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The economic benefit of time-varying surveillance effort for invasive species management

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Summary

1. Government agencies develop invasive species management programmes assuming early detection is key to successful management. Some theoretical studies confirm this intuition, while others, which restrict sampling effort to be constant in time, suggest managers are investing too heavily in sampling to detect new local invader populations.

2. We explore whether these optimal constant-effort strategies underplay the importance of early surveillance and determine how much changing sampling effort through time reduces total management costs.

3. Using optimal control theory to calculate time-dependent surveillance policies that minimize the total cost of sampling, eradication, and damage by the invasive, we find that the best strategies often use intense early sampling, followed by reduced sampling effort.

4. Intense early sampling can drastically reduce costs compared with constant-effort strategies if propagule pressure from outside the managed area is low. However, if new infestations arise from frequent independent introductions from an outside source, constant strategies are cost-effective.

5. *Synthesis and applications*. For invasive species that are initially present, not frequently reintroduced into the managed area, and for which surveillance is reasonably cost-effective, we recommend a simple three-phase management programme that deploys intense early surveillance until the majority of undetected populations have been discovered, followed by medium effort until most of the heavily infested areas have been cleared of the invader and finally low long-term effort to prevent infestations caused by future introductions and spread from populations that escaped surveillance. This programme captures the majority of the economic benefits from varying sampling effort continuously through time.

Key-words: bioeconomics, biological invasions, integrated pest management, *Lymantria dispar*, monitoring, population dynamics, transient dynamics

Introduction

Invasive species cause hundreds of billions of dollars of damage to urban infrastructure, agriculture, livestock, fisheries and natural ecosystems (Davis 2009). There is a rich literature describing the optimal management of established invasive species under complete knowledge of population abundance (for a review, see Epanchin-Niell & Hastings 2010). However, only recently has the focus of theoretical invasive species management shifted towards the design of surveillance programmes for invasive species whose distribution is uncertain (e.g. Haight & Polasky 2010; Horie *et al*. 2013; Keith & Spring 2013; Epanchin-Niell *et al*. 2014; Berec *et al*. 2015).

Several theoretical optimal monitoring programmes clash with management intuition. Biologists and managers widely recognize that intense monitoring and early detection are key components of successful invasive species management (Hobbs & Humphries 1995). In fact, 'early detection and rapid response' is one of five main sections of the USA's official *National Invasive Species Management Plan* (National Invasive Species Council 2008). However, for invasive species, such as insect pests in hardwood forests, which are consistently reintroduced from a source outside the manager's control, the theoretical optimal monitoring strategies in the literature suggest

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that managers sample too much (Bogich, Liebhold & Shea 2008; Epanchin-Niell *et al.* 2012). For example, using data on gypsy moth in Washington, Bogich, Liebhold & Shea (2008) found that managers were deploying traps at densities approximately 20 times greater than the ‘optimal’ constant solution. Is nearly 95% of the sampling deployed in Washington really a waste of money? And if so, how general are these results?

Due to model and methodological simplifications, previous optimal monitoring studies, for pests that are regularly reintroduced, have largely restricted surveillance effort to be static in time by explicitly calculating the most cost-effective sampling effort over a fixed management time frame (Bogich, Liebhold & Shea 2008; Epanchin-Niell *et al.* 2014), or by solving for the surveillance effort that maintains the most cost-effective equilibrium pest density (Epanchin-Niell *et al.* 2012). However, when the invasive is present at the beginning of the management programme, intense early surveillance can lead to early intervention, and therefore, we might expect optimal sampling effort to be front-loaded in time. In this case, time-constant strategies could be vastly underestimating optimal sampling effort.

Other theoretical optimal monitoring studies have shown the potential for large economic benefits of an intense initial search for the invader, especially when the end goal is complete eradication (e.g. Mehta *et al.* 2007; Hauser & McCarthy 2009; Fox *et al.* 2009; Cacho *et al.* 2010; Rout *et al.* 2011; McDermott, Irwin & Taylor 2013). However, the costs of using such strategies have not been compared to the cost of using the best constant surveillance effort. Intuitively, if complete eradication is optimal, sampling beyond the point of eradication can unnecessarily increase costs (Regan *et al.* 2006; Rout, Thompson & McCarthy 2009), so it seems rather obvious that time-varying sampling will be especially important in these cases. Yet when reintroductions exist (but are possibly rare), precluding the possibility of total eradication over long time-scales, the above intuition may no longer hold.

In this study, we generate rules of thumb for when intense initial sampling, followed by a sharp decrease in sampling effort, is more cost-effective than strategies that are constant through time. We find that for invaders with high rates of establishment from an outside source, constant strategies are cost-effective. However, when reintroductions exist, but are infrequent, an intense early search for the invader can drastically reduce costs, depending on initial pest prevalence and the economic benefit-to-cost ratio of sampling.

Materials and methods

ECOLOGICAL MODEL

Determining the importance of changing surveillance effort through time is vital for designing cost-effective invasive species management programmes. A rare invader is costly to find, but cheap to control, while an abundant invader is easy to find, but costly to control. Using this trade-off, our model captures the essence of invasive population dynamics and management to propose clear rules of thumb for when intense early sampling is important.

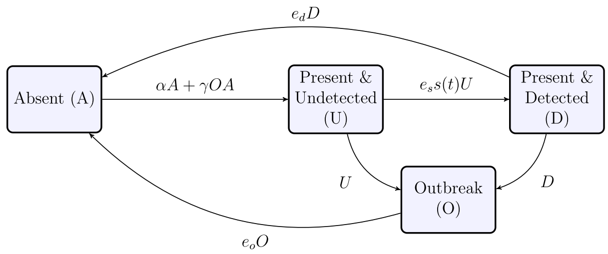

Fig. 1. A flow diagram for the ecological model.

Our model (Fig. 1) considers a landscape of n patches, assuming n is large enough to apply classic metapopulation theory (Etienne 2002). In each patch, the invasive is absent, present but undetected, detected, or present at such high densities and no sampling is required to detect it; we call a patch in the last state an Outbreak. The state variables, $A(t)$, $U(t)$, $D(t)$ and $O(t)$, are the proportion of patches in the Absent, Undetected, Detected and Outbreak states at time t, respectively. In the absence of control, Undetected and Detected patches transition into Outbreaks due to growth of the invasive population. We rescale the model so one time unit is the average time it takes for an Undetected or Detected patch to transition into an Outbreak. We assume Outbreak patches infect Absent patches at rate $\gamma A(t)\ O(t)$, via the law of mass action. Therefore, we call γ the secondary infestation rate, defined as the average number of patches infested by a single Outbreak, over the average lifespan of an Undetected patch, when most patches are Absent. Absent patches can also be infested by an outside source at a constant rate, α. The presence of invasives in Undetected patches is detected via sampling at rate $e_s s(t)$, where e_s is sampling efficacy and $s(t)$ is the *per-patch* sampling effort deployed in Absent and Undetected patches at time t. Detected patches are eradicated at rate e_d. Outbreak patches are also eradicated, but at a slower rate, e_o, as eradicating a large population within a patch is more difficult. These assumptions yield the following:

$$\begin{aligned}
\frac{\mathrm{d}A}{\mathrm{d}t} &= e_o O + e_d D - \alpha A - \gamma O A \\
\frac{\mathrm{d}U}{\mathrm{d}t} &= \alpha A + \gamma O A - e_s s(t) U - U \\
\frac{\mathrm{d}D}{\mathrm{d}t} &= e_s s(t) U - e_d D - D \\
\frac{\mathrm{d}O}{\mathrm{d}t} &= U + D - e_o O
\end{aligned} \qquad \text{(eqn 1)}$$

ECONOMIC MODEL

The assumed goal for the manager is to choose sampling effort, $s(t)$, over a time interval of length T, to minimize the total cost of the invasion, including the costs of sampling, control and the invader’s damage. We assume s_{max} is the maximum sampling effort a manager can deploy at any time. Let k_u be the cost per unit time of the invader’s damage in an Undetected patch, and k_o, and k_d be the sum of the costs of the invasive’s damage and the manager's eradication effort in Outbreak and Detected patches, respectively. Let $f(s)$ be the per-patch cost of deploying s units of sampling effort. All future costs are discounted at rate δ, meaning one dollar now is worth $e^{-\delta t}$ dollars t time units from now (δ is like an interest rate). Therefore, the total discounted cost of the invasion, per patch, is

$$J = \int_0^T e^{-\delta t}[k_u U + k_o O + k_d D + f(s)(A+U)]\mathrm{d}t \qquad \text{(eqn 2)}$$

We assume $f(s) = k_s s + \varepsilon s^2$, where k_s is the per unit cost of sampling. If $\varepsilon = 0$, sampling costs are linear in effort; if ε is small, then sampling costs are approximately linear, until sampling effort reaches such high levels that a scarcity of supplies or labour drives up per-effort costs. In most cases, ε would be much smaller than k_s so that the quadratic term is negligible. However, larger ε's are possible for programmes that require skilled labour, due to diminishing supply and increasing demand for qualified employees.

POSSIBLE SAMPLING STRATEGIES

We compare the economic benefit of deploying four different sampling strategies that are optimal under different constraints on how a manager can change effort through time.

Optimal constant sampling, s_{const}, is the most cost-effective sampling effort, if effort cannot change in time. In other words, it is the level of effort, s_{const}, that minimizes invasion cost J, if $s(t) \equiv s_{const}$.

For any constant sampling effort $s(t) = c$, the proportion of patches in each state will approach and remain at an equilibrium depending on c. We call the value of c that minimizes the total discounted cost of maintaining this equilibrium in the long run, optimal equilibrium sampling, s_{eq}. We refer to the corresponding proportion of Undetected and Outbreak patches as the optimal equilibrium, (U_{eq}, O_{eq}) (for details on calculating equilibrium solutions, see Chapters 1–2 in Conrad & Clark 1987). While optimal equilibrium sampling is a constant-effort strategy, it is unaffected by the length of the management programme and the initial pest density and therefore is at least as costly as optimal constant sampling.

Optimal time-varying sampling is the amount of sampling effort through time, $s(t)$, that minimizes the cost of the invasion, J, assuming sampling effort can change at every moment. The only constraint is that sampling effort is piecewise continuous and bounded between 0 and maximum sampling effort, s_{max}, at all times. For example, this strategy may be constant, change gradually through time or have several discontinuous jumps. We use optimal control theory to calculate which surveillance strategy is most cost-effective over the management time frame. Optimal control theory is a set of methods for determining the best action to take at each time, in a way that minimizes total costs, including the cost of taking an action, the cost of the system state changing in response to that action and the cost of future actions that must be taken due to the resulting system state (see Appendix S1 in Supporting information for the mathematical analysis).

Unfortunately, optimal time-varying sampling must be solved for numerically, and the methods are slow for many parameter combinations, preventing us from feasibly exploring the strategy for all parameters necessary to test the generality of the results. Additionally, because we do not explicitly define the future cost of leaving the landscape with Undetected and Outbreak patches at the end of management, optimal time-varying sampling effort always decreases to zero as time approaches T, as sampling near T incurs costs without producing future benefits. Because constant strategies cannot cease to sample, performance gains from optimal time-varying solutions could be inflated.

To address these issues, we also looked at time-varying sampling effort assuming effort could only change twice, at two specified times. We refer to this strategy as optimal change-twice sampling. To calculate it, we specified two times when effort was allowed to change, t_1 and t_2, and calculated the most cost-effective constant sampling effort over each time interval (0 to t_1, t_1 to t_2 and t_2 to T) using OPTIM in R (R Core Team 2013). This is faster than calculating the optimal time-varying strategy and it is a more practical guideline because managers cannot change surveillance effort continuously through time.

This heuristic strategy is based on a three-phase programme. First, the manager detects most small infestations that already exist. Then, the manager deploys a medium amount of effort to detect new secondary infestations resulting from Outbreaks that have yet to be eradicated. Finally, after eradicating most initial Outbreaks, they detect new introductions and secondary infestations which initially slipped by the detection programme. The two breakpoints separating the three phases are as follows:

$$\begin{aligned} t_1 &= -\ln(1-m_U)/(e_s s_{max}) \\ t_2 &= -\ln(1-m_O)/e_o \end{aligned} \qquad \text{(eqn 3)}$$

where m_U is the proportion of the initial Undetected patches the manager would like to detect in the first phase, if sampling at effort s_{max}. Hence, t_1 is approximately the amount of time it would take to detect m_U proportion of Undetected patches when sampling at effort s_{max}. Similarly, t_2 is the amount of time it takes to eradicate m_O proportion of initial Outbreak patches. We show below that values of m_U and m_O between 0·9 and 0·99 produce simple strategies that come very close to the economic benefits of optimal time-varying sampling over a broad range of parameters.

Additionally, we constrained change-twice sampling, after the second break, to be greater than or equal to the minimum of constant and equilibrium sampling. This ensures economic benefit from using change-twice sampling is not an artefact of ceasing to sample at the end of management.

When comparing the cost of using the above four sampling strategies, we removed the cost of eradicating Outbreaks present prior to management, which is unaffected by sampling. So each strategy costs J for that choice of s, minus $O(0)$ $k_o(1 - \exp\{-(\delta + e_o)T\})/(e_d + e_o)$. We define the proportion of the constant strategy's cost, reduced using time-varying or change-twice sampling, as the *economic benefit* of that strategy.

PARAMETERIZATION

To form a baseline parameterization, we consider management of gypsy moth *Lymantria dispar* an invasive forest pest in the USA that has spread across the north-east. Gypsy moth causes massive defoliation, resulting in economic damage due to tree mortality. It is not well-established on the west coast, and Washington, Oregon and California spend millions of dollars per year sampling to detect and eradicate isolated populations. We used data from California and Washington State's gypsy moth eradication pro-

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grammes and the largest recorded successful eradication in the USA, in Lane County Oregon (a 930 km^2 'Outbreak'), to estimate e_s, k_s, k_o, k_u, e_o and k_d, as displayed in Table 1. Parameters are scaled by area and time, in units 930 km^2 and 13 years, respectively.

We set the initial Undetected and Outbreak patch proportion to match observations during the first five years of Washington state's gypsy moth eradication programme, and let $T = 5$ (65 years) to represent a long but finite management horizon. See Appendix S2, for parameterization details.

We varied the introduction rate, α, based on minimum, median, first and third quartile estimates of establishment rates for all 58 California counties, as reported in Epanchin-Niell *et al.* (2012), rescaled by time and area. No good data exist on gypsy moth spread, so we varied the secondary infestation rate, γ, from 1 to 11. In model (eqn 1), γ is multiplied by the proportion of Outbreak sites, which is always much less than one, so secondary infestations are comparable in importance to external introductions only when γ is substantially larger than α.

To determine how the economic benefit of time-varying sampling is affected by the parameters, we calculated the cost of management using optimal change-twice sampling, constant sampling and equilibrium sampling for four introduction rates (0·0001, 0·001, 0·01 and 0·1), while varying all other parameters randomly, with each parameter spanning multiple orders of magnitude. We generated 1000 parameter combinations, to match with each introduction rate, using a Latin Hypercube design (McKay, Beckman & Conover 1979), with function lhs (Carnell 2012) in R. The ranges for k_u, e_o, e_s and δ are in Table 1. We consider the other parameter values in relation to these parameters. For example, the cost of Detected patches for the i^{th} parameter combination, $k_{d,i}$, is $\beta_i k_{u,i}$, where $k_{u,i}$ is the cost of Undetected patches and β_i is randomly chosen between 1 and 100 (Detected patches are more expensive than Undetected patches, due to eradication costs). Similarly, the cost of Outbreaks is 1–1000 times Detected patch cost, the eradication rate of Detected patches, e_d, is 1–100 times faster than the eradication rate of Outbreaks e_o, the linear per-patch cost of surveillance effort, k_s, is one to seven orders of magnitude less than the cost of an Outbreak, and the local infestation rate is 0·01–100 times the Outbreak eradication rate (all sampled on $\log_{10}$ scale). We show the lowest and highest values for each parameter from the sample in Table 1.

To verify change-twice sampling achieved most of the economic benefit from changing surveillance effort through time, we subsampled 50 parameter combinations from the above analysis, computed the optimal time-varying solution for each value of α and compared the management costs of time-varying and change-twice surveillance.

We repeated the analysis, factorially, for six initial conditions, ($U(0) = 0{\cdot}005$, 0·015, or 0·075, $O(0) = 0{\cdot}005$ or 0·025), and three time horizons (3, 5 and 10). Additionally, we tested initial conditions resulting from simulating an invasion, starting with all patches Absent, until the Outbreak proportion reached 0·02, 0·005, 0·002 or 0·001, which initiated surveillance and control. This yields likely initial conditions for an invasion described by α and γ.

We let $m_U = m_O = 0{\cdot}95$, so that change-twice sampling effort can change after the opportunity to detect 95% of initial Undetected patches and after eradicating 95% of initial Outbreaks. While this choice is arbitrary, we did not see much difference when setting $m_U = m_O = 0{\cdot}9$ or $m_U = m_O = 0{\cdot}99$ (Figs S2–S3, in

Table 1. Variables and parameters. A time unit is 13 years, so per annum rates and costs are those below divided by 13

Symbol	Description	*L. dispar* baseline	Parameter ranges tested
$A(t)$	Proportion of patches where the invader is absent at time t	–	–
$U(t)$	Proportion of patches where the invader is present but undetected at time t	–	–
$O(t)$	Proportion of Outbreak patches at time t	–	
$s(t)$	Per-patch sampling effort in Absent and Undetected patches at time t	–	–
s_{max}	Maximum sampling effort (traps per patch)	3320	$6{\cdot}6 \times 10^2$ to $3{\cdot}3 \times 10^6$
γ	Rate at which Outbreaks infect new patches	varies	$1{\cdot}0 \times 10^{-2}$ to $1{\cdot}0 \times 10^2$
α	Rate at which Absent patches are colonized from an outside source	0·000072, 0·0047, 0·016, 0·042	1×10^{-4} to 1×10^{-1}
e_s	Rate at which a trap detects an Undetected patch	0·1	1×10^{-3} to 5×10^{-1}
e_o	Rate at which Outbreaks are eradicated	3·25	0·5 to 6·5
e_d	Rate at which Detected patches are eradicated	13	1 to 523
k_u	Cost of damage per undetected patch (USD per patch)	$3{\cdot}62 \times 10^4$	$6{\cdot}2 \times 10^2$ to $3{\cdot}6 \times 10^6$
k_o	Cost of damage and control per Outbreak patch (USD per patch)	$8{\cdot}88 \times 10^7$	$3{\cdot}3 \times 10^5$ to $1{\cdot}1 \times 10^{12}$
k_d	Cost of damage and control per Detected patch per unit time (USD per patch)	$5{\cdot}83 \times 10^5$	$8{\cdot}8 \times 10^4$ to $3{\cdot}1 \times 10^9$
k_s	Cost per unit of sampling effort (USD per trap)	$6{\cdot}46 \times 10^2$	1×10^{-2} to $8{\cdot}4 \times 10^9$
T	Length of management time frame	5 (65 years)	3, 5, 10
ε	Weighting of quadratic sampling cost	0·04	$7{\cdot}9 \times 10^{-8}$ to $2{\cdot}5 \times 10^6$
δ	Discount rate	0·13	0 to 0·4

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Appendix S3). The precise choice of t_1 and t_2 is likely unimportant, as long as t_1 is small enough that most of the initial Undetected patches can be detected.

Results

The optimal time-varying strategy, regardless of parameters, is to initially sample (or avoid sampling) such that the Outbreak patch proportion quickly approaches the optimal equilibrium and then to sample at a constant rate to maintain this equilibrium, ultimately ceasing to sample as the end of management approaches (see Fig. 2a for a typical example, and Fig. S1a,c).

If Undetected and Outbreak patches are initially above their optimal equilibrium values, then optimal time-varying sampling is characterized by a period of intense early sampling, followed by a drastic reduction in effort (Fig. 2a, black dotted curve, and Fig. 2b,c for the corresponding patch dynamics). However, if the initial Undetected and Outbreak patch proportion is lower than at the optimal equilibrium, it can be optimal to avoid sampling at first, wait until patch proportions approach equilibrium, and then drastically increase sampling effort towards equilibrium effort (Fig. S1). This happens when sampling is cost-inefficient at low densities (high values of k_s or low values of e_s, Fig. S1c), or the eradication of local Outbreaks is inexpensive or there are zero Undetected patches at the beginning of the management period (Fig. S1a,b). Although waiting to sample is optimal in these cases, it provides relatively little economic benefits over optimal constant sampling. However, when intense early sampling is optimal, this strategy can drastically reduce management costs compared with optimal constant and equilibrium strategies (e.g. Fig. 2d).

For the baseline parameterization corresponding to surveillance and management of gypsy moth, both the secondary infestation rate, γ, and introduction rate, α, are key to determining the economic benefits of time-varying sampling. With the introduction rate equal to the minimum estimate over all California counties, $\alpha = 0{\cdot}00072$, intense initial sampling can reduce management costs by over 50% relative to constant sampling (circles in Fig. 3a). However, if α is the first, second or third quartile of county estimated introduction rates, there is less than a 20% reduction in costs (other symbols in Fig. 3a).

As introduction rates or secondary infestation rates increase, time-varying sampling becomes less important. This is because increasing α flattens time-varying sampling effort as a function of time (compare plots, left to right, within each row of Fig. 4). Additionally, increasing α or γ increases sampling effort, so as these parameters increase, long-term effort gets closer to the high initial effort, mak-

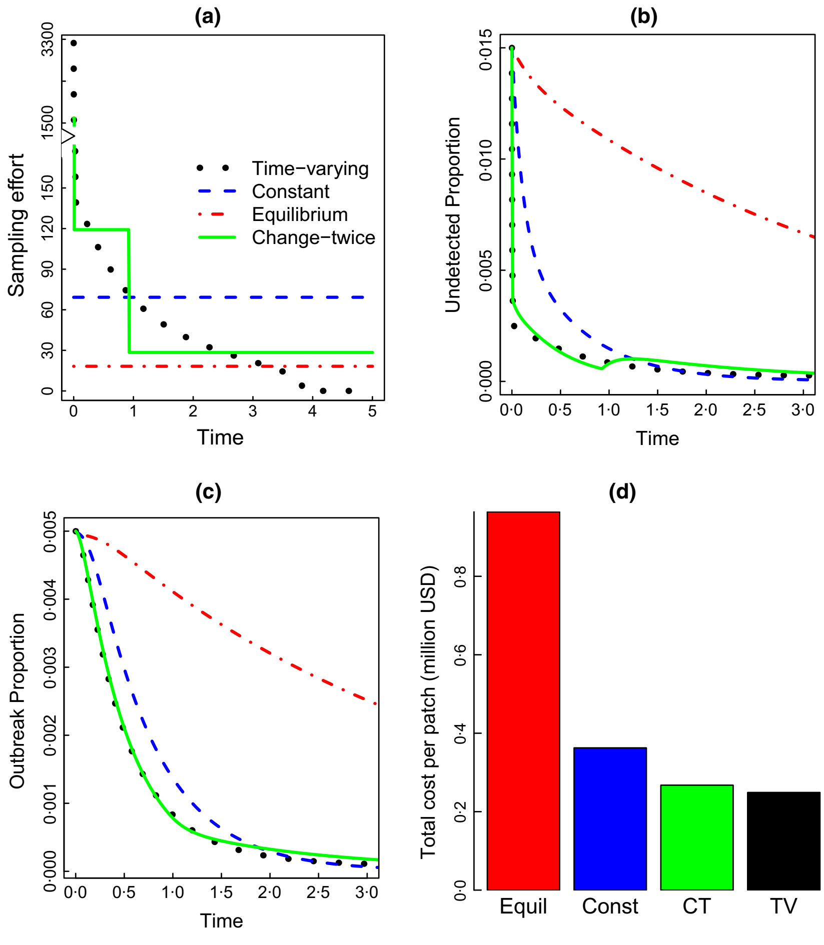

Fig. 2. (a) Per-patch sampling effort vs. time for time-varying (dotted), equilibrium (dot dashed), constant (dashed), and change-twice (solid) strategies. (b) The corresponding dynamics of the proportion of Undetected patches and (c) Outbreak patches. (d) The total per-patch cost (including the cost of damage, sampling and control), in USD, when using the optimal equilibrium, constant, change-twice and time-varying sampling strategies. Parameters are $\alpha = 0{\cdot}000072$, and $\gamma = 9$, with the rest equal to their baseline values (see Table 1).

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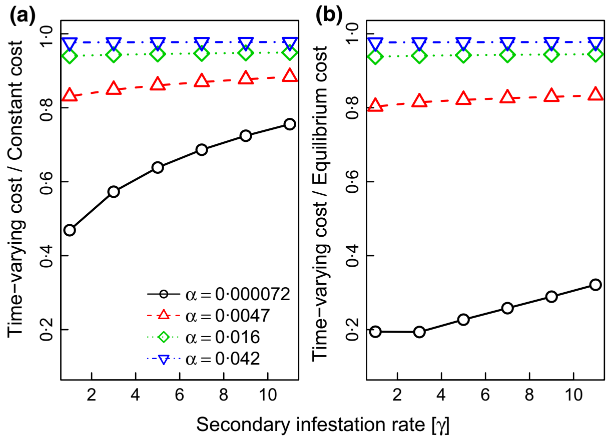

Fig. 3. Per-patch cost of managing gypsy moth using optimal time-varying sampling divided by (a) the cost of using optimal constant and (b) optimal equilibrium sampling vs. the secondary infestation rate, γ, for four introduction rates: the minimum (○), first quartile (△), median (◇), and third quartile (▽) of estimated rates across all Californian counties. Other parameters are the baseline values in Table 1.

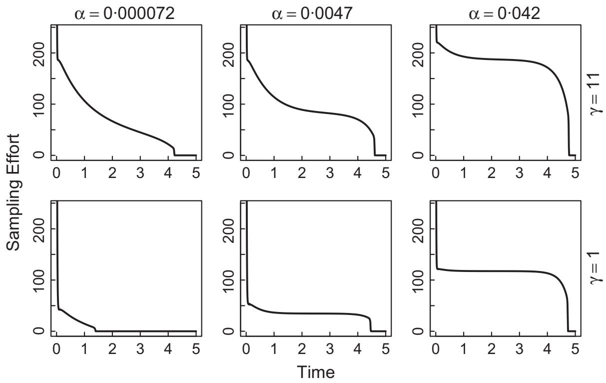

Fig. 4. Optimal time-varying sampling effort for different introduction rates, α (columns), and secondary infestation rates, γ (rows), with other parameters at the baseline. We cut the vertical axis at 250 for display purposes, but initial sampling effort is close to s_{max} for all plots.

ing the optimal strategy effectively more constant (compare plots within each row and bottom to top, within each column of Fig. 4). Combining the results from Figs 3 and 4, we see that changing sampling effort through time is most important when only a minimal amount of surveillance is required to manage the population in the long run. When a pest spreads or is introduced at very high rates, time-varying sampling is not as important because a manager should allocate effort closer to the maximum allowable level at all times.

The economic benefit of time-varying sampling compared with optimal equilibrium sampling is similarly affected by α, and γ; however, it performs considerably worse than the best constant strategies (compare Fig. 3a to b).

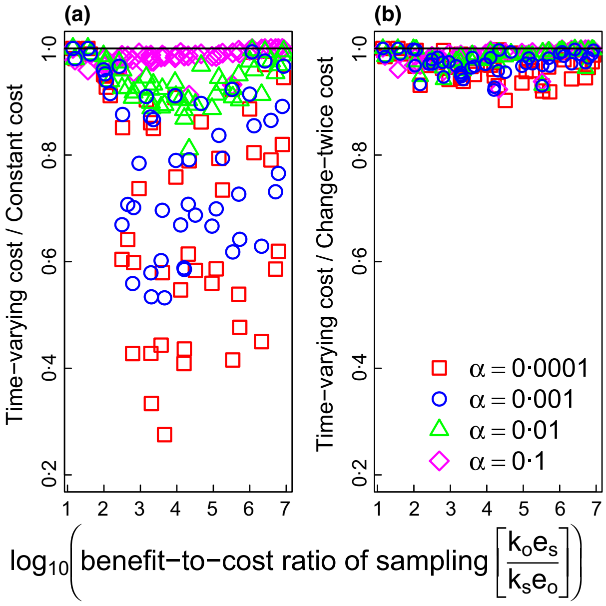

Fig. 5. Per-patch cost of deploying optimal time-varying sampling divided by the cost of optimal constant sampling vs. the benefit-to-cost ratio of sampling $k_o e_s/(k_s e_o)$, on log $_{10}$ scale, for 50 randomly sampled parameter combinations from the global sensitivity analysis, for α = 0·0001 (□), α = 0·001 (○), α = 0·01 (△), and α = 0·1 (◇). (b) Time-varying cost divided by change-twice cost for the same parameter combinations. All values are close to one, meaning change-twice and time-varying strategies are almost equally cost-effective.

GENERALITY OF THE RESULTS

Justification of the change-twice strategy

It is infeasible to compute the optimal time-varying strategy for a large sample of parameter values, so instead, we compared the change-twice strategy with constant-effort strategies. While the change-twice strategy has the potential to under-estimate the benefit of time-varying sampling, we found that this is negligible. Optimal time-varying strategies, computed for a random subsample of the parameters used in the below global sensitivity analysis, reduced costs by up to 75% over the best constant strategies (Fig. 5a), but they never generated more than a 9% cost reduction over the optimal change-twice strategy (Fig. 5b).

Effect of the parameters

When fixing the management time horizon and initial conditions to the baseline values, but varying all other parameters randomly, for four values of the introduction rate (α = 0·0001, α = 0·001, α = 0·01, and α = 0·1), we found that the qualitative trends reported for the gypsy moth parameterization hold across a wide range of parameter space. If the introduction rate is low, there can be major economic benefits to changing sampling in time (Fig. 6a,b). The shading in these figures indicates the cost ratio of managing the invasion using change-twice

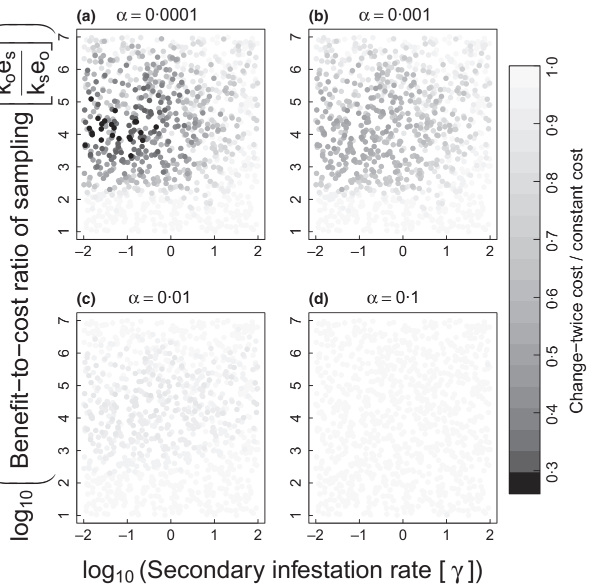

Fig. 6. Per-patch cost of using optimal change-twice sampling divided by the cost of using the best constant strategy, for introduction rates: (a) $\alpha = 0{\cdot}0001$, (b) $\alpha = 0{\cdot}001$, (c) $\alpha = 0{\cdot}01$, (d) $\alpha = 0{\cdot}01$. Other parameters are random, with each circle representing a single parameter combination. Dark circles represent parameters where change-twice sampling generates large cost savings over constant sampling. The vertical axis is the benefit-to-cost ratio of sampling, $k_o e_s/(k_s e_o)$, on $\log_{10}$ scale. A value of 3, for example, means that the expected cost of Outbreak management is three orders of magnitude greater than the cost of sampling effort per detection. The horizontal axis is the secondary infestation rate, γ, on log $_{10}$ scale.

sampling effort versus using the best constant-effort strategy. The darkest points in these figures correspond to a 62% cost reduction using the change-twice strategy, while the lightest points correspond to no cost reduction from changing sampling effort in time. When the introduction rates are low, there are many dark points (Fig. 6a,b). For high introduction rates, there is little value in changing sampling effort (all points are light in Fig. 6c,d).

For lower introduction rates, the importance of changing sampling effort depends critically on the secondary infestation rate, γ, and the benefit-to-cost ratio of sampling, $k_o e_s/(k_s e_o)$, an aggregate parameter measured in the per unit cost savings of preventing Outbreaks, k_o/e_o, divided by the cost-efficacy of sampling k_s/e_s.

As in the baseline parameterization, increasing γ decreases the importance of changing sampling in time (change in shading along the horizontal direction in Fig. 6a,b).

Time-varying sampling is most beneficial for intermediate benefit-to-cost ratios. When the benefit-to-cost ratio of sampling is low (i.e. sampling is expensive or only effective at high effort, or Outbreak eradication is fast or cheap), sampling is avoided until the pest is in so many patches that sampling becomes cost-effective. This creates a high-equilibrium infested patch proportion, and sampling is not very important (light shading along the bottom of Fig. 6a,b). When the benefit-to-cost ratio of sampling is high, sampling is so valuable that the manager in some instances should always deploy high amounts of effort, not just initially, and hence, time-varying sampling gradually becomes less important as the benefit-to-cost ratio of sampling increases to extreme values.

When comparing change-twice sampling to equilibrium sampling, the results are qualitatively similar to Fig. 6, but equilibrium sampling is even more costly than constant sampling (up to 5 times more costly, Fig S2). This agrees with the cost inefficiencies of equilibrium sampling compared with the optimal constant and time-varying sampling for gypsy moth (Fig. 2d and compare the black circles in Fig. 3a to b).

Effect of the time horizon and initial conditions

The length of the management period does not affect the qualitative results in Fig. 6, although changing sampling effort is more important for longer management periods (Figs S9–S24).

The qualitative results in Fig. 6 held for all six fixed initial conditions tested (Figs S9–S24). However, when setting the initial Undetected patch proportion to its value at the end of a simulated invasion process, terminated when 0·005 proportion of the landscape was Outbreak patches, changing sampling effort in time is unimportant for the lowest secondary infestation rates (Fig. 7). This is because slow spread leads to too few Undetected patches at the beginning of a management programme for intense initial sampling to matter. These qualitative findings were not sensitive to the Outbreak threshold triggering management (Figs S5–S8).

UNKNOWN INITIAL FREQUENCY OF THE INVASIVE

When a manager develops sampling protocols, the extent of the invasion is usually unknown. There are two likely scenarios (1) the invader might be present but it has not been detected or (2) an Outbreak has been reported but the presence of smaller populations is uncertain.

In case (1), even if the invasive is present with small probability, time-varying sampling is less costly than the best constant strategy. For example, suppose that a manager (correctly) estimates there is a probability P of the invasive being present in three of 200 patches, and otherwise it is completely absent. Given the gypsy moth parameterization, with $\gamma = 2$ and $\alpha = 0{\cdot}0005$, even if P is as low as 0·1 it is still less costly on average to deploy intense early sampling, as if the species was initially present with absolute certainty, than to sample at the optimal equilibrium or best constant rate (Fig. 8a). This is despite the fact that the constant strategy has perfect knowledge of P, while the time-varying strategy incorrectly assumes $P = 1$.

In case (2), intense initial sampling can be beneficial, even when the Outbreak is the only infested patch. For

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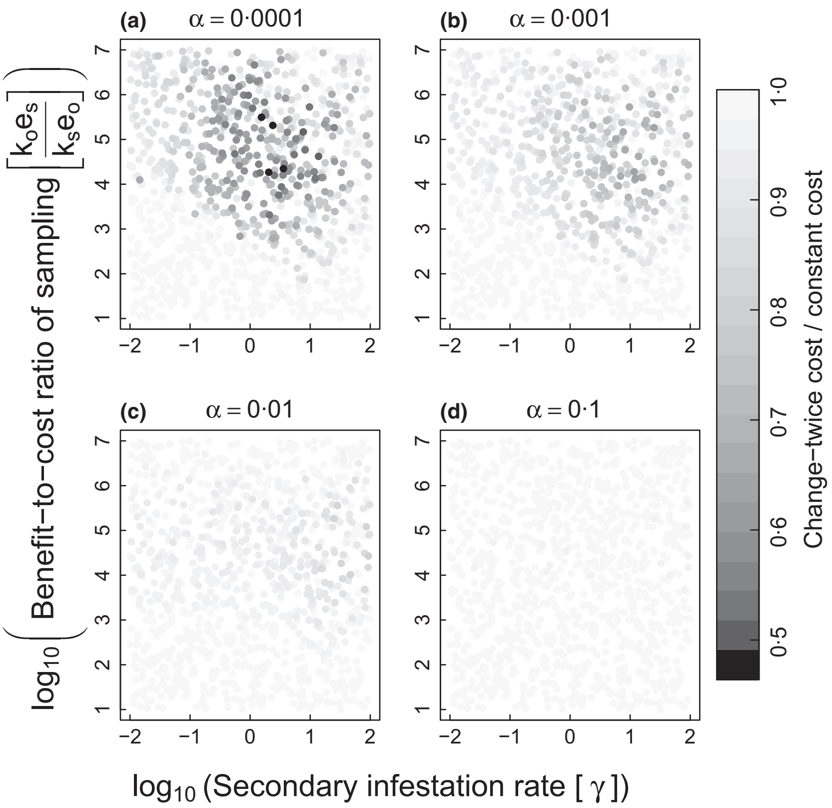

Fig. 7. Cost of change-twice sampling relative to the cost of constant sampling, with axes and shading as in Fig. 6. Unlike Fig. 6 where the initial condition was set to the baseline value, in this figure, the initial condition is the result from simulating the invasion with all patches initially Absent, using introduction rate α, and secondary infestation rate γ, until there was a 0·005 Outbreak proportion.

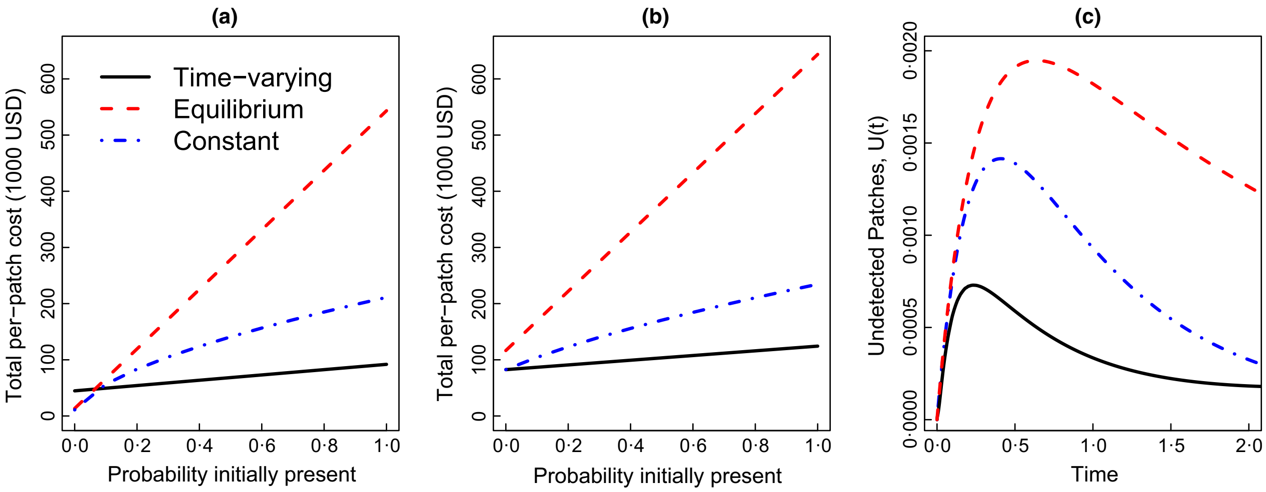

Fig. 8. (a) The expected per-patch cost of management, with an initial landscape of 1·5% Undetected patches with probability P and Absent of the invader with probability $1-P$, under the optimal equilibrium (dashed), the best constant (dot dashed), and time-varying (solid) strategy, vs. P. (b) The expected per-patch cost of management assuming an initial landscape with 0·5% Outbreaks and additionally, with probability P, 1·5% Undetected patches, vs. P. (c) The corresponding Undetected patch dynamics vs. time corresponding to the description in (b) with $P = 0$. The parameters are $\gamma = 2$, $\alpha = 0{\cdot}0001$, and the rest as in Table 1.

example, consider one Outbreak of 200 patches and three Undetected patches with probability P and no Undetected patches otherwise. Given the gypsy moth parameterization with $\gamma = 2$ and $\alpha = 0{\cdot}0005$, even if $P = 0$, it is still more cost-effective on average to deploy intense early sampling than sample at the best constant rate (Fig. 8b). The reason for this is that with an Outbreak patch initially present, even though the intense early sampling strategy overspends to detect non-existent initial Undetected patches, it is able to prevent a build-up of Undetected patches resulting from the Outbreak (Fig. 8c).

Discussion

Recent studies on the optimal control of widespread invasive species show that non-uniform monitoring and eradication effort allocated across space (Hauser & McCarthy 2009; Chadès *et al.* 2011; Baker & Bode 2013, 2015) and time (Chadès *et al.* 2011; Baker & Bode 2015; Bode, Baker & Plein 2015) can greatly improve management outcomes. We have shown that by front-loading effort at the beginning of a management programme, similar benefits can be achieved when sampling to detect rarer invasive species.

When first establishing an early detection surveillance programme, intensive initial sampling, followed by reduced sampling effort is optimal so long as the pest is initially present, and sampling is reasonably cost-effective. In such cases, when the invasive is infrequently reintroduced from an outside source, time-varying sampling can reduce costs by up to 80% compared to the best constant strategies.

When the invasive is frequently reintroduced, the best constant-effort strategies perform near optimally. As a rule of thumb, if the invasive establishes in 1% of patches or more due to introductions from an outside source over the average time required for an Undetected patch to transition into an Outbreak, time-varying strategies never reduce costs by more than 20% over constant-effort costs. This held over the nearly 100 000 cases tested in our sensitivity analysis. For example, using the gypsy moth parameterization, constant-effort searches will be cost-effective if the moth is introduced into one of 200 available patches in Washington every 6·5 years (half the time for transition to an Outbreak). This is satisfied for most managed areas in the USA due to frequent, loosely regulated human travel from the heavily infested east coast. Therefore, the restriction to constant surveillance strategies for gypsy moth on the west coast of the USA (Bogich, Liebhold & Shea 2008; Epanchin-Niell *et al.* 2012) is likely justified. As these sampling rates are much lower than what is deployed in Washington (Bogich, Liebhold & Shea 2008), it is possible that Washington's managers were sampling too intensely.

In the above example, the unit of management was over 100 000 km^2. For smaller units of management, introduction rates can be more variable. While gypsy moth introduction rates are high on average, the lowest introduction rate across all California counties is low enough for constant strategies to perform poorly within this county, if it were infested.

For *Anoplophora glabripennis* Asian long-horned beetle, new introductions into US forest ecosystems are less frequent (Haack *et al.* 2010). Hence, as long as surveillance is cost-effective, optimal constant-effort strategies would underestimate initial surveillance and drastically increase management costs. Intense initial sampling may also be important for the management of *Hydrilla verticillata*, an invasive aquatic weed, within an isolated watershed (Langeland 1996). In 2011, a small Outbreak was reported in an inlet to Cayuga lake, NY. During the following 3 years, surveillance led to the detection of several infestations. Our results suggest that sampling should continue at high levels until local Outbreaks have been eradicated. As hydrilla is uncommon in New York, introductions are likely infrequent, and time-varying effort could reduce management costs.

When high initial surveillance effort is important, we showed that the optimal strategy can be approximated by a simple heuristic. Therefore, a manager need not solve a complicated optimal control problem. They can simply break the surveillance programme into three phases: (i) a high-effort phase, at the beginning of the management period, to detect most of the initial small infestations formed prior to management, followed by (ii) a medium-effort phase, to detect new secondary infestations resulting from Outbreaks that have yet to be eradicated and finally, after most of the initial Outbreaks are eradicated, (iii) a maintenance phase, to detect new introductions and secondary infestations that slipped by the initial surveillance programme and transitioned into Outbreaks.

If the introduction rate is nearly zero, and the pest spreads slower than the Outbreak eradication rate, complete eradication, or the maintenance of a tolerable low infestation density without any long-run sampling effort, is possible. As the introduction or secondary infestation rate increases, the maintenance phase includes more surveillance effort, until finally constant-effort strategies are relatively cost-effective.

The three-phase programme achieves nearly all of the economic benefits achieved by the optimal time-varying strategy. Luckily, minimizing management costs with respect to three numbers (the amount of sampling in the three phases) can be done using a variety of software packages.

The biggest limitation of our model is that it does not incorporate spatial details with respect to costs and local spread. This means the model is inappropriate for determining where to allocate effort. It also means that we could be over- or underestimating optimal total, spatially averaged, sampling effort if there are large variations in the economic benefit of surveillance through space (as in Hauser & McCarthy 2009; Epanchin-Niell *et al.* 2012). Therefore, our model is most applicable to small-scale management areas where costs are more homogeneous, and where the pest can potentially move between all locations within the region during a short amount of time.

Despite the model's limitations, our guidelines are robust to changes in model parameters, initial conditions and management time frames and are important because scientists have used constant-effort optimization to advocate the adoption of invasive species surveillance programmes (Epanchin-Niell *et al.* 2014). Such optimization will be appropriate for systems with high introduction rates, or where a high-effort search for the invader has already taken place (e.g. Epanchin-Niell *et al.* 2014). However, in other cases, constant-effort optimization will greatly underestimate the economic benefit of surveillance

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programmes, and therefore undersell the importance of funding such programmes. In this paper, we showed that front-loading surveillance effort at the beginning of an invasive species management programme can lead to major cost savings over constant strategies when introduction rates are low, the pest is likely present and surveillance is reasonably cost-effective.

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Data accessibility

Data have not been archived because this article does not contain data.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Mathematical analysis.

Appendix S2. Baseline gypsy moth parameterization.

Appendix S3. Supplementary figures.