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Local management in a regional context: Simulations with process-based species distribution models

Tim M. Szewczyk[a,b,*], Tom Lee[a], Mark J. Ducey[a], Matthew E. Aiello-Lammens[c], Hayley Bibaud[a], Jenica M. Allen[a]

[a] Department of Natural Resources and the Environment, University of New Hampshire, United States
[b] Department of Computer Science, University of New Hampshire, United States
[c] Environmental Studies and Science Department, Pace University, United States

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ABSTRACT

Ecological models often strive to inform conservation and management decisions. Occurrence-based distribution models may aid regional management strategies, though many management decisions require information beyond the likely presence of a species provided by such models. Process-based distribution models predict geographic distributions using environmental relationships with biological processes, providing more detailed predictions and a key opportunity for data-driven management. Here, we develop and characterize a novel demography-based regional distribution model and illustrate its use by comparing four management strategies for glossy buckthorn (*Frangula alnus*), a bird-dispersed shrub invasive throughout the northeastern United States. On a gridded landscape in southern New Hampshire and Maine, this population-level simulation includes fruiting, seed dispersal, seed bank dynamics, germination and establishment, and annual survival, with land cover as the dominant environmental driver. We parameterize the model with field and lab studies, supplementing with published data, expert knowledge, and pattern-oriented parameterization with historical records. In a comprehensive sensitivity analysis, we found that the age at which individuals are capable of reproduction and the frequency of long distance dispersal had the strongest influence on the distribution. In our management simulations, we found that immigration prevents total eradication within any property regardless of management frequency or coordination, though management impacts are detectable in nearby un-managed cells via reduced seed deposition. The flexible model structure combines multiple disparate data sources similar to those available for many species into a synthetic framework of local and regional biological processes, allows the incorporation of specific management actions targeting particular processes and life stages into the regional context of a process-based species distribution model, and provides a robust method for evaluating potential management strategies.

1. Introduction

Ecological models are often constructed with a goal of informing conservation and management decisions (Buckley et al., 2004; Elith and Leathwick, 2009; McMahon et al., 2010; Guisan et al., 2013), and encompass a wide range of approaches. Models may help guide the prioritization of efforts by predicting future distributions of many species (Allen and Bradley, 2016), or may identify policy effects on critical life stages for a species of concern (Crowder et al., 1994; Morris and Doak, 2003). In particular, simulation-based approaches naturally incorporate the stochasticity, uncertainty, and complexity of ecologically detailed models (Morris and Doak, 2003; Merow et al., 2011; McGowan et al., 2017). Accounting for inherent variability as well as data and process uncertainty can lead to more informed decisions based on the range of plausible outcomes, and can highlight key data limitations. Further, management actions, though often implemented locally, occur within an interconnected regional landscape that can affect resulting ecological dynamics (Merow et al., 2011).

Species distribution models (SDMs) predict species' geographic distributions based on relationships with the environment, and have been used in a variety of conservation applications. The majority of SDMs are occurrence-based, relying on correlations between observed presences and environmental covariates (Elith et al., 2010; Evans et al., 2016). Occurrence-based SDMs have many uses, such as predicting

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[*] Corresponding author at: Biophore, CH-1015 Lausanne, Switzerland.
E-mail address: timothy.szewczyk@unil.ch (T.M. Szewczyk).

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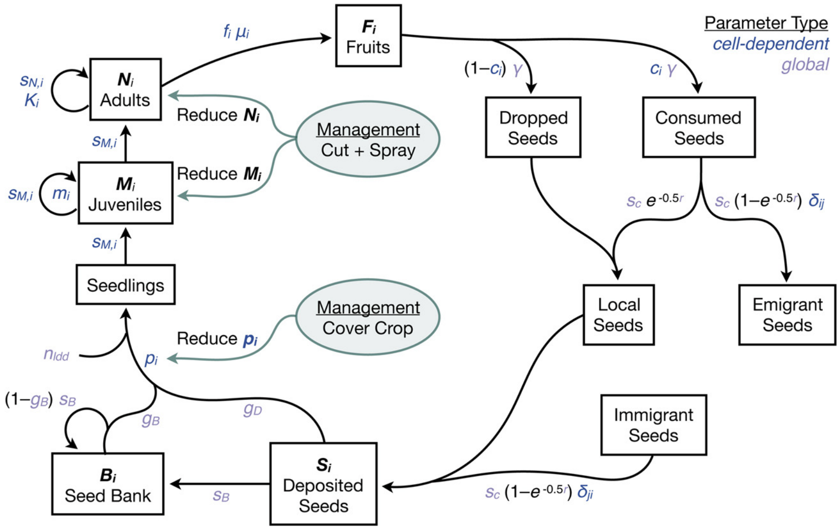

Fig. 1. Annual simulation structure. Boxes represent life stages with abundances, and text along arrows represent parameters. Parameters are either dependent on the cell environment (dark blue, subscript *i*) or global (light purple, no subscript *i*). Manual management actions (i.e., cutting and spraying; ovals) remove individuals prior to reproduction. Fruits are produced according to the number of adults in a given cell, and seeds from consumed fruits are dispersed across the landscape following a negative exponential kernel. Seedlings germinate either directly from seeds produced that year, or from the seed bank. Finally, abundances are updated for the next year, subject to survival rates and carrying capacities. See Table 1 and Appendix A for parameter details. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

current or future distributions and informing conservation priorities by generating maps of potential invasive species risk (Elith and Leathwick, 2009; Guisan et al., 2013; Allen and Bradley, 2016), and are particularly appealing because of the availability of geolocated presence data in online repositories. The predictions of occurrence-based SDMs can be improved by incorporating spatial dynamics, including meta-population and connectivity processes (Mestre et al., 2017). Alternatively, process-based SDMs predict distributions by building relationships between biological processes and environmental covariates, an approach more directly tied to the biology of the species (Kearney and Porter, 2009; Buckley et al., 2010; Dormann et al., 2012; Cuddington et al., 2013; Evans et al., 2016). Options for process-based SDMs are varied; for example, the predictions can be temporally dynamic or static, incorporate dispersal, and utilize either individual-level or population-level relationships (Jongejans et al., 2008; Merow et al., 2011, 2017; Aiello-Lammens, 2014). Compared to occurrence-based SDMs, process-based SDMs require additional data to parameterize, hindering their widespread adoption.

Models for evaluating management strategies are often non-spatial or involve only a small extent (Rees and Paynter, 1997; Buckley et al., 2004; Davis et al., 2006; Ramula and Buckley, 2010), mirroring the local spatial scope of many management actions. As applied models, the structure is typically tailored to the biology and life history of the focal species. The inclusion of particular biological processes allows for the comparison of management actions with differing effects, such as biocontrol agents, cover crops, or manual removal of individuals (Rees and Paynter, 1997; Buckley et al., 2004). With sufficient data to inform impacts on life stages, the predicted population-level effects can be quantified to identify the method most likely to succeed in affecting the species' long term abundance (Davis et al., 2006). However, past work has often made the simplifying assumption that populations occur in isolation, without regional dynamics driven by dispersal of individuals within local neighborhoods and rarer long distance dispersal events.

As spatially explicit models that typically encompass broad geographic areas, SDMs hold great potential for informing the management of rare or invasive species. Occurrence-based SDMs have been constructed to identify locations vulnerable to future invasion (Jiménez-Valverde et al., 2011; O'Donnell et al., 2012; Allen and Bradley, 2016) or particularly valuable critical habitats (Heinrichs et al., 2010). While such products are highly valuable for agencies focused on regional planning, many management decisions occur at finer spatial resolutions than SDMs, or must consider information beyond a species' likely presence or absence as predicted by many SDMs. For instance, managers often must assess the abundance and impact of the focal species, while also balancing logistical constraints (Matzek et al., 2015). Further, management options are diverse. Possible actions for an invasive species may include manual removal, application of herbicide, planting of a cover crop, or introduction of a biocontrol agent, each of which affects the population differently (Rees and Paynter, 1997; Buckley et al., 2004; Davis et al., 2006). The evaluation of management decisions could be greatly aided by models incorporating these differing effects within a broader landscape.

Here, we develop an approach to construct process-based SDMs to simulate local management actions with the expanded realism of regional population dynamics. We link previously disparate models of demographically-driven species abundance, dispersal dynamics, and management actions on specific life stages into a single cohesive modeling framework that is flexible and adaptable to many species. We illustrate with glossy buckthorn (*Frangula alnus*), a bird-dispersed shrub native to Eurasia and invasive throughout the northeastern United States. On a gridded landscape, the model includes mechanistic dispersal and seed bank dynamics in addition to spatially varying flowering probability, fruit production, survival, and seedling establishment. We demonstrate the effect of propagule pressure when managing glossy buckthorn in a regional landscape with heterogeneous management strategies and show the level of spatial coordination needed to achieve local control targets given the species' biology. The flexible structure of the model accommodates modification according to the biology of the focal species, as well as incorporation of biologically realistic effects of management actions. Spatially explicit, process-based models such as this provide a key opportunity to ground management decisions in the species' biology and the best available data.

2. Methods

2.1. Model structure

The model simulates the mechanistic growth and spread of a species across a gridded landscape based on spatially varying biological processes (Fig. 1 and Table 1). The model structure reflects the life history of a bird-dispersed perennial shrub, yet is adaptable to other life histories and dispersal agents. Within each occupied cell, population and life history dynamics are driven by vital rates and demographic parameters which can be global (Fig. 1, light purple) or dependent on the local environment (Fig. 1, dark blue). Populations are connected through the movement of seeds via mechanistic short distance dispersal and random long distance dispersal. We define long distance dispersal as any dispersal event beyond the range of the short distance dispersal neighborhood, including rare, natural disperser movements in addition to intentional and unintentional human-mediated dispersal. Density

Table 1

Parameter definitions. Indexes indicate cells *i* with neighbor *j*. Parameters without an *i* subscript are global, with one value for all cells. Values are for glossy buckthorn. Ranges of values indicate the span among habitable land cover types (i.e., all but *Other*) for parameters that vary with land cover. Minimum and maximum are the limits used in the global sensitivity analysis. Data sources include (a) field studies, (b) lab studies, (c) published literature, (d) pattern-oriented parameterization, and (e) expert knowledge. See Appendix A for additional details.

Symbol	Quantity	Best	Minimum	Maximum	Source
Fecundity parameters					
f_i	Pr(flower|adult)	0.15–0.45	0.11–0.34	0.19–0.56	*a*
μ_i	Mean fruits per flowering adult	14–1948	10–1461	17–2435	*a*
γ	Mean seeds per fruit	2.48	2.38	2.60	*a*
m_i	Age at adulthood [years]	3–7	2–4	4–8	*a, e*
Dispersal parameters					
c_i	Pr(fruit is consumed by a bird)	0.17–0.30	0.12–0.25	0.23–0.33	*a*
r	Short distance dispersal rate [1/cells]	0.0378	0.03	0.5	*c, d*
sdd_{max}	Maximum short distance dispersal distance [cells]	27	4	36	*c, d*
η	Disperser relative habitat preferences	0.05–0.36	0.037–0.27	0.06–0.451	*c*
δ_{ji}	Pr(emigrant from *j* is deposited in *i*)	[a]	[a]	[a]	*c*
n_{ldd}	Annual long distance dispersal events	19	1	20	*c, d*
Survival parameters					
s_c	Pr(seed survival|consumed by bird)	0.59	0.49	0.61	*a*
s_B	Pr(seed survival|seed bank)	0.72	0.64	0.77	*c*
$s_{M,i}$	Pr(juvenile survival)	0.6–0.9	0.45–0.68	0.75–1	*a, c*
$s_{N,i}$	Pr(adult survival)	1	0.9	1	*a, c, e*
K_i	Adult carrying capacity [density/cell]	4162–28,205	1383–19,533	100–38,714	*a, c*
Seedling parameters					
g_D	Pr(germination directly in year produced)	0	0	0	*c*
g_B	Pr(germination from the seed bank)	0.2	0.18	0.28	*a, b*
p_i	Pr(establishment|germination)	0.08–0.42	0.06–0.32	0.10–0.53	*a, b*

[a] Note that δ_{ji} is calculated in each cell based on η, land cover composition, and distance from the source cell.

dependence is implemented by directly limiting the abundance within each cell (Merow et al., 2011). Because of the biological detail, simulated management actions can target particular processes or life stages, such as by reducing seedling establishment through planted cover crops or by reducing abundances through manual removal or herbicide application (Fig. 1).

2.1.1. Fecundity

At the start of each time step *t*, individuals flower and produce fruits. The total number of fruits, *F*, produced in cell *i* in year *t* is calculated as:

$$F_{\mathrm{it}} = N_{\mathrm{it}} f_i \mu_i \tag{1}$$

where N_{it} is the number of adults in cell *i* in year *t*, f_i is the probability that an adult in cell *i* flowers, and μ_i is the mean number of fruits produced by a flowering adult in cell *i*. Both *f* and μ are dependent on the cell environment, as indicated by the subscript *i*.

2.1.2. Dispersal

The fruits produced, F_{it}, are consumed by animal dispersers or drop from the plant to remain in the local population. The seeds in consumed fruits are transported and deposited in the local cell *i* or in the short distance dispersal neighborhood of cell *i*. We assume a single primary natural dispersal vector, though additional dispersal vectors could be readily added. The number of seeds, *S*, in cell *i* in year *t* is therefore:

$$\begin{aligned} S_{\mathrm{it}} &= F_{\mathrm{it}}(1 - c_i)\gamma && \text{not consumed, dropped} \\ &+ F_{\mathrm{it}} c_i \gamma s_c e^{-0.5r} && \text{consumed, deposited in } i \\ &+ \sum_{j=1}^{J_i} F_{\mathrm{jt}} c_j \gamma s_c (1 - e^{-0.5r})\delta_{\mathrm{ji}} && \text{immigrants to } i \text{ from } j \end{aligned} \tag{2}$$

where S_{it} is the number of seeds deposited in cell *i*, c_i is the probability that a fruit in cell *i* is consumed by a disperser, γ is the mean number of seeds per fruit, s_c is the probability that a consumed seed remains viable, $e^{-0.5r}$ is the probability that a consumed seed remains in cell *i* based on an exponential distribution with rate *r* (Merow et al., 2011), δ_{ji} is the probability that an immigrant seed from cell *j* lands in cell *i*, and J_i is the number of cells within the maximum short distance dispersal radius, sdd_{max}. Consequently, each seed produced in cell *i* has four possible fates; a seed may (1) drop in cell *i* without being consumed, (2) be consumed and deposited in cell *i*, (3) be consumed and deposited in a nearby cell, or (4) perish.

The probability of a seed originating in cell *i* dispersing to cell *j*, δ_{ji}, is described by an exponential kernel modified by the expected habitat preferences of the dispersal agents:

$$\delta_{\mathrm{ji}} \propto e^{-|x_j - x_i| r}(L_j \cdot \eta) \tag{3}$$

where $|x_j - x_i|$ is the distance between the centroids of cells *i* and *j*, and the *J* cells in the dispersal neighborhood for *i* are weighted by the expected habitat use of the dispersers (Merow et al., 2011), calculated as the dot product of the land cover composition in the target cell, L_j, and the vector of habitat preferences, η. The exponential kernel with decay rate *r* represents the distribution of distances a dispersal agent is likely to travel between consuming a fruit and defecating to deposit the seeds. However, dispersers will preferentially travel to cells with an abundance of their preferred habitat. Accordingly, the probability for each cell is multiplied by the dot product of the land cover composition and the preference for each land cover type. Thus, for a given distance, dispersal probabilities are higher for cells with a high proportion of disperser-preferred habitat. For each short distance dispersal neighborhood (i.e., the *J* cells surrounding *i*), the probabilities $\delta_{1-J,i}$ are standardized to sum to 1, representing the dispersal probability conditional on first emigrating from the source cell. The calculation of each δ_{ji} therefore incorporates the distance between *i* and *j*, as well as the movement patterns, digestion times, and habitat preferences of the dispersers.

Long distance dispersal is stochastic and inherently difficult to predict, but can be critical to the range expansion of invasive species (Trakhtenbrot et al., 2005; Merow et al., 2011). In addition to rare long distance movements by birds (Merow et al., 2011), which could be considered as rare occurrences following the same mechanism as short distance dispersal, we also include human-mediated dispersal in our definition of long distance dispersal to incorporate unintentional transportation of fruits or seeds and intentional planting of individuals

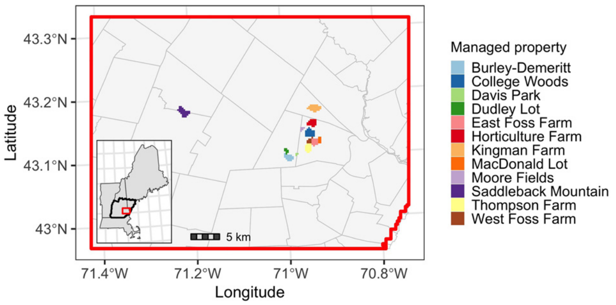

Fig. 2. Map of the study region and properties included in the management simulations. We compared four strategies for controlling the invasive shrub glossy buckthorn on each property: none, stated, actual, and aggressive. The black outline (inset) indicates the region used for the sensitivity analyses and initialization. Gray lines are town boundaries.

(Reichard and White, 2001; Lehan et al., 2013). We therefore include long distance dispersal as a separate component in the model, which also reduces computational requirements by limiting the size of short distance dispersal neighborhoods. Thus, in each year, one successfully established seedling is placed in each of n_{ldd} random cells on the landscape, regardless of whether the cells are already occupied.

2.1.3. Seed dynamics

The S_{it} seeds deposited in cell i in year t may germinate, enter the seed bank, or perish. The number of seeds that establish as seedlings is:

$$M_{i,t+1,1} = S_{\mathrm{it}} g_D p_i + B_{\mathrm{it}} g_B p_i \tag{4}$$

where $M_{i,t+1,1}$ is the number of one-year-olds in cell i in the following year, g_D is the probability that a seed deposited in year t germinates in year t, p_i is the probability that a germinant successfully establishes in cell i, B_{it} is the number of seeds in the seed bank at the start of year t, and g_B is the probability that a seed germinates from the seed bank.

Seeds added to cell i in year t that do not germinate may enter into the seed bank. The seed bank abundance in cell i is:

$$B_{i,t+1} = B_{\mathrm{it}}(1 - g_B)s_B + S_{\mathrm{it}}(1 - g_D)s_B \tag{5}$$

where s_B is the probability that a seed survives one year in the seed bank.

2.1.4. Survival

We define adults as individuals that are capable of reproducing based on age. Plants are considered juveniles until they reach this age, m, and juveniles survive each year with probability $s_{M,i}$, where survival is dependent on the environmental conditions in i. The number of juveniles of each age is stored as M_{itk}, with ages $k = 2, \ldots, m - 1$, and calculated as:

$$M_{i,t+1,k} = M_{i,t,k-1} s_{M,i} \tag{6}$$

such that individuals advance in age each year, diminished by annual mortality.

Once individuals reach an age where they may potentially reproduce, m, they are considered adults. The number of adults in cell i in each year t, N_{it}, is limited by a ceiling-type carrying capacity, K_i, based on the environmental conditions within each cell. The number of adults is:

$$N_{i,t+1} = \min\left\{\begin{array}{l} K_i \\ N_{\mathrm{it}} s_{N,i} + M_{i,t,m-1} s_{M,i} \end{array}\right. \tag{7}$$

where K_i is the carrying capacity in cell i and $s_{N,i}$ is the annual adult survival rate. The number of adults in each cell will increase based on the propagule pressure (i.e., the sum of local and immigrant seeds), juvenile survival, and adult survival until the carrying capacity is reached (Morris and Doak, 2003; McGowan et al., 2017).

This process-based model was written in R, and all simulations and analyses were performed in R 3.5.2 (R Core Team, 2018). The model and landscape have been made available as the R package *gbPopMod* (https://github.com/Sz-Tim/gbPopMod). R code for the simulations and analyses is provided in the appendixes.

2.2. Model application

2.2.1. System description

We illustrate the model using glossy buckthorn (*Frangula alnus*), a shrub native to Eurasia that was introduced in North America by 1879 and has since become invasive in much of the northeastern United States (Catling and Porebski, 1994; Johnson et al., 2006; Webster et al., 2006; Aiello-Lammens, 2014). Glossy buckthorn persists in forest understories, but forms dense thickets in open canopy (Burnham and Lee, 2010). In addition to reducing recreational value, glossy buckthorn causes particular damage to forestry operations; after trees have been harvested, buckthorn densities increase dramatically in canopy gaps, out-competing commercial timber species such as eastern white pine (Frappier et al., 2003; Lanzer et al., 2017; Lee et al., 2017). Glossy buckthorn produces fleshy fruits throughout the summer that are consumed and dispersed by a variety of bird species (Craves, 2015). In the northeastern United States, the most likely dispersers include European Starlings, American Robins, and Cedar Waxwings (McCay et al., 2009).

We focus on southern New Hampshire and Maine in the northeastern United States, an area where glossy buckthorn is abundant and eastern white pine forests are reasonably common (Fig. 2, black outline in inset). Within this regional extent, we assume that land cover type is the dominant factor affecting glossy buckthorn biological rates (Pearson and Dawson, 2003). The landscape consists of 240,656 grid cells (4,813,120 acres ≈ 19,478 km^2) with a resolution of 20 acres (8.1 ha ≈ 285 × 285 m). We specify biological rates for glossy buckthorn in six land cover classes (*Open*, *Deciduous Forest*, *Mixed Forest*, *White Pine Forest*, *Other Evergreen Forest*, and *Other*) where possible, using the land cover composition in each cell to calculate aggregate expected rates across the landscape. We used a land cover map of the predicted proportion of each land cover class in each 20 acre cell (Appendix A). The map was created to represent glossy buckthorn habitat affinities via a modeled synthesis of two land cover datasets: the 2001 National Land Cover database (Homer et al., 2007) and the more detailed New Hampshire land cover map (Justice et al., 2002). We used environmental, anthropogenic, and topographic data to predict discrepancies between the land cover datasets and to align categorization differences to produce a single compositional land cover map across the study extent at the desired resolution (Szewczyk et al., in review).

2.2.2. Parameterization and sensitivity analyses

To parameterize the model, we used a combination of field and lab experiments, supplemented by published data from the literature, expert knowledge, and pattern-matching (Table 1 and Appendix A). When data for glossy buckthorn were unavailable, we used ecologically similar species, namely the woody shrub *Lindera benzoin* and the fleshy-fruit producing invasive vine *Celastrus orbiculatus*. See Appendix A for extensive parameter-specific details and additional information regarding data sources.

The earliest record of glossy buckthorn within the study area (Fig. 2, black outline in inset) is in southern New Hampshire in 1922 (Aiello-Lammens, 2014). This record served as the initial introduction site for the sensitivity analysis and population initialization. We used historical records to identify the dispersal parameters that best captured the observed spread (Aiello-Lammens, 2014; EDDMap, 2016). Then, we ran 1000 iterations for 96 years (1922–2018) each, using the average abundances in each cell to represent the predicted abundance of glossy buckthorn in the study region from initial introduction to the year 2018. This final distribution served as the initial year in simulations comparing management strategies, such that the management actions

Table 2

Details for four simulated management scenarios (no action, stated, actual, and aggressive) for the invasive shrub glossy buckthorn on 12 centrally managed properties in southeastern New Hampshire, USA. Management actions include cutting, spraying, and planting a cover crop, and may be implemented only in specific land cover types (e.g., *Open* or *Forests*), only when glossy buckthorn abundances exceed a threshold, or only in certain years.

Property	Acres	No action	Stated	Actual	Aggressive
Burley-Demeritt	130	No action	Cut if $N > 500$/acre	No action	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
College Woods	250	No action	Cut annually in *Forests* + spray annually in *Open*	Cut annually	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
Davis Park	11	No action	Cut if $N > 500$/acre	No action	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
Dudley Lot	21	No action	No action	No action	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
East Foss Farm	164	No action	No action	Cut in *Open* in years 1 & 2 on a 5-year cycle	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
Horticulture Farm	156	No action	No action	No action	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
Kingman Farm	334	No action	No action	Cut in *Open* in years 1 & 2 on a 5-year cycle	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
MacDonald Lot	79	No action	No action	Cut in *Open* in years 1 & 2 on a 5-year cycle	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
Moore Fields	118	No action	Cut if $N > 500$/acre	Spray in years 1 & 2 on a 5-year cycle	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
Saddleback Mountain	277	No action	Cut if $N > 500$/acre	No action	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
Thompson Farm	205	No action	No action	Cut in *Open* in years 1 & 2 on a 5-year cycle	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle
West Foss Farm	92	No action	No action	Cut in *Open* in years 1 & 2 on a 5-year cycle	Cut & spray in *All* types + cover crop in *Open* in years 1, 2, & 3 on a 5-year cycle

occur in the present environment as predicted by the model.

We performed a global sensitivity analysis to explore the plausible parameter space and understand model behavior (Prowse et al., 2016; Aiello-Lammens and Akçakaya, 2017). Rather than performing sensitivity analyses for each parameter in isolation, a global sensitivity analysis simultaneously selects values for all parameters. This approach effectively marginalizes across any interactions between parameters to provide a holistic estimation of the effect of each parameter on the model predictions.

We set plausible parameter ranges based on field studies, lab studies, the literature, and expert opinion (Table A.1). We drew random values from uniform distributions within these ranges to generate 25,000 parameter sets, running one iteration of the model for each parameter set (Prowse et al., 2016). Despite the stochastic dispersal in the model, a single iteration allows for a more efficient exploration of the parameter space compared to multiple iterations per draw with a more limited number of draws (Prowse et al., 2016). For each draw, we simulated the population for 50 years from the initial introduction, and then calculated the proportion of cells occupied by adults, the proportion of cells with a seed bank, the proportion of occupied cells that had reached carrying capacity, the mean and median abundance in occupied cells, and the variance in abundance among occupied cells.

To evaluate each parameter's effect on each response metric, we used boosted regression trees (BRTs) with all parameters included as predictors (Elith et al., 2008; Prowse et al., 2016). BRTs use the machine learning technique of boosting to create an ensemble model of regression trees to optimize predictive performance. Using the weights of the regression trees included in the ensemble model, the relative influence of each parameter can then be calculated (Elith et al., 2008). We compared tree complexities of 1, 3, and 5. To ensure that the parameter space was adequately explored, each BRT was fit with bootstrapped subsets of varying size, with cross-validation deviance and stability of the relative influence estimates calculated across subsets (Prowse et al., 2016). For parameters that varied by land cover type, we included the value for each of the six land cover types as predictors to fit the BRT, and summed the relative influence. For example, we fit each BRT with f_{Open}, …, f_{Other} included as separate predictors, then summed the relative influence to calculate an overall relative influence for f. See additional detail in Appendix B.

We used pattern-oriented parameterization to identify the best estimates for dispersal (Grimm et al., 2005; Merow et al., 2011; Grimm and Railsback, 2005). We compiled geo-located presences of glossy buckthorn by combining herbarium records (Aiello-Lammens, 2014) and occurrences from the EDDMapS database (EDDMap, 2016). For each cell with an observation, we calculated the earliest observation. We varied the mean short distance dispersal distance, $1/r$, the maximum short distance dispersal distance, sdd_{max}, and the number of annual long distance dispersal events, n_{ldd}, in the same manner as the main global sensitivity analysis, with all other parameters set to best estimates, taking 5000 samples. Each iteration was initialized as above and run for 96 years, representing the predicted spread through 2018. Then, we selected the median values for each parameter from the parameter draws that correctly predicted at least 90% of the historical spread.

2.2.3. *Management simulations*

The University of New Hampshire manages woodland properties throughout the state of New Hampshire. These properties vary in size from 11 to 334 acres and are centrally managed with goals aimed toward a variety of purposes, including recreation, wildlife habitat, and academic uses. The abundance of glossy buckthorn and other invasive plants is variable among properties, and stated management strategies range from monitoring to regular treatment to no action (https://colsa.unh.edu/woodlands/managed-properties). In practice, the realized management actions on each property depend on a combination of logistical constraints and broader goals.

We simulated possible strategies for managing glossy buckthorn on 12 of the woodland properties in southeastern New Hampshire (Fig. 2 and Table 2). To initialize the landscape, we ran 1000 simulations for 96 years each (1922–2018), using best estimates for each parameter (Table A.1) and calculating the mean abundance across simulations of the seed bank and of each age category within each land cover type in each cell. For computational efficiency, the landscape and initial distribution were then truncated to the bounding box enclosing 2 × sdd_{max} around the focal properties (Fig. 2, red outline). Then, we evaluated four sets of management plans: no management, the stated management plan, the actual management actions, and an aggressive plan (Table 2). Each strategy was implemented for 1000 simulations of 20 years each to assess the effect of management actions on glossy buckthorn populations within and around each property.

3. Results

Our model predicts not only the probability of occurrence in each cell of the landscape, but also the abundance of each life stage and the spatial distribution of biological processes and rates. In our illustration with glossy buckthorn, the predicted abundance of adults was highest in cells with more *Open* habitat and less *Forest* (Fig. 3a), reflecting the affinity of glossy buckthorn for higher light levels (Cunard and Lee, 2009; Burnham and Lee, 2010). In contrast, seedling establishment rates show less geographic variation, despite varying among land cover types (Fig. 3b). The total propagule pressure (i.e., the total seeds deposited in a cell), is high only near the abundance hotspots (Fig. 3c). Individuals produce more fruit under open canopies, and the pattern of per capita seed production thus mirrors that of adult abundance and propagule pressure (Fig. 3d). Based on the total propagule pressure and the number of seeds immigrating to each cell (Fig. 3e), the relative abundance of local and immigrant seeds can be calculated (Fig. 3f). Thus, process-based SDMs allow the examination of the spatial variation in each biological rate or process, providing information valuable for management decisions.

The relative influence of parameters was stable for all metrics across sample sizes greater than 20,000 (Fig. B.2), and we base our analysis on 25,000 samples of the parameter space. The parameters with greatest influence varied with the metric of interest (Fig. 4). The number of annual long distance dispersal events, n_{ldd}, and the age of adulthood, m, primarily drove the proportion of cells occupied, both for adults and for seeds, with smaller effects of the short distance dispersal rate, r, and juvenile survival, s_M. The proportion of occupied cells reaching carrying capacity and the mean and median abundance were most strongly affected by the age of adulthood with secondary effects of the juvenile survival rate and, for mean abundance, carrying capacity, K. In contrast, the variance of abundance in occupied cells was driven by carrying capacity.

The number of annual long distance dispersal events had a large impact on the ability to accurately predict the historic spread of glossy buckthorn, reaffirming the results of the global sensitivity analysis. The short distance dispersal rate had a moderate influence, while the maximum short distance dispersal distance had little effect. The accurate prediction of the distribution required abundant long distance dispersal (n_{ldd} = 19 annual events) with a short distance dispersal rate of 0.0378 and a maximum distance of 27 cells (≈7.7 km).

In the management simulations, glossy buckthorn density on each property approached or reached carrying capacity in the absence of management actions (Fig. C.16). The stated plan, actual actions, and aggressive strategy all decreased buckthorn adult and seed density relative to no action on properties that implemented management (Fig. 5). However, even the aggressive strategy failed to fully eliminate

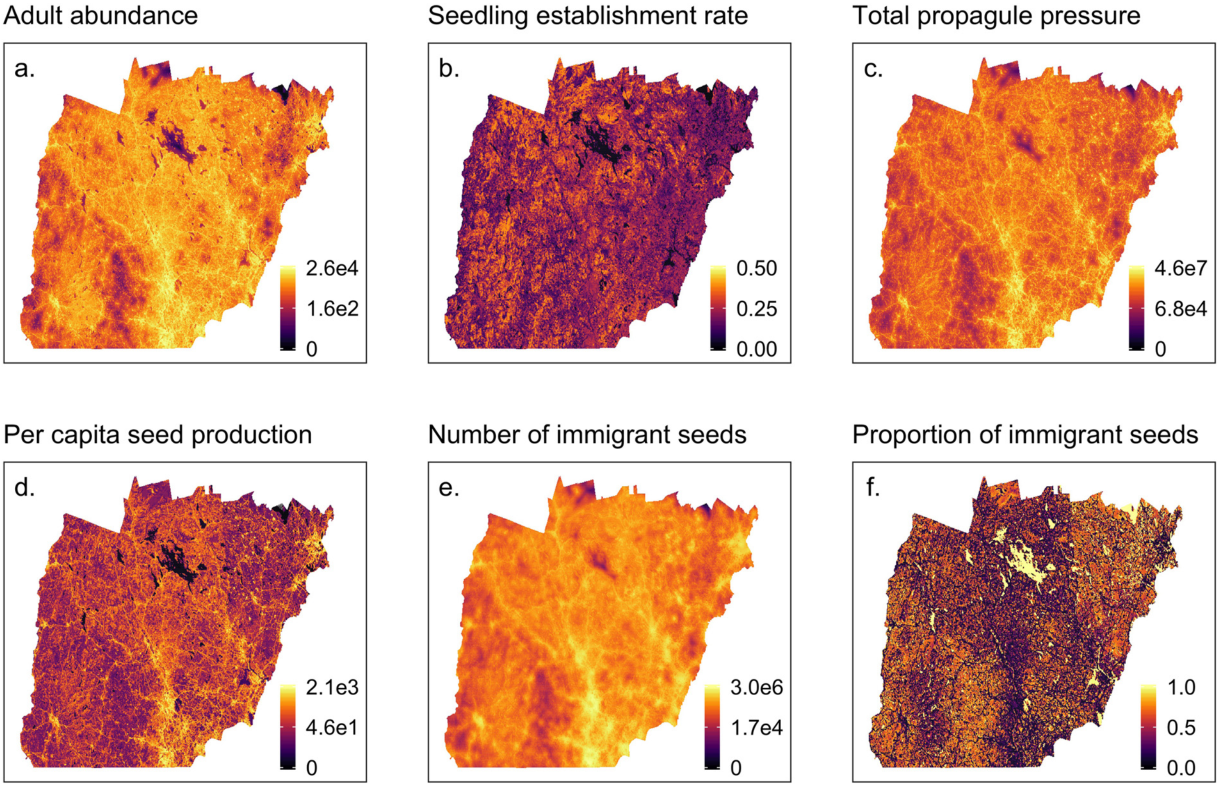

Fig. 3. Maps of model output. Process-based species distribution models can predict numerous aspects of the species' biology in addition to simple presence or absence. As constructed here, the model generates predictions of abundance for (a) adults, juveniles, and the seed bank, in addition to (b) the predicted seedling establishment rate, (c) total propagule pressure (i.e., the total number of seeds deposited in each cell), (d) per capita seed production, (e) immigrant seeds, and easily calculable quantities such as (f) the relative influence of immigration on propagule pressure. The modeled extent includes southern New Hampshire and Maine as indicated by the black outline in Fig. 2 inset.

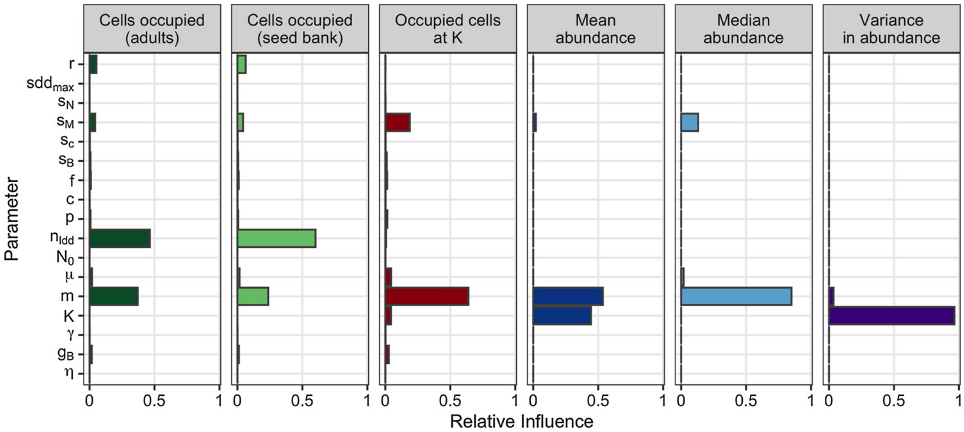

Fig. 4. Relative influence of parameters in a global sensitivity analysis. We varied all parameters simultaneously within data-based ranges (Tables 1 and A.1), and used boosted regression trees to calculate the relative influence of each on the number of cells occupied by adults, the number occupied by seeds, the proportion of occupied cells at carrying capacity, and the mean, median, and variance in adult abundance for occupied cells.

glossy buckthorn (Fig. 5, right column), despite repeated cutting, spraying, and planting of cover crops (minimum density per property: 1.4–101 adults/20 acre). The seed bank was reduced, but maintained at a lower equilibrium by the remaining adults as well as immigration from nearby cells (Fig. 5, bottom row). Consequently, the abundance of glossy buckthorn adults quickly rebounded in the intervening years between treatments due to the surviving juveniles and the persistent propagule pressure from surrounding cells.

4. Discussion

The process-based SDM presented here incorporates several biological processes in the context of a bird-dispersed shrub. The flexible structure makes this framework suitable for a wide array of species and life histories. The added complexity confers several key benefits, including insight into the geographic variation in vital rates, and the ability to simulate specific, targeted effects of management actions, with local decisions implemented in the broader regional context. We illustrated such a use by evaluating management strategies for the invasive shrub glossy buckthorn on 12 centrally managed properties in southeastern New Hampshire, showing persistent spillover effects from nearby un-managed cells.

Process-based SDMs provide much more detailed predictions than occurrence-based SDMs (Merow et al., 2011, 2017). By incorporating biological rates and processes that vary across environmental gradients, they allow for spatial predictions of processes such as germination or flowering rates (Merow et al., 2017). Exploration of these predictions may highlight management methods or locations that are likely to be most fruitful, whether for reducing the abundance of an invasive species or, conversely, increasing the abundance of a threatened species. For example, a regional strategy for managing glossy buckthorn may involve targeting populations that produce a large number of emigrant seeds to efficiently reduce the propagule pressure of the surrounding area (Fig. C.12). Incorporating mechanistic dispersal in a simulation framework extends the possibilities further. Temporally dynamic simulations may identify dispersal corridors for species, highlighting areas to protect or monitor. Compared to SDMs with simple population growth (Merow et al., 2011), the model presented here includes age structured populations and reproductive processes. Aggregating and collecting data to inform these processes across an adequate environmental gradient may be more logistically feasible than estimating intrinsic growth rates across a similar gradient. Further, a model built directly on biological processes may produce more accurate predictions in the face of a changing climate, particularly if parameterized with warming or transplant experiments (Jiménez-Valverde et al., 2011; Evans et al., 2016).

In the global sensitivity analysis, we constrained the range of each parameter according to available data. The relative influence therefore reflects a combination of the inherent sensitivity of the output to that parameter and the breadth of the plausible range. In contrast, using the full allowable range for each parameter (e.g., [0–1] for a probability) reveals solely the sensitivity that is structural in the model. Incorporating data-driven constraints on the ranges highlights parameters for which additional data would be most valuable and lead to the greatest improvements in predictions. If a distinction between the influence of structural sensitivity and data uncertainty is required, one could compare a sensitivity analysis performed with data-driven ranges to one performed with full possible ranges. Our results show that the number of annual long distance dispersal events, the age of maturity, and the juvenile survival rate are influential across several grid-wide

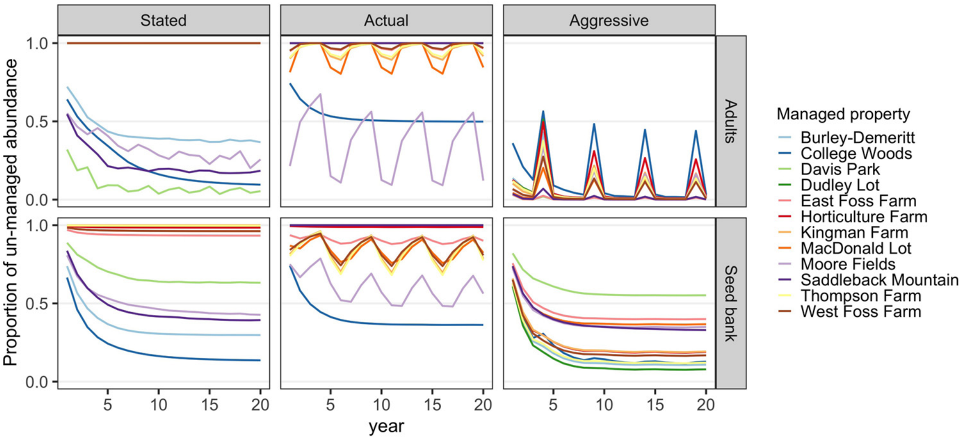

Fig. 5. Proportion of ‘No action’ abundances under each management regime.

metrics. While long distance dispersal is inherently difficult to predict (Higgins and Richardson, 1999; Buchan and Padilla, 1999), future models of glossy buckthorn would most benefit from additional data clarifying juvenile mortality and the age at which individuals are capable of producing fruit across a range of environments.

We identified best estimates for each dispersal parameter using a pattern-oriented approach with historical records of glossy buckthorn. Compared to *Celastrus orbiculatus*, a bird-dispersed invasive vine in New England, our model of glossy buckthorn required broader short distance dispersal and more annual long distance dispersal events (Merow et al., 2011). We propose three hypotheses for this difference relative to previous work. First, our definition of long distance dispersal is broader, including not only rare long distance bird dispersal, but also unintentional and intentional human-mediated events. Like many invasive plants, glossy buckthorn was planted in gardens as an ornamental shrub, particularly early in its introduction history (Catling and Porebski, 1994; Reichard and White, 2001; Aiello-Lammens, 2014), and so a high number of 'dispersal' events reflects this history. Second, we modeled a relatively modest regional extent, and glossy buckthorn occurs beyond our study borders (Catling and Porebski, 1994; Aiello-Lammens, 2014; Craves, 2015). Increased long distance dispersal could reflect dispersal from beyond our landscape boundaries, a phenomenon likely to be less influential in the model of *C. orbiculatus* across the entirety of the northeastern United States. Third, we used a high resolution grid to evaluate management scenarios, and consequently, dispersing seeds must cross more grid cells per unit distance. Because dispersal probability exponentially decreases with distance from the source cell, dispersal requires more 'steps' on a high resolution grid than on a coarser grid, which is compensated for by a flatter exponential distribution for short distance dispersal.

Process-based SDMs, which construct distributions based on biological processes, are often assumed to be superior to occurrence-based SDMs, which construct distributions by relating occurrence data to environmental variables (Jiménez-Valverde et al., 2011; Evans et al., 2016; Merow et al., 2017). However, the application of grid-based simulations with simple population growth and mechanistic dispersal for predicting species distributions has been minimal (Merow et al., 2011). More complex integral projection models incorporate individual-level data into vital rate regressions, and can be used to predict population growth rates across a region (Merow et al., 2014, 2017). The data that are available or feasibly collected constrain the plausible choices for process-based SDMs. Estimating intrinsic population growth rates typically requires population estimates across several years and the accuracy is quite sensitive to inter-annual stochastic variation (Morris and Doak, 2003; McCain et al., 2016; Loehle and Weatherford, 2017). Similarly, integral projection models require multi-year, labor-intensive studies to measure and track individuals across a sufficiently broad environmental gradient (Aiello-Lammens, 2014; Merow et al., 2014, 2017). The model presented here represents an alternative that uses data that may be more readily available in the literature or more quickly collected in the field, with intermediate model complexity.

Often, SDMs are built at fairly coarse resolutions with pixels on the order of multiple square kilometers (Elith and Leathwick, 2009; Ibánez et al., 2009; Merow et al., 2011; Bellard et al., 2013; Allen and Bradley, 2016). At these scales, regional variables such as climate tend to be most influential (Huston, 1999; Pearson and Dawson, 2003; Keil et al., 2012; Fraterrigo et al., 2014), and the models are agnostic regarding sub-pixel variation in the species' occurrence or abundance. Stakeholders deciding how to monitor and manage individual properties require more detailed predictions than coarse-scale models can provide. These managers would benefit most from high resolution models predicting the probable abundance or risk within each property (Matzek et al., 2015). Hyper-local plant distributions are often determined by variables such as light availability, soil type, or canopy species (Guisan and Thuiller, 2005; Elith and Leathwick, 2009; Burnham and Lee, 2010), as well as the stochastic placement of individuals (Grimm et al., 2005). While a model can be parameterized using these local variables, predictions may then be limited to hypothetical 'good' or 'bad' local habitats since the local variables are unknown at a regional extent (Merow et al., 2017). Thus, there is a critical scale mismatch between the models ecologists are often able to build and the models that would be most useful for applied management decisions (Matzek et al., 2015). Process-based regional models such as the model presented here are a step toward rectifying this mismatch, and could be combined with statistical downscaling to predict local distributions on particular properties (Wu and David, 2002; Keil et al., 2013; Barwell et al., 2014).

The specific model presented here describes a bird-dispersed woody shrub. However, the structure is easily modified for different life histories or dispersal methods. For example, a biennial plant could be modeled by setting the age at maturity to 2 and adult survival to 0. To model a wind-dispersed species, short distance dispersal neighborhoods could be increased in size and modified by wind patterns if data are available (Nathan et al., 2011). Importantly, additional variables such as climate, topography, or even the distribution of competitor species can be included rather than solely land cover, such that parameters are calculated in each cell based on regressions (Merow et al., 2017; Carlo et al., 2018; Fern et al., 2019). In the absence of available data to inform these regressions, sensitivity analyses could identify the impact of data-based uncertainty. Further, simulations could incorporate parameter uncertainty by selecting values from a specified distribution in each iteration, essentially adopting a Bayesian approach to produce a more robust assessment of the likely distribution (Morris and Doak, 2003; Clark, 2005; Szewczyk and McCain, 2019). Rather than assuming simplistic dynamics among habitat types, density-dependent habitat selection could be included, depending on the species' life history (Menezes and Kotler, 2019). This model employs average population values, assuming that individual variation is negligible to the metrics of interest. A similar grid-based structure could be combined with regression models of individual-based traits and the environmental conditions within each cell to account for individual differences as in integral projection models (Merow et al., 2014, 2017). However, a key benefit of a population-level model is the lower data requirement compared to an individual-level model, where tagged individuals must be monitored and measured across years.

Dynamic SDMs with mechanistic dispersal and biologically realistic processes hold great potential for management planning. While we focused on an established invasive, a newly introduced species could be projected into the future to identify unoccupied areas highly vulnerable to invasion, and the local and regional success of management options weighed. Alternatively, policies for increasing the abundance or distribution of rare species could be evaluated. For example, populations of grassland birds such as the Bobolink and Eastern Meadowlark have seen dramatic declines in the northeastern United States resulting from changes in land use (Bollinger et al., 1990; Foster, 2002; Foster et al., 2002). State agencies and non-governmental organizations are currently attempting to increase their abundance by preserving or creating suitable grassland habitat (Foster and Motzkin, 2003; Hill et al., 2014). With the modelling framework presented here, managers could compare the effects of improving habitat in different locations to maximize the impact of their efforts. Further, conservation organizations advocate for several strategies to align agricultural practices with nesting habits, including delaying hay harvests to lower juvenile mortality and reducing grazing to minimize nest destruction (Bollinger et al., 1990; Hill et al., 2014). The relative effectiveness of these options could be compared, incorporating regional heterogeneity in their effects. Thus, this model structure provides the ability to identify the most sensitive life stages and processes, as well as the most critical localities.

The interconnected regional context in our management simulations includes cells beyond the purview of the focal manager, and we assumed that glossy buckthorn was not controlled in any non-focal cells. Future work could predict management within each cell of the landscape. For example, integration with decision models could allow each simulated land owner to decide how to manage the species (Epanchin-Niell and Wilen, 2014). Alternatively, coordinated regional strategies could be evaluated, representing cooperation among land owners or a large agency such as the U.S. Forest Service centrally managing the majority of the study region (Sims et al., 2010). Further, we evaluated just four pre-determined management strategies. Management actions could instead be optimized across a broad range of possibilities using machine learning techniques (Adelman and Mersereau, 2008; Boutilier and Lu, 2016). Lastly, we defined our set of possible management actions by those that have been evaluated for glossy buckthorn (Fig. 1). However, the demographic structure of the model provides the valuable opportunity to assess any actions relevant to the species of interest, such as the introduction of a biocontrol agent that reduces seed production or the strategic application of fire (Buckley et al., 2004; Davis et al., 2006).

Grid-based population models hold great potential for applications in conservation and management. By incorporating both local and regional biological processes, simulated management actions can target particular life stages within a limited spatial extent, while the resultant effects occur within the context of the full landscape. These models can help to clarify not only which management actions are likely to be most effective, but also the locations that are most likely to lead to success. The flexible nature of process-based SDMs allows for their application across a wide variety of taxa and management goals. Process-based, regional models are an opportunity to provide managers with data-driven, science-based, actionable information to maximize the success of conservation decisions.

Authors' contribution

Tim M. Szewczyk: Conceptualization; data curation; formal analysis; investigation; methodology; software; visualization; writing – original draft; writing – review & editing.

Tom Lee: Conceptualization; funding acquisition; data curation; investigation; methodology; writing – review & editing.

Mark J. Ducey: Conceptualization; funding acquisition; investigation; methodology; writing – review & editing.

Matt Aiello-Lammens: Data curation; investigation; methodology; writing – review & editing.

Hayley Bibaud: Data curation; investigation; writing – review & editing.

Jenica M. Allen: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; visualization; writing – review & editing.

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Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolmodel.2019.108827.

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