

Finding the best management policy to eradicate invasive species from spatial ecological networks with simultaneous actions

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Summary

1. Spatial management of invasive species is more likely to be successful when multiple locations are treated simultaneously. However, selecting the best locations to act is difficult due to the many options available at any time.

2. We design a near-optimal policy for applying multiple actions simultaneously for faster invasive species control within a network. Our method uses a recent optimisation tool, the graph-based Markov decision process (GMDP). Since the policy can be difficult to interpret, we extracted a simpler policy using classification trees. We applied our approach to the eradication of invasive mosquitofish *Gambusia holbrooki* from the habitat of the red-finned blue-eye *Scaturiginichthys vermeilipinnis*, a critically endangered fish with a global population that is restricted to seven artesian springs in Queensland, Australia.

3. The policy returned by the GMDP was to manage springs occupied by mosquitofish and their connected neighbours, unless the neighbours were occupied by red-finned blue-eyes.

4. Simultaneous management resulted in rapid declines in simulated mosquitofish occupancy even if eradication effectiveness was low; however, the cost of simultaneous eradication was high and sustained eradication effort was necessary to maintain low mosquitofish occupancy.

5. *Synthesis and applications.* Our paper finds a near-optimal, multi-action control policy to remove an invasive species from a multi-species spatial network. We introduce the graph-based Markov decision process and apply it to a real case study – eradication of invasive mosquitofish from the habitat of the red-finned blue-eye. We find that the graph-based Markov decision process can generate policies for networks with extremely large state spaces; however, it works best when nodes have fewer than five neighbours. We conclude that simultaneous eradications are effective for rapid control of invasive species; however, managers should consider the cost and time required for an effective eradication program.

Key-words: classification trees, computational sustainability, conservation, *Gambusia*, invasive species, Markov decision processes, network, optimal control, optimisation, *Scaturiginichthys vermeilipinnis*

Introduction

Species that occupy spatially distinct habitats form ecological networks consisting of habitat nodes connected by migration (Hanski 1994). Managers of species in ecological networks operate in uncertain environments, yet must decide which management actions to take, and where and when to apply them. Making inefficient or ineffective decisions may result in extinction, so managers have a

strong incentive to apply management policies that make the best use of limited conservation resources (Bottrill *et al.* 2008).

In an ecological network, management actions can be taken simultaneously at many locations or nodes, requiring managers to decide which action to take at each node. A policy is a decision rule that prescribes where to apply actions at each timestep, as a function of the current state of the ecological network. The most efficient policy maximises the probability of achieving a targeted objective. In principle, this policy can be found using optimisation. However, because each node interacts with its neighbours,

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each combination of management actions affects the network differently (Chadès *et al.* 2011). As the number of network nodes increases, the number of possible combinations of actions increases exponentially (Nicol & Chadès 2011). The huge number of possible combinations of actions often means that computing an optimal policy that considers all combinations is intractable in practice.

Previous attempts to optimally schedule management of spatial networks circumvent the issue of simultaneous management by either restricting the number of nodes that can be managed in each timestep to one or two (Possingham 1996; Westphal *et al.* 2003; Costello & Polasky 2004; Nicol *et al.* 2015a); or working on small networks (Lubow 1996; Shea & Possingham 2000; Nicol & Chadès 2011). Acting in many nodes simultaneously may provide greater ecological benefits than acting at only one node, but existing optimisation models cannot determine whether this is true. Here, we use a technique developed for problems with many interacting managed units, the graph-based Markov decision process (GMDP) (Sababadi, Peyrard & Forsell 2012). This approach uses the interaction structure of the network to find a near-optimal policy for choosing the set of multiple nodes to manage at each timestep.

Global policies express the recommended management action for each state of the system at each timestep. However, large networks contain many possible states, so policies may be hard to communicate to managers. Heuristics or 'rules of thumb' are commonly presented in the literature, derived either from an analytical approximation to the solution (Chadès *et al.* 2008) or from intuition then tested by simulation (Wilson *et al.* 2006; McBride *et al.* 2007; Nicol & Chadès 2011). While these heuristics often perform well, they do not provide any guarantee of how well they approximate the original policy and every problem requires a different approach, so it is not always apparent how to formulate a rule of thumb. Here, we show for the first time how classification trees can simplify a policy to a desired accuracy level and provide a structured way to simplify any complex policy.

Materials and methods

ECOLOGICAL CASE STUDY

Our approach is motivated by the need to manage a network of artesian springs containing two competing fish species, the critically endangered red-finned blue-eye *Scaturiginichthys vermeilipinnis* (RFBE) and the invasive mosquitofish *Gambusia holbrooki*. The RFBE is a native fish whose global distribution is restricted to just seven springs within the network of springs at Edgbaston reserve in central western Queensland, Australia. Mosquitofish reduce RFBE persistence (Nicol *et al.* 2015b) and are implicated in local extinctions of RFBE after invasion of a spring by mosquitofish (Fairfax *et al.* 2007). Both species can colonise new springs through episodic flood events, although the RFBE has only been observed to do this on one occasion.

The management objective at Edgbaston is to increase populations of RFBE, which includes preventing the spread of mosquitofish and eradication wherever possible (Fensham, Ponder & Fairfax 2010). The objective requires either eradicating mosquitofish from springs or moving RFBE to new springs. While relocation of RFBE remains a promising management policy to reduce the risk of population extinction (Fairfax *et al.* 2007), there are few candidate springs that are unlikely to be recolonised by mosquitofish, and all of these have already been used in relocation trials (Kerecsy & Fensham 2013; Nicol *et al.* 2015b). In this paper, we find a policy for mosquitofish eradication, with the assumption that eradicating mosquitofish will create suitable habitat for RFBE relocations. We use optimisation to inform managers of when and where to eradicate mosquitofish to maximise the number of springs occupied by RFBE over time.

Fifty RFBE and mosquitofish occupancy surveys were completed over 37 of the springs at Edgbaston from November 1990–October 1997 (Fairfax *et al.* 2007) and March 2009–October 2013 (A. Kerecsy, pers. comm.). Surveys were converted to annual occupancy data for likelihood estimation. Springs where presence was recorded at any time during the year were assumed to be occupied in that year. During the annual surveys, four colonisation and five local extinctions (including two exterminations completed by managers) were recorded for mosquitofish; and 11 colonisation events (including 10 assisted recolonisations) and seven local extinction events were recorded for RFBE. Additional transitions occurred but were preceded by missing data, so the timing of the transition could not be determined.

MODEL FOR SPECIES DYNAMICS

We model the dynamics of the fish populations using a two-species occupancy-based metapopulation model (Richmond, Hines & Beissinger 2010). We assume that the mosquitofish dynamics are independent of the presence of RFBE, but that the dynamics of RFBE depend on the presence of mosquitofish.

We model the system as a network of Θ springs. Each node represents a spring. Edges represent colonisation pathways between springs. The set of all springs connected to spring i is the neighbourhood of i , denoted $N(i)$, $N(i) \subset \{1, \dots, \Theta\}$.

Throughout the manuscript, we use the superscript M to represent mosquitofish and R to represent RFBE. The state of the mosquitofish in spring i is denoted $s_i^M \in \{0, 1\}$ and the state of the RFBE is $s_i^R \in \{0, 1\}$. Using this notation, the state of the network is given by $s = \{s_1, \dots, s_\Theta\}$, where $s_i = (s_i^M, s_i^R)$. The timestep of the model and all simulations in the manuscript is annual.

In our model, managers can choose to eradicate mosquitofish from a spring i (denoted $a_i = 1$; with success probability erad_i^M) at a cost or do nothing (denoted $a_i = 0$). The set of actions taken at all springs in a timestep is given by $a = \{a_1, \dots, a_\Theta\}$. We assume that the effects of the eradication action last for a full timestep. If managers do nothing, we assume that the population of spring i goes extinct with probability d_i . The probability of colonisation of spring i from spring j is denoted ρ_{ji} . Because mosquitofish can colonise springs from outside the system during flooding, we allow a small probability (0.075) that spring i is colonised spontaneously, denoted source_recol_i^M . RFBE cannot recolonise from outside the system so $\text{source_recol}_i^R = 0$ in the RFBE model. Colonisation occurs during floods; however, as we do not know which springs are connected during a flood nor the flood frequency, we assume that floods occur every year and

connect all springs when they occur. This assumption will result in precautionary management policies as the probability of flooding will be overestimated by the model.

The transition probabilities for the mosquitofish M at node i , given management action $a_i \in \{0, 1\}$, are defined as $\Pr(s_i^{M'} | s_i^{M'^{-1}}, s_{N(i)}^{M'^{-1}}, a_i^{t-1})$, where $s_{N(i)}^{M'^{-1}}$ is a Θ -vector that denotes the presence of mosquitofish (0/1) in the neighbourhood of node i .

Transition probabilities without management action

In the absence of management action ($a_i = 0$), the transition dynamics for mosquitofish are:

$$\Pr(0|0, s_{N(i)}^{M'^{-1}}, 0) = \prod_{j \in N(i), s_j^{M'^{-1}}=1} (1 - \rho_{ji}^M) (1 - \text{source_recol}_i^M) \quad \text{eqn 1}$$

$$\Pr(0|1, s_{N(i)}^{M'^{-1}}, 0) = d_i^M \quad \text{eqn 2}$$

The transition probabilities for the RFBE (R) are defined so that the state depends on the presence of mosquitofish: $\Pr(s_i^{R'} | s_i^{R'^{-1}}, s_{N(i)}^{R'^{-1}}, a_i^{t-1})$. The form of the equations for the RFBE transition dynamics is the same as eqns (1) and (2); however, the parameter values are different. The colonisation probability ρ_{ji}^M in eqns (1) and (2) is replaced with $\rho_{ji}^{R|M}$ (the probability of colonisation of node i from node j given the presence ($M = 1$) or absence ($M = 0$) of the mosquitofish in node i). The extinction probability is replaced with $d_i^{R|M}$ (the baseline extinction probability for node i , given the occupancy state of the mosquitofish).

Transition probabilities when management action is applied

If eradication is applied ($a_i = 1$), the transition probabilities for mosquitofish are:

$$\Pr(0|0, s_{N(i)}^{M'^{-1}}, 1) = (1 - \text{erad}_i^M) \Pr(0|0, s_{N(i)}^{M'^{-1}}, 0) + \text{erad}_i^M \quad \text{eqn 3}$$

$$\Pr(0|1, s_{N(i)}^{M'^{-1}}, 1) = \text{erad}_i^M + (1 - \text{erad}_i^M) \Pr(0|1, s_{N(i)}^{M'^{-1}}, 0) \quad \text{eqn 4}$$

For RFBE, the structure of the transition probability equations is similar to eqns (3) and (4); however, eradication actions eliminate RFBE with probability erad_i^R (note that this action would never be applied to a spring containing RFBE in practice).

A full description of all model transition probability equations is contained in Data S1, Supporting Information.

PARAMETERISATION

Currently, the most successful eradication policy has been to remove mosquitofish from springs using the piscicide Rotenone. The efficacy of eradication with Rotenone varies, but with repeated application it is likely to achieve eradication (Kerezy & Fensham 2013). We used a probability of $\text{erad}_i^M = \text{erad}_i^R = 0.9$ for both species, based on the assumption that Rotenone would be applied as frequently as required to achieve a high likelihood of eradication (we vary this assumption in the Results section).

Applying the above assumptions, the model has six unknown parameters (Table 1). The unknown α and β values are fit from data using maximum likelihood techniques. We assume that

colonisation probability decreases with increasing distance between springs and that extinction probability is inversely related to spring area (Hanski 1994).

The respective log-likelihood functions for the mosquitofish and RFBE models are (Data S1):

$$\log L^M = \sum_{i=1}^{\Theta} \sum_{2 \leq t \leq 14} \ln \left(\Pr(s_i^{M'} | s_i^{M'^{-1}}, s_{N(i)}^{M'^{-1}}, a_i^{M'^{-1}}, \alpha^M, \beta^M) \right)$$

$$\log L^R = \sum_{i=1}^{\Theta} \sum_{2 \leq t \leq 14} \ln \left(\Pr(s_i^{R'} | s_i^{R'^{-1}}, s_{N(i)}^{R'^{-1}}, a_i^{R'^{-1}}, \alpha^{R|M=0}, \beta^{R|M=0}, \alpha^{R|M=1}, \beta^{R|M=1}) \right)$$

During parameterisation, we assume that all springs can be connected, so $N(i) = \{1, \dots, \Theta\}$, $\forall i \in \{1, \dots, \Theta\}$. After parameterisation, neighbourhoods are defined using a colonisation threshold. Two springs are neighbours (i.e. connected by a link) if the probability of colonisation by either fish between the springs is greater than 0.05. To reduce the number of nodes, we aggregated springs that were connected by mosquitofish colonisation probabilities greater than 0.33; after aggregation, the model contained 32 springs.

After parameter estimation, we found that the probability that RFBE and mosquitofish cohabit the same spring was very low (see $d_i^{R|M=1}$ in Table 1; note that $\text{area}_i < 1 \forall i$). Consequently, we reduced the number of model states by assuming that the probability of cohabitation was zero.

NETWORK SENSITIVITY TO COLONISATION PARAMETER

A key model uncertainty is the mosquitofish colonisation probability. In our model, the colonisation probability is estimated from survey data, and therefore may be valid only for the environmental conditions present during that survey. However, the environment at Edgbaston is variable. Changes in the frequency of flooding may alter the frequency that the springs are connected and the probability of mosquitofish colonisation (recall that two springs are connected if the colonisation probability is > 0.05). To model the effect of a change in mosquitofish colonisation, we varied the colonisation parameter α^M by $\pm 10\%$. We denote the three scenarios as wet ($-10\% \alpha^M$; more frequent floods, wetter climate, more connected network), current conditions ($+0\% \alpha^M$) and dry ($+10\% \alpha^M$; less frequent floods, drier climate, less connected network).

OPTIMISATION: THE GRAPH-BASED MARKOV DECISION PROCESS

The objective of this study is to determine the optimal timing and location of mosquitofish eradication actions to maximise a reward function that values springs based on RFBE and mosquitofish occupancy, less management costs. We model the problem as a Markov decision process (MDP). MDPs are used to model discrete-time stochastic processes where the system is partially controllable (Puterman 1994). The solution to a MDP is an optimal policy π that links every system state with the management action that offers the highest probability of achieving the objective over an infinite time horizon (Puterman 1994). In practice, the policy is obtained by maximising a value function defined as the expected sum of rewards over time, where rewards $R(s, a)$ are the immediate benefits of being in a state and taking actions at each node – they specify the quality of a state relative to the objective.

Table 1. List of the parameters of the species dynamics model. Figures in square brackets following the maximum likelihood parameter values list empirical 95% confidence intervals for each parameter estimate. area_i represents the area of node i (ha); distance_{ij} represents the Euclidean distance between patches i and j (km)

Parameter	Function	Description	Maximum likelihood parameter value
d_i^M	$\min\left(\frac{\beta^M}{\text{area}_i}, 1\right)$	Mosquitofish local extinction probability	$\beta^M = 9.3 \times 10^{-4}$ [8.4×10^{-3} , 10.5×10^{-3}]
ρ_{ji}^M	$e^{-\alpha^M \times \text{distance}_{ij}}$	Probability mosquitofish colonise node i from node j	$\alpha^M = 10.68$ [10.14, 10.81]
$d_i^{R M=0}$	$\min\left(\frac{\beta^{R M=0}}{\text{area}_i}, 1\right)$	RFBE local extinction probability given mosquitofish not present	$\beta^{R M=0} = 6.3 \times 10^{-3}$ [6.1×10^{-3} , 8.8×10^{-3}]
$d_i^{R M=1}$	$\min\left(\frac{\beta^{R M=1}}{\text{area}_i}, 1\right)$	RFBE local extinction probability given mosquitofish present (assumed to be 1)	$\beta^{R M=1} = 0.20$ [0.14, 0.20]
$\rho_{ji}^{R M=0}$	$e^{-\alpha^{R M=0} \times \text{distance}_{ij}}$	Probability RFBE colonise node i from node j given mosquitofish not present in i	$\alpha^{R M=0} = 30.86$ [23.12, 38.04]
$\rho_{ji}^{R M=1}$	$e^{-\alpha^{R M=1} \times \text{distance}_{ij}}$	Probability RFBE colonise node i from node j given mosquitofish present in i (assumed to be 0)	$\alpha^{R M=1} = 354.08$ [91.36, 366.70]

Although traditional solution methods for MDPs have wide application in decision theory and pest eradication, their application to spatial problems is limited by the size of the problem (Taylor & Hastings 2004). Here, this ‘curse of dimensionality’ is problematic because the state space is large (3^Θ states) and eradication actions can occur at any node (2^Θ possible actions), making the number of combinations that must be considered during optimisation excessively large. While factored representations can overcome large state space constraints (Degris & Sigaud 2010), few techniques exist to deal with large action spaces. We apply a method developed for spatial problems, the graph-based Markov decision process (GMDP) (Sabbadin, Peyrard & Forsell 2012). The GMDP requires that each node has a local neighbourhood of connected nodes with which it communicates. Defining these neighbourhoods allows decomposition of the computation of transition probabilities and rewards into local functions, which can then be solved using a mean-field approximation of the policy iteration algorithm (MF-API) (Peyrard & Sabbadin 2006; Sabbadin, Peyrard & Forsell 2012).

In the mean-field approximation, we propose a method to avoid the curse of dimensionality. First, instead of computing the value function via the iterative Bellman equation (Puterman 1994), we express the value function as an *occupation measure* (Altman 1999). Roughly speaking, the occupation measure $Pr_{S,\pi}(y)$ measures the proportion of time spent in state y (discounting future occupations by a factor γ), given initial state x and policy π (Altman 1999; Sabbadin, Peyrard & Forsell 2012):

$$Pr_{S,\pi}(y) = (1 - \gamma) \sum_{t=0}^{\infty} \gamma^t Pr_{\pi}(S^t = y | S^0 = x), \forall y \in S$$

where $Pr_{\pi}(S^t = y | S^0 = x)$ is obtained from the transition matrix as:

$$Pr_{\pi}(S^t = s^t | S^0 = s^0) = \sum_{s^1, s^2, \dots, s^{t-1}} \prod_{t'=0}^{t-1} Pr(s^{t'+1} | s^{t'}, \pi(s^{t'}))$$

The value function can be computed from the occupation measure using:

$$V_{\pi}(x) = \frac{1}{1 - \gamma} \sum_{y \in S} Pr_{S,\pi}(y) R(y, \pi(y))$$

Using this expression to evaluate the value function avoids having to solve a fixed point equation. However, computing the occupation measure $Pr_{S,\pi}(y)$ exactly is usually intractable, as it may require too much storage space (the space of y is huge, due to the curse of dimensionality).

Sabbadin, Peyrard & Forsell (2012) use the GMDP structure to propose a ‘mean-field’ approximation of $Pr_{S,\pi}(y)$ and to approximate $V_{\pi}(x)$.

For a local policy $\pi = \{\pi_1, \dots, \pi_n\}$, the value can be decomposed as:

$$V_{\pi}^i(x) = \sum_{t=1}^n \sum_{t=0}^{\infty} \gamma^t \sum_{y \in S} Pr_{\pi}(S^t = y | S^0 = x) R_i(y_{N(i)}, \pi(y_{N(i)}))$$

We look for an approximation to the conditional probability $Pr_{\pi}(S^t = y | S^0 = x)$ that has simple structure and will allow us to approximate $V_{\pi}^i(x)$ by a function that depends only on $x_{N(i)}$. That is, we seek an approximation that depends only on the initial occupancy state of the neighbourhood rather than the full transition history of the process.

To approximate $V_{\pi}^i(x)$, we seek a distribution of independent variables that is as close to $Pr(y|x)$ as possible (‘closeness’ is measured using the Kullback–Leibler divergence $KL(Q|P) = E_Q[\log(\frac{Q}{P})]$); the solution is referred to as the mean-field approximation and has the effect of replacing the spatio-temporal influence of the neighbourhood with its mean value (Sabbadin, Peyrard & Forsell 2012). Here, the ‘mean value’ means replacing the transition probability with the expectation of the transition probabilities for all possible configurations of the neighbourhood. Making this approximation removes the dependence of the occupation measure $Pr_{S,\pi}(y)$ on the history of the process, simplifying the computation of the value function $V_{\pi}^i(x)$. For further explanation of the mean-field approximation and a full derivation of the approximation applied to GMDP, refer to Sabbadin, Peyrard & Forsell (2012).

Graph-based Markov decision processes have six components – states, actions, transition probabilities, a discount factor, a neighbourhood function and a reward function. The state of the network is $s = \{s_1, \dots, s_{\Theta}\} \in S_1 \times \dots \times S_{\Theta}$, where $s_i = (s_i^M, s_i^R)$. Because RFBE and mosquitofish cannot occur in the same spring, we impose $(s_i^M, s_i^R) \neq (1, 1)$, so that there are three possible states per spring. There are two possible actions for each spring i , so that an action is $a = \{a_1, \dots, a_{\Theta}\}$, where $a_i \in \{0, 1\} = \{\text{do nothing, eradicate}\}$ (note

that the GMDP framework is not limited to binary actions). Transition probabilities are defined by eqns (1–4). The neighbourhood of spring i , $N(i)$, is defined as all springs that have a probability of colonisation by either fish that is greater than 0.05.

The reward for spring i is defined by $R_i^t(s_i^t, a_i) = \delta_R s_i^{R^t} - \delta_M s_i^{M^t} - c_i(a_i^t)$ where $c_i(a_i^t)$ is the cost of action a in spring i at time t ; δ_R is the relative value of having RFBE present in a spring and δ_M is the relative cost of having mosquitofish present in a spring. For this model, we set $\delta_R = \delta_M = 10$, so that the value of a spring occupied with RFBE is 10 units and the value of a spring occupied with mosquitofish is -10 units (we also tried models where the value of a spring occupied with RFBE was 50 or 100 units; however, increasing the relative value of RFBE had no impact on the resulting policy, probably because RFBE colonisation probability is very low). We set the cost of eradication (1 unit) to be lower than the value of having fish species present. Indeed, the largest management cost is getting a manager to Edgbaston rather than the expense of eradication (A. Kerecsy, pers. comm.). A biologist regularly monitors fish populations at Edgbaston, so management could be conducted as part of this visit if supported by decision-makers. Doing nothing had no cost.

In this problem, finding the optimal policy for all nodes is intractable for the MDP solution (3^{32} states). Although the GMDP policy solves problems that are independent of the size of the state space, networks containing nodes with many neighbours are intractable for the GMDP because the computation of the mean-field approximation becomes difficult when there are many neighbours. The number of connected neighbours in this problem forced us to break the network into smaller subgraphs (i.e. subsets of vertices and edges in which each vertex is connected by an edge to another vertex in the subgraph, but vertices are not connected to any vertices outside the subgraph) before obtaining the GMDP simultaneous action policy. The network was split into subgraphs by applying the connectivity threshold (Parameterisation section).

We solved the GMDP using the GMDP Toolbox (<http://www.inra.fr/mia/T/GMDPtoolbox>) running on MATLAB R2012a. The solution to a GMDP is a set of local policies, one per spring. The local policy prescribes 'do nothing' or 'eradicate' depending on the occupancy of both fish species in the spring of interest and its neighbours.

A HEURISTIC FOR APPLYING ONE ACTION PER TIMESTEP

Once the graph is disconnected into subgraphs, we can solve the simultaneous action problem, but we still require a solution to the single action problem to be able to compare the expected rewards

from acting simultaneously to acting at a single location. To quantify these rewards, we compared the GMDP solution to a heuristic allowing only one action per timestep for the entire network: at each timestep, the heuristic first selects a subgraph and then utilises the optimal MDP policy on this subgraph to decide which spring to manage. In the MDPs for each subgraph, we assumed perfect eradication effectiveness, so that the MDP policy is an approximate best scenario for the number of springs occupied by mosquitofish in each subgraph. In each timestep, the subgraph with the fewest springs occupied by mosquitofish (>0) was selected first. This heuristic assumes that eradicating mosquitofish from subgraphs with few occupied springs is easier than eradicating mosquitofish from subgraphs with many occupied springs.

Results

THE GMDP POLICY

Acting at multiple nodes simultaneously has higher expected rewards than taking a single action per timestep and results in rapid declines in mosquitofish occupancy that cannot be achieved with a single eradication per timestep (Fig. 1). If eradication effectiveness probability is high (≥ 0.5), then mosquitofish occupancy can be halved in a single year of action. In contrast, acting in one node at a time is unlikely to suppress mosquitofish – after 25 years, mosquitofish remain present in 19 springs on average, despite perfect eradication effectiveness. Although taking simultaneous actions can result in fewer springs occupied by mosquitofish, taking multiple actions per timestep requires many more eradication actions over time than acting in a single node (Fig. 2).

If no management action is taken for 25 years, RFBE are likely to go extinct in all but one spring (1.4 ± 1.1 springs occupied; note that \pm error statistics represent 1 standard deviation throughout the manuscript) and mosquitofish will occupy most of the springs (28.5 ± 3.7 springs occupied, Fig. 3). Management effectiveness is a key parameter in determining the impact of the eradication program. Under current conditions, the number of springs occupied by mosquitofish after 25 years may vary from 13.6 ± 6.6 ($\text{erad}_i^M = 0.2$) to 3.4 ± 1.7 ($\text{erad}_i^M = 0.9$). A relatively ineffective program (e.g. $\text{erad}_i^M = 0.2$) could more than halve the expected number of occupied springs, but

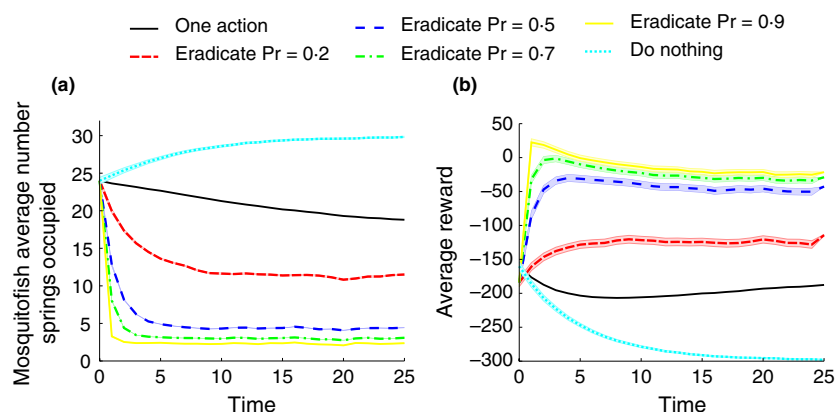


Fig. 1. Comparison of (a) expected number of springs occupied by mosquitofish and (b) expected rewards after applying simultaneous actions or a single action per timestep. Results are generated from the average of 1000 simulations using the current number of occupied springs as the initial state. [Colour figure can be viewed at wileyonlinelibrary.com]

once the program becomes very effective, it may be difficult to get further gains (e.g. increasing pois_i^M from 0.7 to 0.9 changes the number of occupied springs after 25 years from 4.3 ± 2.5 to 3.4 ± 1.7). While it seems promising that even a relatively ineffective program might have substantial gains, the average cost of an ineffective program is substantially more than that of an effective program (Fig. 3) because repeated applications are often required (compare policies in Figs S1 and S2 in Data S2). Regardless of the effectiveness of mosquitofish eradication, RFBE numbers are unlikely to increase without additional management. Doing nothing results in 1.4 ± 1.1 springs occupied by RFBE, but a highly effective mosquitofish eradication program ($\text{erad}_i^M = 0.9$) only results in 1.8 ± 1.5 springs occupied by RFBE after 25 years.

Although wetter conditions increase the number of connected nodes in the network (Fig. 4), changes to the colonisation parameter of mosquitofish are unlikely to affect management performance (wet, existing and dry scenarios in Fig. 3). The value of learning the correct colonisation parameter can be computed from the difference in the value of the expected rewards after managing using the correct parameter value and the number occupied using an incorrect parameter value (Data S3). In this problem, there is no value in learning the correct colonisation probability ($\pm 10\%$; see Table S2 in Data S3).

DERIVING A SIMPLIFIED MANAGEMENT POLICY USING CLASSIFICATION TREES

Optimal strategies are complex to represent and difficult to communicate. Simple heuristics or rules of thumb are

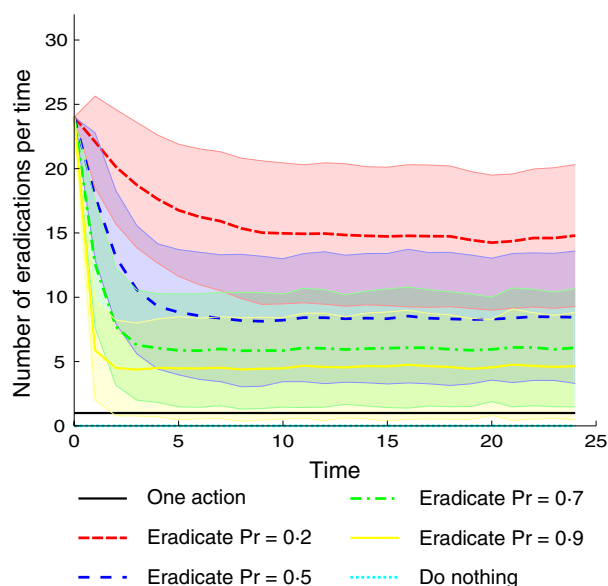


Fig. 2. Expected number of eradication actions per timestep using simultaneous actions and one action per timestep. Results are shown for 1000 simulations of 25 years using the current number of springs containing mosquitofish as the initial state; error intervals represent 1 standard deviation. [Colour figure can be viewed at wileyonlinelibrary.com]

more easily applied, so a challenge is to obtain a compact rule set that represents the solution with a reasonable degree of accuracy (Possingham *et al.* 2001). In previous studies, rules of thumb are often created by observing the solution and then tested by simulation. Here, we use classification trees (Therneau & Atkinson 2015) to express the GMDP policy in a binary tree. As well as providing an automated approach to obtain a rule of thumb, the classification tree can be used to measure the loss of performance that results from simplifying a policy by simulating the classification rule against the original policy.

We generated a classification tree using the *rpart* package in *R* (Fig. 5a). *Rpart* works in two stages (Therneau & Atkinson 2015). First, a tree is constructed by recursively splitting based on the predictor variables (i.e. information about the state of a node or its neighbourhood) which best separates the data until subgroups (i.e. collections of node and neighbourhood states for which the same action is prescribed by the classification tree) reach a minimum size or no further improvement can be made. Splits are based on minimising the misclassification rate (the proportion of states for which the action prescribed by the classifier is different from the one prescribed by the GMDP policy). Second, because the complete tree is complex and has too many terminal nodes, cross-validation is used to prune the tree until a user-specified misclassification rate is achieved, i.e. splits in the tree are removed if they make little difference to the overall error. In our application, the classification tree (Fig. 5a) has a negligible misclassification rate of 0% and performs similarly to the GMDP policy in simulations (Fig. 5b).

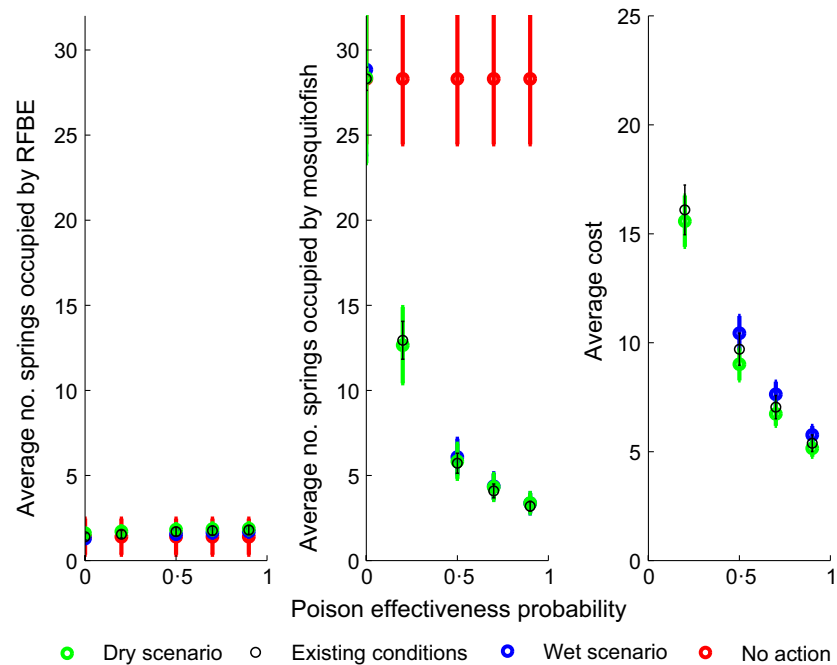
In the *rpart*-derived rule of thumb (Fig. 5a), the key decision factor is whether RFBE are present in the target spring. If they are present, then the spring should not be poisoned. If they are absent, then whether to act depends on whether the mosquitofish are present in the neighbourhood and the target patch. Poisoning should occur whenever mosquitofish occur in the neighbourhood of the target patch. This is consistent with examination of simulations of the species dynamic model following the GMDP policy, which suggests that a good policy is to eradicate mosquitofish in all springs where it occurs, as well as eradicating all neighbouring springs (unless RFBE are present in the neighbouring springs; Data S2).

Discussion

IS ACTING SIMULTANEOUSLY AN EFFECTIVE WAY TO ERADICATE MOSQUITOFISH?

In this paper, we demonstrated how acting simultaneously may result in faster decline of an invasive species than if single actions were taken in each timestep (Fig. 1). Our results suggest that local eradication is a promising approach if it can be carried out on a broad scale across multiple nodes simultaneously. We showed that acting in many nodes is superior to acting in a single node (Fig. 2),

Fig. 3. Change in performance with eradication effectiveness for three colonisation parameter scenarios. The best performance occurs in the dry scenario when mosquitofish has the lowest probability of colonisation. The GMDP policy for the wet scenario (most connected) with an eradication effectiveness probability of 0.2 could not be computed due to excessive computational time. Error intervals depict 1 standard deviation. [Colour figure can be viewed at wileyonlinelibrary.com]



and that under these circumstances even a low (i.e. 0.2) probability of success may have a substantial impact on mosquitofish occupancy.

Acting in many nodes at once requires many more eradication actions in total than acting at a single node (Fig. 2) (Menz, Coote & Auld 1980; Wadsworth *et al.* 2000). Although the cost of simultaneous eradications at Edgbaston may be low, widespread use of controversial actions such as piscicides for eradication may be undesirable and a compromise policy may be useful. We tested a one-off treatment where all eradications were applied in the first timestep and no action was taken for the remainder of the simulated management period; however, we found that this treatment was little better than taking no action after 25 years (Data S4). The rapid recolonisation of the network by mosquitofish that occurs after the initial treatment is probably due to the source recolonisation probability in the model that allowed springs to be recolonised from outside the network. In networks that are not closed to immigration, sustained eradication efforts will be required to control invasives (Bomford & O'Brien 1995).

Another alternative to global simultaneous eradication could use the variation in colonisation between spring complexes. The network splits into subgraphs (Fig. 4) which are robust to small changes in mosquitofish colonisation probability ($\pm 10\%$). It may be possible to reduce the number of eradications required by concentrating eradication efforts on subgraphs of springs that have limited probabilities of recolonisation from other complexes. The effectiveness of this approach would depend on the probability of recolonisation from non-spring sources that were not included in the model, such as the bore drains present at Edgbaston.

IMPACT OF COLONISATION POTENTIAL ON MANAGEMENT

Our rule of thumb advocates eradication efforts in the target spring and its immediate neighbours in the network. This rule is likely to work well in systems where colonisation is limited (Kleczkowski *et al.* 2011); in this study, both species of fish had low colonisation potential to reach springs other than their geographic neighbours. In systems with greater invasive colonisation potential, a global control policy may need to be developed (Kleczkowski *et al.* 2011).

Investing effort to better understand mosquitofish colonisation probability is likely to be less productive than investing effort into controlling mosquitofish, as it does not affect management performance if the colonisation probability is incorrect (within $\pm 10\%$; Data S3). This may be due to the generally low colonisation probabilities for mosquitofish at Edgbaston – if colonisation probabilities were higher, a 10% change may make a greater qualitative difference to network connectivity than under current conditions (Fig. 4).

Red-finned blue-eye are extremely unlikely to colonise other springs without assistance. The eradication policy for mosquitofish is unlikely to recover RFBE populations without additional management actions (Fig. 3) such as the ongoing program of RFBE reintroductions (Kerezy & Fensham 2013). An outstanding question from our modelling is, given that mosquitofish have been eradicated from a set of springs, which spring should RFBE be relocated to? As well as the potential for recolonisation of the target relocation spring by mosquitofish, this would depend on biological characteristics of individual springs (Nicol *et al.* 2015b) that were not modelled here. Given that RFBE appear unlikely to colonise springs by

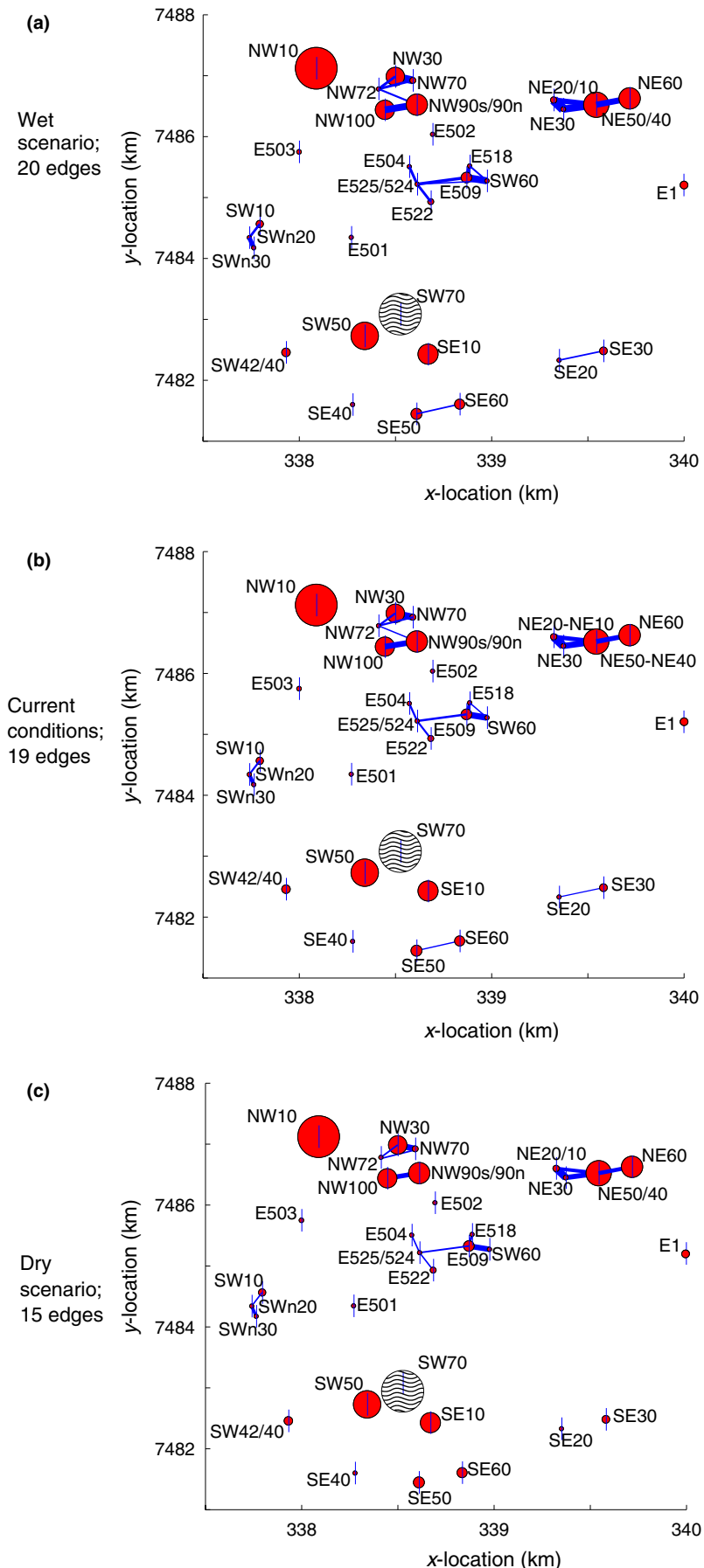


Fig. 4. Network connectivity under wet (a), current conditions (b) and dry (c) scenarios. The area of each spring relative to the second-largest spring (NW70) is indicated by the size of the circle at the spring location; minimum circle size is 10% of the area of NW70. The largest spring (SW70; wavy circle) is twice as large as NW10 – it is depicted smaller for ease of visualisation. Edges represent colonisation probabilities between pairs of springs; the total number of network edges in each scenario is included in the subfigure label. Thicker edges between springs represent connections with higher mosquitofish colonisation probabilities. [Colour figure can be viewed at wileyonlinelibrary.com]

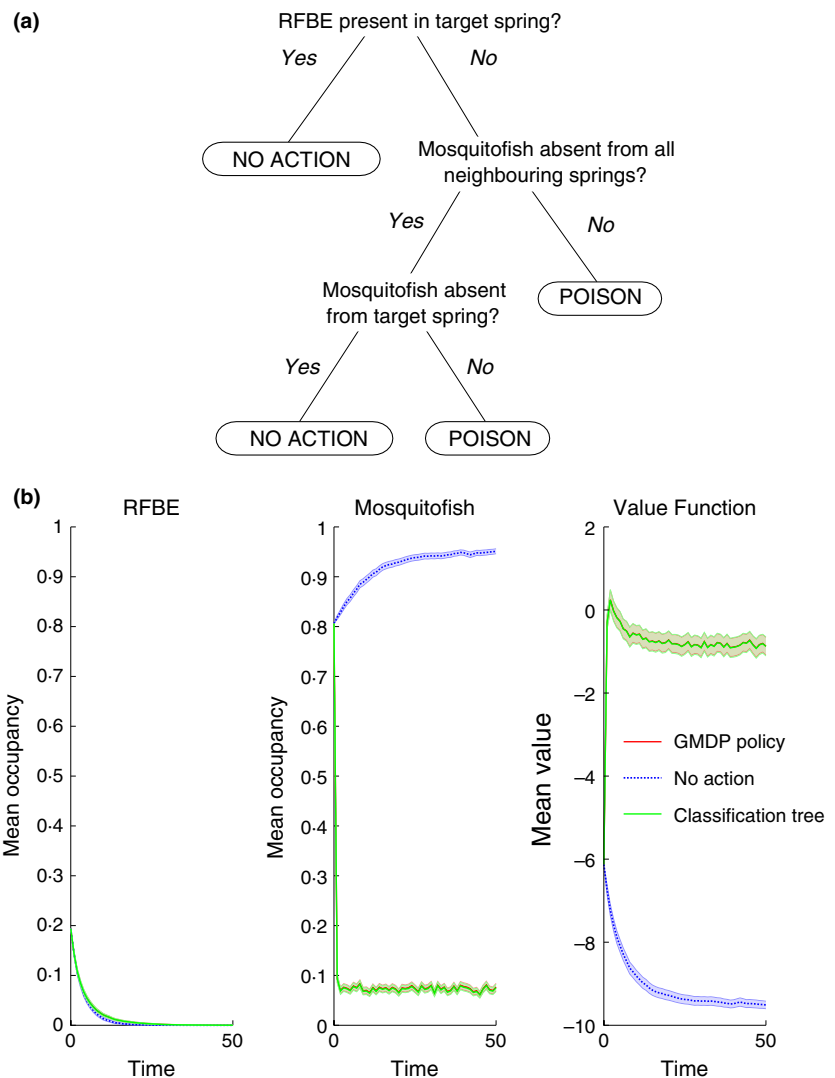


Fig. 5. A classification tree for selecting best management action (a) performs similarly to the GMDP policy (b; note that the dash-dot red 'GMDP policy' line follows the solid green 'Classification tree' line where it is not otherwise visible). In (b), the mean occupancy of each species and the mean value function are computed from 1000 simulations for a 50-year time horizon. Shaded regions depict one standard error. In both simulations, the probability of eradication success is 0.9. [Colour figure can be viewed at wileyonlinelibrary.com]

themselves, relocation efforts should be refined to be as successful as possible.

In the paper, we presumed that mosquitofish eradication will be achieved by poisoning, because this is the only proven eradication strategy to date (manual fishing to local extinction requires excessive time). However, the effectiveness of Rotenone remains unproven beyond a handful of trials and the effects on non-target organisms remain a subject of ongoing research (Kerezy & Fensham 2013). In this paper, we do not advocate a particular approach – our results depend on the eradication effectiveness, not the eradication mechanism (Fig. 1).

GMDP CONSIDERATIONS AND LIMITATIONS

While the GMDP framework allows consideration of large, spatially distributed combinations of actions, it has some limitations. Most importantly, the computational complexity of the GMDP grows exponentially with the number of neighbours associated with each network node, rather than the total number of network nodes. The

Edgbaston network is quite dense, and we had to apply a connectivity threshold (nodes were connected if the probability of colonisation between them was >0.05) that split the graph into multiple subgraphs with fewer neighbours, so that the GMDP could find a near-optimal policy. For this case study, splitting the network into subgraphs resulted in subgraphs that were small enough to be solved exactly, but this is specific to our case study network and is not a general result. Many networks in spatial management problems are well-connected but have low degree (e.g. grid lattice networks have four connected neighbours). To illustrate the power of the GMDP to generate management policies for large networks that have nodes of low degree (i.e. few neighbours), we constructed a modified version of the Edgbaston network with the full 32 nodes, but with a maximum of three neighbours per node. This modified network has a state space that is too large to be solved exactly (3^{32} states), but the GMDP found a solution to this problem in 1 h (Data S5). As a rough guide, graphs containing nodes with more than four neighbours should be simplified if possible, as the

GMDP computational time becomes impractical with more than four neighbours.

Although the GMDP approach requires specification of the costs of action at each site, it does not explicitly allow a total budget to constrain the policy (i.e. it cannot limit the number of actions per timestep according to a maximum budget because the global policy is comprised of unconstrained policies that are generated independently based on local costs and rewards within each neighbourhood). This can be an advantage because it allows decision-makers to determine the most effective policy and then consider their constraints, rather than finding a constrained policy that may be suboptimal. Knowing what resources are required to be effective may aid managers to negotiate budgets and may empower them to be more efficient over the long term. If budgetary constraints must be applied, the total cost of a GMDP policy can be computed by simulation. The reward function of the GMDP can be altered and a new GMDP policy can be calculated until an acceptable total cost is achieved.

There are three main approximations made by the GMDP compared to an optimal MDP solution. First, unlike the global policy returned by a typical MDP solver, the GMDP seeks local policies (one per node) prescribing whether or not to eradicate, depending on the state of the spring and its neighbours. Second, unlike in an optimal MDP solver, where the policy is optimal for all starting states, the best local policy found by the GMDP solver depends on an initial probability distribution over starting states. We assumed that this initial distribution was uniform (this assumption allows us to generate policies that are more generally relevant than policies for specific starting states, but note that the GMDP toolbox allows the user to input alternative initial distributions). Finally, the GMDP toolbox applies an approximate solution algorithm (MF-API) to find a policy given the initial belief (Sabbadin, Peyrard & Forsell 2012). The practical significance of these three assumptions is that although previous experiments with GMDP suggest that the error is limited (Peyrard & Sabbadin 2006; Sabbadin, Peyrard & Forsell 2012; Cheng *et al.* 2013), it does not have the performance guarantee of a solver that finds a globally optimal solution. We encourage testing the GMDP solution against other heuristics that are expected to perform well. In our case study, the GMDP consistently outperformed a common-sense heuristic (Table S1 in Data S3).

USING CLASSIFICATION TREES TO DERIVE SIMPLIFIED POLICIES

We demonstrated that using a classification tree to simplify a complex policy can give near-optimal performance with a known misclassification rate. This new approach to policy simplification is promising, as previous studies employing state-based methods have struggled to communicate usable policies in a rigorous way, resorting to heuristics that are based on observation.

The risk of using decision trees is that the rules are generated automatically, so they need to be checked by humans to make sure that the resulting classifier makes sense. One issue is that the probability of occurrence is not reflected in the misclassification rate: choosing the incorrect action may have a greater impact for highly probable states. This can be overcome by weighting each state according to the stationary distribution; however, in our case including the weights resulted in a tree that recommended poisoning all springs occupied by mosquitofish, regardless of the presence of RFBE (Data S6). This solution was accurate but practically undesirable, so we did not present this example here. This exercise highlighted a more challenging issue for classification trees: the consequence of the action is not expressed by the misclassification rate, so that in some cases taking the wrong action can have major impact on the objective. Modellers should take care to interpret the results of automated classifiers by combining simulations of the performance of the classification tree with the experience of managers, particularly as the classifiers become more complex.

Conclusion

Competing species in time and space require special consideration. Managing unwanted competitors may be more effective if simultaneous actions are taken than if management occurs at a single node per timestep over an ongoing period of time. We derived a management policy for local eradication of unwanted species in spatially structured populations, showing that the best plan is to act at the target node as well as its connected neighbours.

Authors' contributions

All authors conceived the ideas and designed methodology; S.N. analysed the data, wrote the models and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Occupancy data for RFBE and mosquitofish, as well as R and MATLAB scripts used in the analysis are included in online Data S7 and uploaded to Dryad Digital Repository <https://doi.org/10.5061/dryad.3r1v5> (Nicol *et al.* 2017). The GMDP toolbox is available from: <http://www7.inra.fr/mia/T/GMDPtoolbox/>.

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Supporting Information

Details of electronic Supporting Information are provided below.

Data S1. Species dynamics model description.

Data S2. Species dynamics simulations under the GMDP policy.

Data S3. Value of information analysis and performance against a heuristic.

Data S4. Effectiveness of a one-off treatment.

Data S5. GMDP effectiveness on large networks.

Data S6. Weighted classification trees.

Data S7. Occupancy data files and scripts used in the analysis (R and MATLAB).