

# Optimizing search strategies for invasive pests: learn before you leap

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## Summary

1. Strategic searching for invasive pests presents a formidable challenge for conservation managers. Limited funding can necessitate choosing between surveying many sites cursorily, or focussing intensively on fewer sites. While existing knowledge may help to target more likely sites, e.g. with species distribution models (maps), this knowledge is not flawless and improving it also requires management investment.

2. In a rare example of trading-off action against knowledge gain, we combine search coverage and accuracy, and its future improvement, within a single optimization framework. More specifically we examine under which circumstances managers should adopt one of two search-and-control strategies (cursorily or focussed), and when they should divert funding to improving knowledge, making better predictive maps that benefit future searches.

3. We use a family of Receiver Operating Characteristic curves to reflect the quality of maps that direct search efforts. We demonstrate our framework by linking these to a logistic model of invasive spread such as that for the red imported fire ant *Solenopsis invicta* in south-east Queensland, Australia.

4. Cursorily widespread searching is only optimal if the pest is already widespread or knowledge is poor, otherwise focussed searching exploiting the map is preferable. For longer management time-frames, eradication is more likely if funds are initially devoted to improving knowledge, even if this results in a short-term explosion of the pest population.

5. *Synthesis and applications.* By combining trade-offs between knowledge acquisition and utilization, managers can better focus – and justify – their spending to achieve optimal results in invasive control efforts. This framework can improve the efficiency of any ecological management that relies on predicting occurrence.

**Key-words:** adaptive management, containment, eradication, invasive species, optimal management, receiver operating characteristic (ROC) curve, species distribution models, state-dependent management, stochastic dynamic programming (SDP), value of information

## Introduction

Invasive species comprise one of the main threats to global biodiversity (Sala *et al.* 2000) and their annual economic impact is substantial (Pimentel *et al.* 2001). While considerable economic resources can be allocated to invasive species management, it is important to strategise spending in a coherent decision-making framework, to maintain cost-efficiency as well as increase the likelihood of programme success (Regan *et al.* 2006; Bogich & Shea 2008). Such a framework should ideally take account of all economic factors in the programme, includ-

ing investing in knowledge acquisition to improve future management. This notion of learning now, to make better decisions later, underpins adaptive management (Walters 1986) and theories of learning in animal behaviour (Stephens & Krebs 1986). In this paper we investigate how best to allocate a restricted budget among options for research and control of an invasive pest when we have some information about its distribution, as well as the ability to improve that information.

For any detection-and-control programme constrained by time, budget and human resources, trade-offs exist between the different search strategies and the acquisition of information to inform future searches. Therefore managers are confronted with the following questions: How many sites should we search, which ones, and at what intensity? Should we invest

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resources in refining our methods for choosing sites, to improve future search success? The first questions have been addressed to some extent in the literature. For example, controlling new satellite populations may be preferable to reducing the density of the core pest population (Moody & Mack 1988), although this may not be optimal when costs are taken into account (Whittle, Lenhart & Gross 2007). For pest metapopulations, it may be optimal to attempt eradication of medium-density sub-populations, while still balancing colonization from, and containment of, high-density patches (Bogich & Shea 2008). With enough money, however, prioritizing high-density patches can become optimal (Taylor & Hastings 2004). Within a patch, detection probability depends on both the search method and search intensity or coverage, which in turn depend on budget (Cacho, Hester & Spring 2007). The trade-off between cursory and focussed searching has not yet been examined in the context of (mis-) information about the distribution of the species.

Predicting a pest's distribution and spread often involves a species distribution model of its likely occurrence (e.g. Baret *et al.* 2006; Hauser & McCarthy 2009), allowing some degree of strategic searching within a region. The predictive accuracy of species distribution models is commonly assessed using Receiver Operating Characteristic (ROC) curves (Pearce & Ferrier 2000; Wintle, Elith & Potts 2005; Latimer *et al.* 2009), which graph the rates of occurrence of true vs. false positives. In species distribution models (henceforth, 'maps') this translates as rates of classifying occupied sites as being occupied, vs. rates of misclassifying unoccupied sites as occupied, implying when searches would be worthwhile or futile, respectively. As maps can be improved at some cost, namely redirecting funds from active control (Murray *et al.* 2009), optimal investment in research can be determined if we know the future benefit of having better predictive maps that will result from the short term reduction in on-ground effort. The trade-off of knowledge gain vs. immediate action is implicit in every area of applied ecology. Despite the practical benefits and broader implications of exploring such a trade-off, however, this has not yet been done in a theoretical or practical framework. Although some cost-benefit analysis has been applied to the use of ROC curves in clinical settings (Swets & Pickett 1982; Metz 1986), this has focussed on the direct costs of treating false-positive vs. true-positive diagnoses rather than deferring treatments while diagnostic tests are improved.

As no map can predict a pest's distribution with 100% precision, some unoccupied sites will inevitably be searched (Václavík & Meentemeyer 2009). As the overall search area increases we expect to reach more of the occupied sites, but we also experience a concomitant increase in the proportion of empty sites that are searched. In the extreme case, exhaustive searching entails looking for the pest throughout the entire area of unsuitable habitat as well as in all the more likely sites. Therefore it may be better to select fewer sites and increase the search effort at each site to increase the probability of detecting the pest, similar to intensive vs. extensive search modes of animal foraging behaviour (Fortin 2002). The search strategy for an invasive species will ideally incorporate some idea of how

accurate the distribution predictions are, and therefore what proportion of searches are likely to be futile due to an incorrect choice of site. Consequently it may even be beneficial to redirect resources to refining our knowledge of the organism's expected distribution, to better identify candidate sites for future searches.

We address these issues here by optimizing the trade-offs among widespread and more focussed search areas (allowing low and high search intensity per site, respectively), against knowledge acquisition to improve future searches. We use stochastic dynamic programming (SDP), a procedure that identifies optimal strategies by considering the possible changes in the states of a system over time (Bellman 1957). We also compare, by simulation under different assumptions, the relative performances of the SDP recommendations and alternative management strategies. SDP is commonly applied in behavioural ecology (Mangel & Clark 1988; McNamara & Houston 1996), including examining when foraging organisms should learn about resource distribution by moving between patches (Eliassen *et al.* 2009). It is being used increasingly to solve state-dependent management problems in ecology: choosing between fire management options (Richards, Possingham & Tizard 1999; McCarthy, Possingham & Gill 2001), how to allocate management effort within or among sites (Baxter *et al.* 2007; McDonald-Madden, Baxter & Possingham 2008), and when to cease management or monitoring altogether (Regan *et al.* 2006; Chadès *et al.* 2008).

We frame our analysis around the invasion of red imported fire ants *Solenopsis invicta* Buren in the Brisbane, Queensland, region, dating from February 2001 (Jennings & McCubbin 2004). Native to South America, their establishment as an invasive alien species is greatly facilitated by anthropogenic disturbance (King & Tschinkel 2008), and they are capable of considerable environmental, social and economic damage (Williams 1994; Callcott & Collins 1996). The fire ant incursion into Australia is therefore potentially very serious, given extensive suitable habitat (Moloney & Vanderwoude 2002; Sutherst & Maywald 2005), and the invasion has been listed as a Key Threatening Process under the 1999 Commonwealth Environment Protection and Biodiversity Conservation Act. The Queensland invasion dynamics have been modelled previously (Scanlan & Vanderwoude 2006), allowing reasonable biological parameterisation for our purposes. In the absence of detailed management cost data, however, we keep our approach general and demonstrate the method in a form broadly applicable to invasive species management (and indeed to applied ecology in general), rather than presenting a specific case analysis of the fire-ant invasion. This novel approach shows how current and future prediction capability should affect current and future search strategies to optimize invasive species control and planning.

## Materials and methods

In order to model the maps' predictive quality, we use a family of ROC curves. In practice, ROC curves can take any shape between (0,0) and (1,1), with one measure of map quality being the area under

the curve (AUC); the closer AUC gets to one, the better the map (Swets 1988; but see Lobo, Jiménez-Valverde & Real 2008). We assume a family of ROC curves given by

$$y = x^{1/a} \quad \text{eqn 1}$$

(Fig. 1a; after Swets 1986), and bounded at (0,0) and (1,1) as required. For this equation, the area under the curve takes a simple form,  $\text{AUC} = a/(a+1)$ , which asymptotically approaches one as  $a$  increases. Therefore a higher value of  $a$  implies a more reliable map ( $a = 1$  essentially implies no knowledge and random searches).

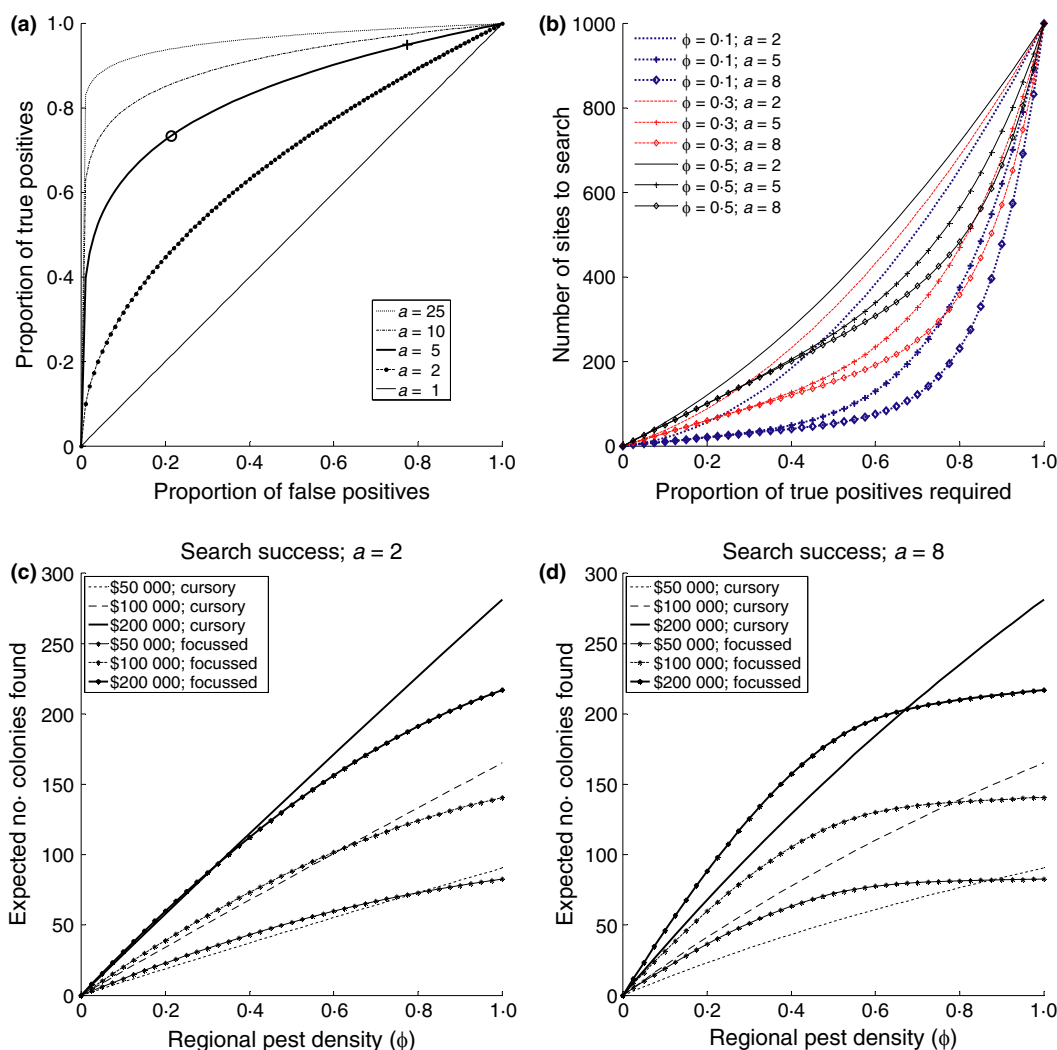
#### SEARCH STRATEGY AND SUCCESS

We assume that a pest is present at some density  $\phi$  within a region of area  $A$  (we list symbols and parameters in Table 1). In a map,  $A$  can be measured as the number of cells in a grid covering the region (i.e.

number of sites in which the pest may potentially occur), and  $\phi$  as the proportion of those cells that are infested. The map directing our searches will produce sites labelled as occupied, either correctly (in eqn 1, proportion  $y$  of occupied sites) or incorrectly (proportion  $x$  of empty sites). When we use the map to choose  $sA$  sites to search (a proportion  $s$  of the region), eqn 1 allows us to express this in terms of the sites searched that are either occupied ( $\phi Ay$ ) or unoccupied ( $[1-\phi]Ax$ ):

$$\begin{aligned} sA &= \phi Ay + (1 - \phi)Ax \\ \Rightarrow s &= \phi y + (1 - \phi)x^a. \end{aligned} \quad \text{eqn 2}$$

The value of  $s$  increases with  $y$ ,  $A$  and  $\phi$  (Fig. 1b). We can use eqn 2 to find the proportion of a region,  $s_1$ , needed to be searched in order to visit some proportion  $y_1$  of the occupied sites. Alternatively we could search fewer sites (proportion  $s_2 < s_1$ ), spending longer in each, giving:



**Fig. 1.** Relationships underpinning the framework of active searching vs. knowledge acquisition. (a) Family of theoretical Receiver Operating Characteristic curves, described by  $y = x^{1/a}$ , where higher values of  $a$  reflect better predictive capability. Two example search strategies are indicated for a habitat map quality of  $a = 5$ . The cursory-widespread strategy ('+') attempts to find 95% of the infestation (380 sites) and the focussed strategy ('o'), visits half that number, allowing double the search time per site. (b) The total number of sites (empty and occupied) required to search, to visit given proportions of occupied sites, depending on regional infestation density,  $\phi$ , and quality of habitat map,  $a$ . (c, d) Expected number of colonies detected in one time step as a function of regional pest density, for three different budgets and the two search strategies (cursory and focussed). Two levels of map quality are shown, (c)  $a = 2$  and (d)  $a = 8$ .

**Table 1.** Parameters used, with their symbols and values (where applicable; otherwise indicated as a variable or a function  $f(\dots)$  of other parameters)

Symbol	Description	Value
$\phi$	proportion of region infested	variable
$\phi_0$	initial proportion of region infested in simulations	0.01
$\lambda_{\max}$	maximum rate of invasion spread	1.19
$\lambda_d$	rate of spread due to detected colonies	$f(\phi), \leq 1.09$
$\lambda_u$	rate of spread due to uncontrolled colonies	$f(\phi), \leq 1.19$
$A$	area of region (#grid cells in species distribution model)	1000
$B$	budget per time-step	\$100,000
$D_i$	expected proportion of colonies detected with action $i$	$f(\phi, A, B, k, s_i, y_i)$
$S_{95}$	value of $s$ giving 95% worthwhile searches	$f(\phi, a)$
$a$	ROC curve exponent	variable
$a_0$	initial ROC curve exponent in simulations	2
$d$	probability of detecting a colony if present	$f(v, k)$
$k$	search effort at which $d = 0.5$	\$500
$s$	proportion of region to be searched	$f(y, \phi, a)$
$v$	search effort per site (\$)	$f(A, B, s)$
$x$	proportion of all futile sites searched ('false positive proportion')	0–1
$y$	proportion of all worthwhile sites searched ('true positive proportion')	0–1, $f(x, a)$

ROC, Receiver Operating Characteristic.

$$s_1 = \phi y_1 + (1 - \phi) y_1^a$$

and

$$s_2 = \phi y_2 + (1 - \phi) y_2^a,$$

eqn 3

with  $y_1 > y_2$  when  $s_1 > s_2$  (Fig. 1b). For example we can set  $s_1 = S_{95}$ , which we define as the proportion of sites needed to include 95% of all occupied sites ( $y_1 = 0.95$ ):

$$s_1 = S_{95} = 0.95\phi + (1 - \phi)0.95^a$$

eqn 4

(Fig. 1a, '+'). If we want to find the 'hit' rate  $y_2$  for searching half those sites we can use the equation

$$s_2 = 0.5S_{95} = \phi y_2 + (1 - \phi) y_2^a,$$

eqn 5

and (knowing  $S_{95}$  and estimating  $a$  and  $\phi$ ) we can find  $y_2$  numerically (Fig. 1a, 'o'). For example, for a regional infestation density of  $\phi = 0.4$ , and map quality  $a = 5$ , we get  $S_{95} = 0.844$ , and  $y_2 = 0.735$  (giving  $s_2 = 0.422 = 0.5S_{95}$ ). This means that, for an area of 1000 sites, in order to search in 380 sites that are occupied (95% of the 400 infestations), we need to search in 844 sites in total, as our map will misdirect us to 464 sites (so 55% of searches are futile – still better than random, which would lead to 60% of searches being futile). By halving the number of sites searched (422), our map would send us to  $0.4(0.735) = 294$  occupied sites, and leave us with 128 futile searches (30% of all searches). Therefore when we employ the map, reducing the total search coverage also reduces the proportion of searches that are futile. Furthermore, searching half the sites allows us to double our per-site search effort, increasing the detection probability at occupied sites. Nonetheless, the increase in proportion of worthwhile searches and detection probability must be traded off against the reduction in overall search coverage.

#### PROBABILITY OF DETECTION

Detecting a pest at an occupied site is more likely if we expend more effort searching the site. Assume the probability of pest detection (conditional on its presence),  $d$ , is a saturating function of search effort ( $v$ ):

$$d = v/(k + v), \quad \text{eqn 6}$$

where we have a 50% chance of finding an infestation if we search with effort  $v = k$ . Search effort could reflect, for example, time spent at a site, number of fieldworkers and different search methods used. It is convenient therefore to measure effort in terms of its total cost, which gives the effort per site searched as

$$v = B/sA, \quad \text{eqn 7}$$

where the budget for the management period is \$ $B$ . Combining eqns 6 and 7 gives the detection probability in an occupied site as a function of budget, proportion of areas searched, and the area of the region:

$$d = B/(ksA + B). \quad \text{eqn 8}$$

#### IMPROVING THE SPECIES DISTRIBUTION MODEL

Another possible strategy is to defer searching to concentrate resources on improving the predictive accuracy of the map (increasing  $a$  in eqn 1). These improvements could come from updating habitat-predictive algorithms, or acquiring more or better environmental data relating to pest habitat, including development of novel techniques to do so.

#### DECISION TRADE-OFFS

In this example, therefore, we choose from three actions ( $i$ ) at each time step:

$i = 1$ : search proportion  $s_1 = S_{95}$  of the region, visiting 95% of all occupied sites,  $0.95\phi A$ . In each we have a probability  $B/(ks_1A + B)$  of detecting the pest, but we also search  $A(1 - \phi)0.95^a$  sites in vain, and leave  $(1 - S_{95})A$  sites unsearched;

$i = 2$ : search proportion  $s_2 = 0.5S_{95}$  of the region, which gives us  $\phi y_2 A$  occupied sites in which we have a probability  $B/(ks_2A + B)$  of detecting the pest. We will also search  $(1 - \phi)y_2^a A$  empty sites and leave  $(1 - 0.5S_{95})A$  sites unsearched; or

$i = 3$ : postpone searching ( $s_3 = 0$ ) and develop a better map (increase  $a$ ).



For the first two options, the expected proportion of colonies detected and destroyed is

$$D_i = \frac{\phi y_i AB}{k s_i A + B} \quad i = 1, 2 \quad \text{eqn 9}$$

(Fig. 1 c,d). For the third option ( $i = 3$ ) we assume that all  $\phi A$  colonies remain undetected ( $D_3 = 0$ ).

## PARAMETERIZATION AND OPTIMIZATION

### Cost parameters

For purposes of illustration, we assume that the map covers  $A = 1000$  sites, or grid-cells, each of which may or may not contain the pest species; that the budget per time step is  $B = \$100\,000$ ; and that the cost of the effort required to have 50% chance of detecting a pest present on an infested site is  $k = \$500$ . These values give a detection probability per occupied site of  $d = 0.17$ , if all sites are searched, increasing to  $d = 0.67$  if only 10% of the region is searched.

### Invasion parameters

The spread of the infestation will depend on both the organism's biology and search-and-control success. In this example we use simplified fire ant population dynamics to demonstrate our approach. Scanlan & Vanderwoude (2006) modelled the spread of fire ants in Australia at two spatial scales, and assumed that invasion extent doubled every 2–4 years when measured at the broader scale (10 000-km<sup>2</sup> blocks), with faster dynamics at local scales. We compromise between these two scales and assume a maximum doubling period, in the absence of control or density-dependence, of 24 months. Thus, in a 6-month management period, the maximum rate of spread is  $\lambda_{\max} = 2^{(6/24)} \approx 1.19$ . We assume that the increase in regional density follows logistic growth (Scanlan & Vanderwoude 2006; see also Shryock *et al.* 2008), giving a rate of increase of

$$\lambda_u(\phi) = 1 + (\lambda_{\max} - 1)(\phi - 1)/1 \quad \text{eqn 10}$$

if colonies are uncontrolled (the denominator of 1 indicates the 'carrying capacity' of  $\phi = 1$  in a fully colonized area). Even if a colony is detected and destroyed, it may already have reproduced. Assuming that colonies are discovered on average halfway through their reproductive cycle, the rate of increase of detected-and-removed colonies is

$$\lambda_d(\phi) = \lambda_u(\phi)^{1/2}. \quad \text{eqn 11}$$

For  $\lambda_u = 1.19$  at its maximum value, this implies that at most 9% of detected ant colonies will have spread prior to their destruction ( $1.19^{1/2} \approx 1.09$ ).

For the optimization (Appendix S1, Supporting Information), we describe the system state by the combination of map quality ( $a$  in eqn 1) and regional pest density  $\phi$ . The system undergoes transitions between states with probabilities governed by the outcome of each management option. Expected future pest density depends on the rates of spread from controlled and uncontrolled sites, and we assume that learning improves the map quality  $a$  by one (with probability 0.2) or two (probability 0.8) units, giving diminishing increases in AUC. We accord a 'utility' value to each state depending on the pest density only (map quality has no utility apart from improving future searches): utility increases linearly as pest density decreases, with a 100-fold bonus if the pest is eradicated (this high bonus could reflect renewed access to export markets in the case of agricultural pests

(Fraser *et al.* 2006), avoided costs of ongoing management, or even societal values).

## PERFORMANCE EVALUATION

To test the performance of employing the optimization (SDP) results vs. three simpler management regimes, we simulated 20-year management of a pest invasion with dynamics as above (Table 1), beginning at 1% regional infestation; this level would in practice be dependent on both timeliness of detection and the spatial resolution of the map. We assumed an initial knowledge level of  $a = 2$ , reflecting a reasonable lower-end AUC value (Latimer *et al.* 2009; Václavík & Meentemeyer 2009). The alternative management regimes were based on those used for the SDP formulation and comprise: always search  $S_{95}$  sites; always search  $S_{95}/2$  sites (doubling effort-per-site); or rotate between search and learning modes. The 'rotating strategy' iteratively followed the sequence: widespread control ( $S_{95}$ ) - upgrade map (increase  $a$ ) - focussed control ( $S_{95}/2$ ).

## Results

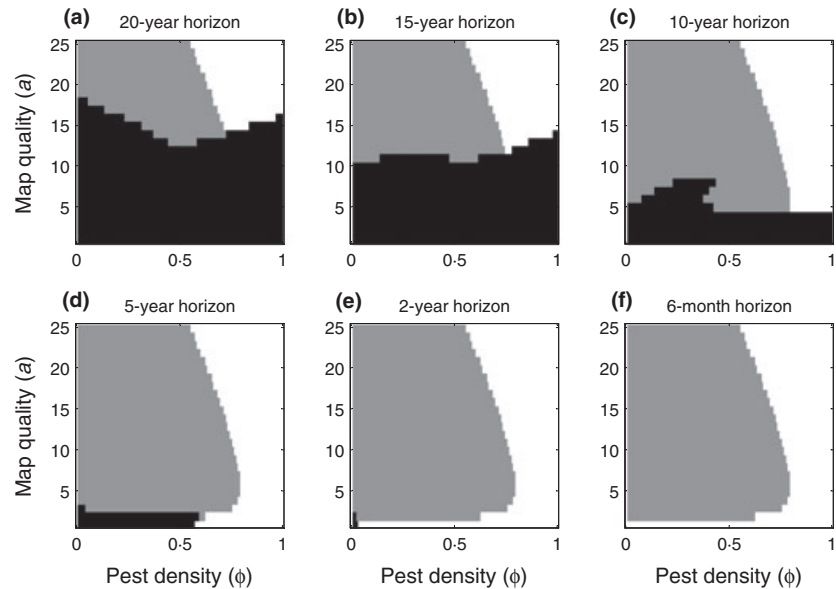
### STATE-DEPENDENT OPTIMIZATION

The optimal strategies for learning about and controlling an invasion (i.e. the SDP solution; Fig. 2) depend on the system state (pest infestation density  $\phi$  and map quality  $a$ ), and on the management time horizon  $T$ . We first consider long-term management recommendations (e.g. more than a decade; Fig. 2a–c). For the longest management horizon considered, 20 years, improving the predictive quality of the map initially takes precedence over either search method for most of the system states. Exceptions are when our map is already excellent ( $a > 15$ , or AUC > 0.9375; not unrealistically high values; Zurell *et al.* 2009) or when the infestation is at moderate densities. If the infestation is at very low densities we can afford to delay searching until we have a better map to improve targeting of future searches. On the other hand, if the infestation is widespread then searching with a restricted budget will have little effect on pest density and so we again delay searching until we have a better map.

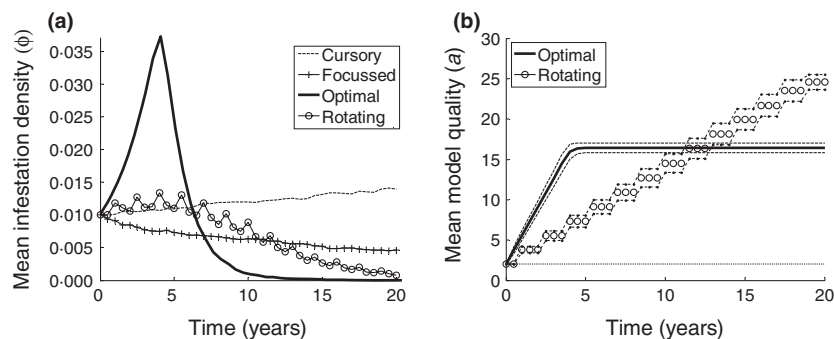
If we strive for shorter-term success (Fig. 2d–f) the value of improving the map diminishes and the optimal strategy is usually immediate search-and-control. Generally, if the pest is already widespread, then cursory widespread searching is optimal ( $i = 1$  above), as even undirected searches will have high success. If the pest is at lower densities then we should use targeted site-intensive searching ( $i = 2$ ). This strategy depends on having a reasonable-quality map to exploit: if the map is very poor, we should still use cursory searches (close in effect to random searches:  $a \approx 1$ ). Nonetheless, at all but the shortest management timeframes, it is always recommended to improve a very poor map if the infestation is still at low levels (e.g.  $\phi = 0.01$ ; bottom-left of Fig. 2a–e).

## PERFORMANCE EVALUATION

As expected, the state-dependent optimization performed better in our simulations than the alternative strategies (Fig. 3a,



**Fig. 2.** Optimal strategies depending on regional infestation density ( $\phi$ ) and current quality of species distribution model ( $a$ ), over a selection of management time horizons. The optimal strategies for each ( $\phi$ ,  $a$ ) state are indicated as: white = cursory widespread searching ( $s_1 = S_{95}$ ); grey = fewer, more focussed and intensive searches ( $s_2 = S_{95}/2$ ;  $v_2 = 2v_1$ ); black = re-direct funding towards improving the species distribution model.

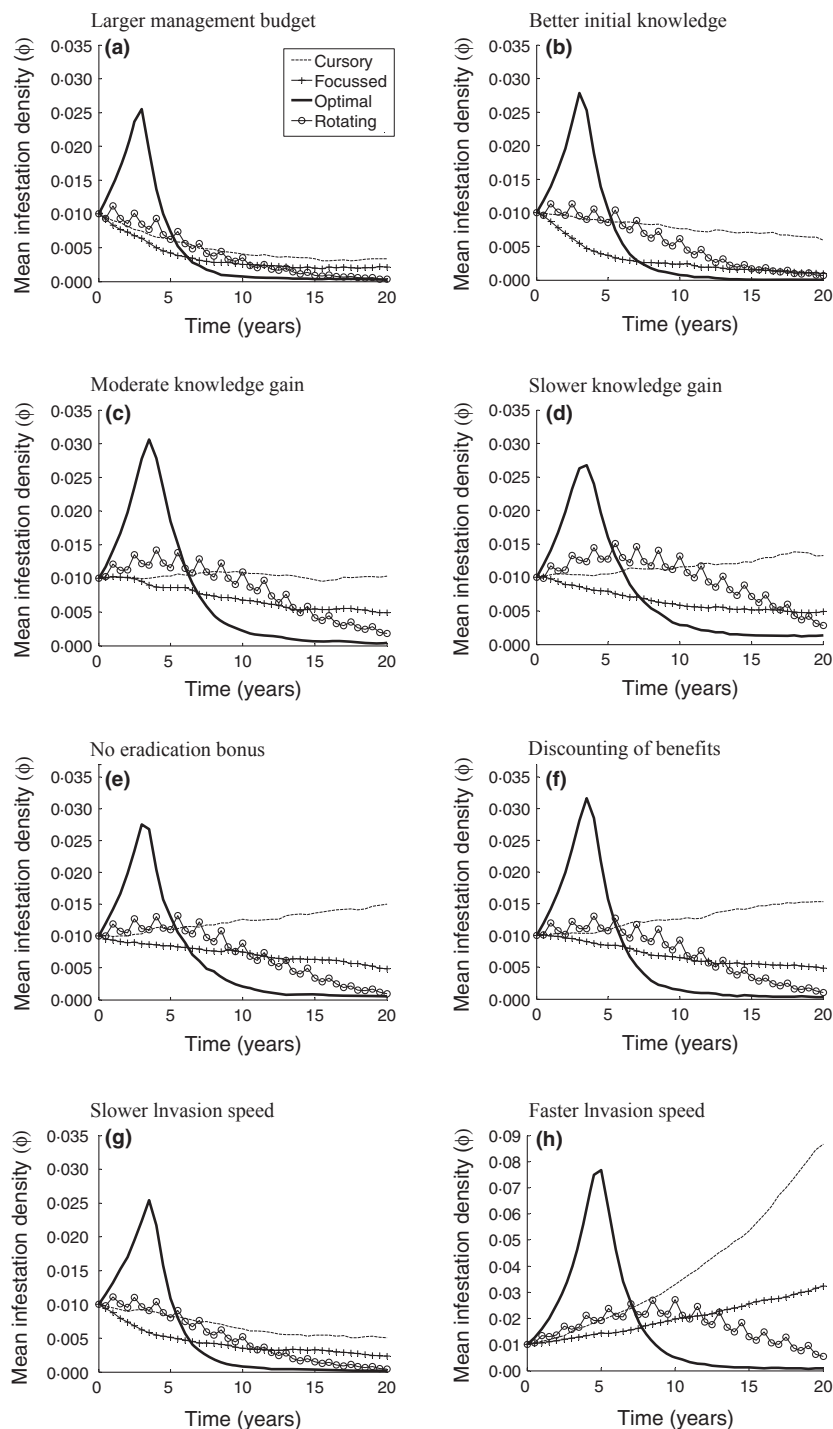


**Fig. 3.** Simulated performance of pest management over 20 years under default model assumptions. (a) Comparison of four management strategies: cursory widespread searches; intensive focussed searches; optimal state-dependent strategy recommended by stochastic dynamic programming; and continual rotating between cursory search, model-improvement and focussed search. (b) Acquisition of knowledge when the optimal and rotational strategies are implemented, showing mean ( $\pm$ SD) values of the Receiver Operating Characteristic curve exponent  $a$ . The two non-learning strategies (cursory and focussed searching) remain at the initial level of  $a = 2$  (dotted line).

mean trajectories shown), usually achieving eradication by year 20. This eventual success is dependent on tolerating an initial increase in pest density as funds are initially devoted to improving the map (Fig. 3b). Other strategies avoid the initial ‘spike’ in pest density but fail to achieve eradication over the long-term. The cursory-widespread search strategy performs worst, with the site occupancy steadily increasing. The ‘focussed’ strategy results in a steady, but slow, decrease in density. The ‘rotating’ strategy allows some map improvement as well as search-and-control efforts, and thus performs comparatively well. Nonetheless, in terms of achieving eradication the optimal strategy performed considerably better, eradicating the pest in 97% of simulations (compared to 59% for the rotating strategy, and never for the two non-learning strategies).

We also investigated departures from our default assumptions and parameter values (Fig. 4). Increasing the budget by 50% (Fig. 4a) improved the performance of all strategies (unsurprisingly), with most strategies achieving high levels of

suppression. Starting with a better map ( $a = 5$ ; Fig. 4b) also led to improvements in all strategies, particularly the ‘focussed’ strategy, which particularly depends on reliable site selection for its success. We also examined our assumption that research increases the value of  $a$  by 2 units with probability  $p_a = 0.8$ , however, this appeared to have little overall effect on results (Figs 4c,d). The spike in pest density when the optimization solution is applied decreases with  $p_a$ , because managers will be less willing to allow temporary population explosions if the scope for improving the map is reduced, and so switch to search/control operations sooner. Similar effects resulted from eliminating the eradication bonus (Fig. 4e) or incorporating a 3% discount rate (Fig. 4f): these scenarios reduce the emphasis on eradication vs. containment (Odom *et al.* 2003; Fraser *et al.* 2006) either in the longer-term (discounting) or permanently (no bonus), leading to decreased incentive to improve knowledge. All strategies had more success controlling slower invasions (Fig. 4g), while rapidly-spreading invasions (Fig. 4h) were only able to be suppressed by the optimal and rotating



**Fig. 4.** Mean performances of four management strategies (as Fig. 3a) under alternative parameter values and assumptions. (a) Budget per time-step of \$150 000; (b) initial good quality species distribution model ( $a = 5$ ); (c) 50% and (d) 20% probability of increasing  $a$  by 2 units (otherwise  $a$  increases by 1 unit); (e) no eradication bonus given; (f) applying a 3% discount rate to the performance benefits; and maximum doubling time of invasion set to (g) 30 months ( $\lambda_{\max} = 0.15$ ) and (h) 18 months ( $\lambda_{\max} = 1.26$ ; note different vertical scale).

strategies. Overall, the ranking of performances was robust to changes in assumptions (including others not shown; e.g. higher initial pest density). The tendency of the SDP solution to allocate approximately 3–4 years' initial funding to map improvement was similarly consistent.

## Discussion

We have introduced and demonstrated an approach for trading-off actions that search for and remove a pest, against an action that only gains knowledge. Our optimizations indicate

that spending time improving knowledge about the pest's habitat preferences, before searching for it, is optimal. We were surprised to discover this, as deciding to improve knowledge while a pest incursion grows exponentially seems like fiddling while Rome burns. Nevertheless this highlights the value of learning even when at the expense of control operations under seemingly urgent conditions.

With a long-term perspective, it is optimal to learn rather than take direct action at the start of an invasion (Fig. 2), but exactly for how long we should delay action and learn depends on many factors. These include the cost of learning relative to

on-ground search and control operations, the desire for eradication vs. containment, the likely improvement in our knowledge of habitat preferences and the biological characteristics of the pest species (Fig. 4). Once the initial learning phase is over, searching should be focussed and intensive, rather than widespread and cursory, when we have less widespread infestation or intermediate predictive capabilities (Fig. 2d–f).

Simulation of alternative plausible management strategies confirmed the expected superiority of the optimization approach (Fig. 4). The overall similarity of trajectories under different assumptions also highlighted that at the initial stages of pest incursion (when  $\phi$  is still small), allowing some spread of the infestation may be acceptable so long as we can improve our map to better predict and control the pest in future. This is partly because our management objective gives more weight to eventual eradication than to merely suppressing the population (cf. Fig. 4e), and increased knowledge is ultimately required to improve searching for and removing the invader. This result raises the interesting question of whether the best emergency response to a new incursion is actually to ‘do nothing’ – take no immediate direct action but concentrate funds into developing high-quality predictive maps to maximize efficacy of future management. By taking a long-term focus (and deferring control), it could be argued that managers are being more pragmatic, trading off the apparent urgency of a new incursion against the strategic allocation of resources to knowledge acquisition and better chance of success further in the future. This however must also be evaluated in the light of the structure and assumptions presented here. For example, the framework can be expanded to include many different strategies (e.g. more search areas  $s_i$  and their corresponding search intensities). More refined budgetary options in the optimization could allow both searching and habitat modelling simultaneously by selecting the proportion of funds allocated to learning vs. control, instead of the all-or-nothing choice presented here. Alternatively some funding could be allocated to improving detection probability at occupied sites by developing enhanced on-site search techniques. Pursuing this research will provide further insights into knowledge/action trade-offs.

The optimization (Fig. 2) indicates cases where we should search and control straight away rather than improving a map. The most obvious case is when we already have a reasonable quality map. The simulation results indicate that the switch from knowledge acquisition to active control takes place after about 3–4 years’ research (average map quality of  $a = 16.4$ ,  $AUC = 0.94$ ), but of course this depends on other factors such as the severity of the incursion and the management time horizon. Nonetheless, the shorter the management timeframe, the less the relative merits of acquiring additional information and the more likely control action will be taken. This diminishing return on investment in data acquisition has recently been shown for conservation of South African fynbos flora (Grantham *et al.* 2009), in which case optimal decisions on choosing patches to reserve could be made after a relatively small initial data-gathering effort. Other cases demanding quicker action are when the pest population spreads quickly, or the management timeframe imposes too tight a deadline to be able to act

on the research results. These two aspects reflect increased urgency in countering the invasion, either in terms of spatial spread or the wish to produce positive outcomes quickly. Another factor to favour immediate action is having a large budget, which allows greater search effort and better success even with poor predictive ability. The size of the budget may itself reflect an urgent desire to control an invasion. This was the case in the Queensland fire-ant incursion, for which a large budget was available from the outset (AU\$123 million; George 2007). Such well-funded programmes allow us the luxury of immediate action as well as simultaneous production of a predictive map; however many conservation efforts operate on much tighter budgets, making trade-offs between knowledge gain and control efforts unavoidable. Even in the fire-ant case success has proven elusive despite more than AU\$200 million invested (Williams 2010).

While we deliberately used simple models to demonstrate the learn-or-act trade-off, the assumptions made in developing our framework should be noted, particularly if being applied to a real-world situation. For example, we have assumed that diversion of funds into research will definitely have a (measurable) positive outcome, that  $a$  will increase precisely by either 1 or 2 (with probability 0.2 and 0.8 respectively); while altering the relative values of these probabilities had little effect on simulated performance (Fig. 4c,d), the possibilities of no map improvement, or even perverse disimprovement, were not considered. We have assumed that this improvement costs the same per time-step as searching for the pest; the actual costs and benefits of map improvement would need to be estimated based on acquiring suitable personnel and infrastructure (software, data layers etc.), and anticipating the projected map improvements (reduction in level of false positives with an improved map) – these estimates, while uncertain, may provide sufficient insight into whether greater weight should be given to searching or knowledge improvement. The current value of  $a$  could be estimated from the map’s performance in predicting the species’ native range (with caution), or from previous search results if available.

We have disregarded the spatio-temporal dynamics of the infestation. In reality dispersing ants may not find all suitable available habitat in which to found a new colony, so our assumptions also (conservatively) overestimate doubling speed. Just as a searched site may be ideal habitat, but not yet colonized by a dispersing pest, a site deemed to be of marginal suitability may become colonized if the surrounding area is already saturated with colonies. We have also assumed that the map extends to all possible areas of spread – judgement may be required to trade its spatial extent off against sufficient grain to provide meaningful information on finer scales.

We could use more sophisticated optimization methods to address some of our assumptions. D’Evelyn *et al.* (2008) demonstrate the value of incorporating search results directly into estimates of pest population density, in order to choose the optimal effort of control in later years, emphasizing, as here, the value of early learning (in their case via control). Our optimization is dependent on both infestation density and map accuracy, both of which may be imprecisely known (Václavík



& Meentemeyer 2009). We could therefore re-express the problem in terms of our belief of what the current values of  $\phi$  and  $a$  are, in a partially-observable Markov decision process (POMDP), to optimize our future 'belief state' rather than the actual, but unknowable, state of the system (for ecological examples see Lane 1989; White 2005; Chadès *et al.* 2008).

In terms of economic simplifications, we have ignored the costs of travelling between sites; so that the selection of many sites to search may incur extra costs if extensive travel is involved. McDonald-Madden, Baxter & Possingham (2008) demonstrate a succinct approach to this problem when the locations of the populations are known. We have also assumed that the cost of pest removal, once discovered in a site, is negligible, or integrated into the search costs. Similarly we ignore the possibility of multiple pest occurrences on one site which would influence both the search success and removal costs; or other aspects of spatial contagion that also affect costs and strategy performance.

We have made these assumptions and simplifications so that we could get to the heart of the act-or-learn problem in invasion management; some of these assumptions will be relaxed in future work. Nonetheless, striking results emerge, particularly the consistent recommendation that learning first, and looking (more successfully) later on, is the long-term optimal approach to new pest incursions.

## Acknowledgements

We thank Iadine Chadès, Hedley Grantham, Cindy Hauser, Dane Panetta, the editor and two anonymous reviewers for helpful discussions and comments. Financial support was provided by the Australian Centre of Excellence for Risk Analysis (ACERA) and the Applied Environmental Decision Analysis (AEDA) research hub, a Commonwealth Environmental Research Facility.

## References

- Baret, S., Rouget, M., Richardson, D.M., Laverigne, C., Egoh, B., Dupont, J. & Strasberg, D. (2006) Current distribution and potential extent of the most invasive alien plant species on La Réunion (Indian Ocean, Mascarene islands). *Austral Ecology*, **31**, 747–758.
- Baxter, P.W.J., Wilcox, C., McCarthy, M.A. & Possingham, H.P. (2007) Optimal management of an annual weed: a stochastic dynamic programming approach. *MODSIM 2007 International Congress on Modelling and Simulation* (eds L. Oxley & D. Kulasiri), pp. 2223–2229. Modelling and Simulation Society of Australia and New Zealand, [http://www.mssanz.org.au/MODSIM07/papers/41\\_s34/OptimalManagement\\_s34\\_Baxter\\_.pdf](http://www.mssanz.org.au/MODSIM07/papers/41_s34/OptimalManagement_s34_Baxter_.pdf).
- Bellman, R.E. (1957) *Dynamic Programming*. Princeton University Press, Princeton, NJ.
- Bogich, T. & Shea, K. (2008) A state-dependent model for the optimal management of an invasive metapopulation. *Ecological Applications*, **18**, 748–761.
- Cacho, O.J., Hester, S. & Spring, D. (2007) Applying search theory to determine the feasibility of eradicating an invasive population in natural environments. *Australian Journal of Agricultural and Resource Economics*, **51**, 425–443.
- Callcott, A.M.A. & Collins, H.L. (1996) Invasion and range expansion of imported fire ants (Hymenoptera: Formicidae) in North America from 1918–1995. *Florida Entomologist*, **79**, 240–251.
- Chadès, I., McDonald-Madden, E., McCarthy, M.A., Wintle, B., Linkie, M. & Possingham, H.P. (2008) When to stop managing or surveying cryptic threatened species. *Proceedings of the National Academy of Sciences*, **105**, 13936–13940.
- D'Evelyn, S.T., Tarui, N., Burnett, K. & Roumasset, J.A. (2008) Learning-by-catching: Uncertain invasive-species populations and the value of information. *Journal of Environmental Management*, **89**, 284–292.
- Eliassen, S., Jørgensen, C., Mangel, M. & Giske, J. (2009) Quantifying the adaptive value of learning in foraging behavior. *The American Naturalist*, **174**, 478–489.
- Fortin, D. (2002) Optimal searching behaviour: the value of sampling information. *Ecological Modelling*, **153**, 279–290.
- Fraser, R.W., Cook, D.C., Mumford, J.D., Wilby, A. & Waage, J.K. (2006) Managing outbreaks of invasive species: eradication versus suppression. *International Journal of Pest Management*, **52**, 261–268.
- George, C.R.R. (2007) *Establishment risk modelling of invasive organisms: Solenopsis invicta as a case study*. PhD Thesis, University of Queensland, Brisbane.
- Grantham, H.S., Wilson, K.A., Moilanen, A., Rebelo, T. & Possingham, H.P. (2009) Delaying conservation actions for improved knowledge: how long should we wait? *Ecology Letters*, **12**, 293–301.
- Hauser, C.E. & McCarthy, M.A. (2009) Streamlining 'search and destroy': cost-effective surveillance for invasive species management. *Ecology Letters*, **12**, 683–692.
- Jennings, C. & McCubbin, K. (2004) *The National Red Imported Fire Ant Eradication Program Overview – October 2004*. Fire Ant Control Centre, Queensland Department of Primary Industries, Brisbane, Australia.
- King, J.R. & Tschinkel, W.R. (2008) Experimental evidence that human impacts drive fire ant invasions and ecological change. *Proceedings of the National Academy of Sciences*, **105**, 20339–20343.
- Lane, D.E. (1989) A partially observable model of decision-making by fishermen. *Operations Research*, **37**, 240–254.
- Latimer, A.M., Banerjee, S., Sang Jr, H., Mosher, E.S. & Silander Jr, J.A. (2009) Hierarchical models facilitate spatial analysis of large data sets: a case study on invasive plant species in the northeastern United States. *Ecology Letters*, **12**, 144–154.
- Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, **17**, 145–151.
- Mangel, M. & Clark, C.W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton, NJ.
- McCarthy, M.A., Possingham, H.P. & Gill, A.M. (2001) Using stochastic dynamic programming to determine optimal fire management for *Banksia ornata*. *Journal of Applied Ecology*, **38**, 585–592.
- McDonald-Madden, E., Baxter, P.W.J. & Possingham, H.P. (2008) Subpopulation triage: how to allocate conservation effort among populations. *Conservation Biology*, **22**, 656–665.
- McNamara, J.M. & Houston, A.I. (1996) State-dependent life histories. *Nature*, **380**, 215–221.
- Metz, C.E. (1986) ROC methodology in radiologic imaging. *Investigative Radiology*, **21**, 720–733.
- Moloney, S. & Vanderwoude, C. (2002) Red imported fire ants: a threat to eastern Australia's threatened wildlife? *Ecological Management and Restoration*, **3**, 167–175.
- Moody, M.E. & Mack, R.N. (1988) Controlling the spread of plant invasions – the importance of nascent foci. *Journal of Applied Ecology*, **25**, 1009–1021.
- Murray, J.V., Goldizen, A.W., O'Leary, R.A., McAlpine, C.A., Possingham, H.P. & Choy, S.L. (2009) How useful is expert opinion for predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillata*. *Journal of Applied Ecology*, **46**, 842–851.
- Odom, D.I.S., Cacho, O.J., Sinden, J.A. & Griffith, G.R. (2003) Policies for the management of weeds in natural ecosystems: the case of scotch broom (*Cytisus scoparius*, L.) in an Australian national park. *Ecological Economics*, **44**, 119–135.
- Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.
- Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture Ecosystems & Environment*, **84**, 1–20.
- Regan, T.J., McCarthy, M.A., Baxter, P.W.J., Panetta, D.F. & Possingham, H.P. (2006) Optimal eradication: when to stop looking for an invasive plant. *Ecology Letters*, **9**, 759–766.
- Richards, S.A., Possingham, H.P. & Tizard, J. (1999) Optimal fire management for maintaining community diversity. *Ecological Applications*, **9**, 880–892.
- Sala, O.E., Chapin, F.S., Armesto, J.J. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Scanlan, J.C. & Vanderwoude, C. (2006) Modelling the potential spread of *Solenopsis invicta* Buren (Hymenoptera: Formicidae) (red imported fire ant) in Australia. *Australian Journal of Entomology*, **45**, 1–9.

- Shryock, K.A., Brown, S.L., Sanders, N.J. & Burroughs, E. (2008) A reaction-diffusion equation modeling the invasion of the Argentine ant population, *Linepithema humile*, at Jasper Ridge Biological Preserve. *Natural Resource Modeling*, **21**, 330–342.
- Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, N.J.
- Sutherst, R.W. & Maywald, G. (2005) A climate model of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae): Implications for invasion of new regions, particularly Oceania. *Environmental Entomology*, **34**, 317–335.
- Swets, J.A. (1986) Indexes of discrimination or diagnostic-accuracy – their ROCs and implied models. *Psychological Bulletin*, **99**, 100–117.
- Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science*, **240**, 1285–1293.
- Swets, J.A. & Pickett, R.M. (1982) *Evaluation of Diagnostic Systems: Methods From Signal Detection Theory*. Academic Press, New York.
- Taylor, C.M. & Hastings, A. (2004) Finding optimal control strategies for invasive species: a density-structured model for *Spartina alterniflora*. *Journal of Applied Ecology*, **41**, 1049–1057.
- Václavík, T. & Meentemeyer, R.K. (2009) Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions? *Ecological Modelling*, **220**, 3248–3258.
- Walters, C.J. (1986) *Adaptive Management of Renewable Resources*. Macmillan, New York.
- White, B. (2005) An economic analysis of ecological monitoring. *Ecological Modelling*, **189**, 241–250.
- Whittle, A.J., Lenhart, S. & Gross, L.J. (2007) Optimal control for management of an invasive plant species. *Mathematical Biosciences and Engineering*, **4**, 101–112.
- Williams, D.F. (1994) Control of the introduced pest *Solenopsis invicta* in the United States. *Exotic Ants: Biology, Impact, and Control of Introduced Species* (ed. D.F. Williams), pp. 282–292. Westview Press, Boulder, CO.
- Williams, B. (2010) Fire ants advance. *Courier Mail* 31 March 2010. News Limited, Brisbane, pp 1–2.
- Wintle, B.A., Elith, J. & Potts, J.M. (2005) Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of NSW. *Austral Ecology*, **30**, 719–738.
- Zurell, D., Jeltsch, F., Dormann, C.F. & Schröder, B. (2009) Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography*, **32**, 733–744.

Received 27 January 2010; accepted 30 September 2010

Handling Editor: Andy Sheppard

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