A method for plant invasions. *Journal of Applied Ecology*, 48(1), 76–85. https://doi.org/10.1111/j.1365-2664.2010.01915.x

Richardson, D. M., & Pyšek, P. (2008). Fifty years of invasion ecology—the legacy of Charles Elton. *Diversity and Distributions*, 14(2), 161–168. https://doi.org/10.1071/981444329988

Rodriguez, N. (2015). On an integro-differential model for pest control in a heterogeneous environment. *Journal of Mathematical Biology*, 70(5), 1177–1206.

Rosen, R. (1981). Pattern generation in networks. *Progress in Theoretical Biology*, 6, 497–525.

Runge, M. C. (2011). An introduction to adaptive management for threatened and endangered species. *Journal of Fish and Wildlife Management*, 2(2), 220–233. https://doi.org/10.3989/jfwm.045

Runge, M. C., Converse, S. J., & Lyons, J. E. (2011). Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. *Biological Conservation*, 144(4), 1214–1223. https://doi.org/10.1016/j.biocon.2010.12.020

Runge, M. C., Converse, S. J., Lyons, J. E., & Smith, D. R. (2020). *Structured decision making: Case studies in natural resource management*. Baltimore: Johns Hopkins University Press.

Schmolke, A., Thorbek, P., DeAngelis, D. L., & Grimm, V. (2010). Ecological models supporting environmental decision making: A strategy for the future. *Trends in Ecology and Evolution*, 25(8), 479–486. https://doi.org/10.1016/j.tree.2010.05.001

Schumaker, N. H., & Brookes, A. (2018). *HexSim*: A modeling environment for ecology and conservation. *Landscape Ecology*, 33(2), 197–211. https://doi.org/10.1007/s10980-017-0605-9

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8, 1–9. https://doi.org/10.1038/ncomms14453

Sharov, A. A., Liebhold, A. M., & Roberts, A. E. (1998). Optimizing the use of barrier zones to slow the spread of gypsy moth.
Walters, C. J. (1986). Adaptive management of renewable resources. Basingstoke: Macmillan.

Walters, C. J., & Hilborn, R. (1978). Ecological optimization and adaptive management. *Annual Review of Ecology and Systematics*, 9(1), 157–188.

Wang, M. H., & Kot, M. (2001). Speeds of invasion in a model with strong or weak Allee effects. *Mathematical Biosciences*, 171(1), 83–97. https://doi.org/10.1016/S0025-5564(01)00048-7

Wang, M. H., Kot, M., & Neubert, M. G. (2002). Integrodifference equations, Allee effects, and invasions. *Journal of Mathematical Biology*, 44(2), 150–168. https://doi.org/10.1007/s002850100116

Wangersky, P. J. (1978). Lotka-Volterra Population Models. *Annual Review of Ecology and Systematics*, 9(1), 189–218.

Westgate, M. J., Likens, G. E., & Lindenmayer, D. B. (2013). Adaptive management of biological systems: A review. *Biological Conservation*, 158, 128–139. https://doi.org/10.1016/j.biocon.2012.08.016

Wilensky, U. (1999). NetLogo (and NetLogo user manual). Center for connected learning and computer-based modeling, Northwestern University. Retrieved from http://ccl.northwestern.edu/netlogo

Williams, B. K., & Brown, E. D. (2014). Adaptive management: From more talk to real action. *Environmental Management*, 53(2), 465–479. https://doi.org/10.1007/s00267-013-0205-7

Williams, B. K., & Brown, E. D. (2016). Technical challenges in the application of adaptive management. *Biological Conservation*, 195, 255–263. https://doi.org/10.1016/j.biocon.2016.01.012

Wilson, J. R. U., Dormontt, E. E., Prentis, P. J., Lowe, A. J., & Richardson, D. M. (2009). Something in the way you move: Dispersal pathways affect invasion success. *Trends in Ecology and Evolution*, 24(3), 136–144. https://doi.org/10.1016/j.tree.2008.10.007

Wolfram, S. (1984). Cellular automata as models of complexity. *Nature*, 311(5985), 419–424. https://doi.org/10.1038/311419a0

Zhang, B., & DeAngelis, D. L. (2020). An overview of agent-based models in plant biology and ecology. *Annals of Botany*, 126, 539–557. https://doi.org/10.1093/aob/mca043

**How to cite this article:** 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