

LETTER

Optimal surveillance and eradication of invasive species in heterogeneous landscapes

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Abstract

Cost-effective surveillance strategies are needed for efficient responses to biological invasions and must account for the trade-offs between surveillance effort and management costs. Less surveillance may allow greater population growth and spread prior to detection, thereby increasing the costs of damages and control. In addition, surveillance strategies are usually applied in environments under continual invasion pressure where the number, size and location of established populations are unknown prior to detection. We develop a novel modeling framework that accounts for these features of the decision and invasion environment and determines the long term sampling effort that minimises the total expected costs of new invasions. The optimal solution depends on population establishment and growth rates, sample sensitivity, and sample, eradication, and damage costs. We demonstrate how to optimise surveillance systems under budgetary constraints and find that accounting for spatial heterogeneity in sampling costs and establishment rates can greatly reduce management costs.

Keywords

Biological invasions, cost efficient, detection, eradication, gypsy moth, *Lymantria dispar*, monitoring, pest management, resource allocation, risk management.

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INTRODUCTION

Invasive species threaten ecosystem stability worldwide (Simberloff 2000; Pimentel *et al.* 2001), and may inflict sizable economic damage, including expenditures for control and losses of market and non-market benefits (Aukema *et al.* 2011). For example, the invasion of the emerald ash borer (*Agrilus planipennis* Fairmaire) in the United States alone is expected to cost homeowners and municipalities nearly \$10 billion over the next decade for landscape tree treatment or removal (Kovacs *et al.* 2010). Unintentional introductions of non-indigenous species are by-products of international travel and trade, and cumulative numbers of established species continue to rise despite regulatory measures designed to prevent introductions (Aukema *et al.* 2010). Enhanced efforts to detect and eradicate newly established species are critical to reducing their ecological and economic harms (Lodge *et al.* 2006).

In resource management, integrating monitoring and treatment is important to ensure maximum utility of the resulting information (Nichols & Williams 2006; McDonald-Madden *et al.* 2010). Monitoring is coupled with treatment in adaptive management frameworks to gather information and reduce uncertainty about resource dynamics (Walters & Hilborn 1976; Probert *et al.* 2011; Williams 2011). Monitoring also is used to reduce uncertainty about the state of a resource and improve the quality of treatments, with applications in erosion control (Tomberlin & Ish 2007), environmental compliance (White 2005) and endangered species management (Chadès *et al.* 2008). A wide range of modeling tools are available for designing and evaluating post-border surveillance systems for biosecurity

(Hester *et al.* 2010), although few integrate monitoring and management activities.

Cost-effective surveillance systems for invasive species must balance the intensity and cost of surveillance with the costs of eradicating newly detected populations. Greater surveillance effort requires larger upfront investment, but increases the likelihood of detecting invasions earlier when they are less costly to control and cause less damage (Epanchin-Niell & Hastings 2010). Conversely, lower surveillance effort may increase the resources available for eradication, but increase the chance that invasions are large and difficult to deal with when detected. Previous studies accounting for these trade-offs have provided important insights about factors that influence optimal levels of surveillance. Their applicability to optimising surveillance efforts for real-world biosecurity concerns depends on underlying assumptions about the invasion process and the decision-making environment, which differ across studies.

Mehta *et al.* (2007) optimised surveillance for an invasive population, assuming that costs and damages increased with delayed detection. Homans & Horie (2011) optimised surveillance for small populations establishing ahead of an advancing front; they embedded a model of optimal post-detection management and examined how optimal surveillance differed with distance from the invasion front. In contrast to these studies, Bogich *et al.* (2008) assumed that the likelihood of detecting a population increases with population size. These three studies all assumed that the number and size of target populations is known, which is not often the case for biosecurity surveillance systems.

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While previous approaches employed dynamic optimisation methods, Hauser & McCarthy (2009) developed a static model to optimise one-time surveillance effort across multiple sites when species' presence is uncertain prior to detection, accounting for heterogeneity in species presence and detectability across sites. Their approach considers species' presence or absence and defines a parameter that captures all future costs and damages from failing to detect the species when present. They found this parameter to be among the most important determinants of optimal surveillance effort. While this parameter may be difficult to estimate in practice, this approach allowed the authors to derive elegant analytical solutions for optimal one-time surveillance and to suggest important insights.

Here, we present a new model for designing optimal long-term surveillance programs for high concern invasive species, to minimise the total costs of preventing their long-term establishment and spread. Our motivation is to include additional features of the management environment that are not included in previous work. Specifically, our model allows for (1) repeated invasion events over time, (2) stochastic invasion establishment and detection, (3) unknown number, size, and location of populations prior to their detection and (4) increasing detectability and costs with increasing population size. In addition, our model provides significant flexibility for adaptation to designing surveillance for specific invaders and is based on mechanistic processes, facilitating parameterisation.

We use the model to show how optimal surveillance intensity and management costs depend on population establishment rates, rates of spatial expansion by local populations (which we refer to henceforth as growth rate), sample sensitivity, and sample, eradication, and damage costs. We further develop the approach to optimise surveillance across heterogeneous landscapes, allowing for a region-wide budget constraint, and illustrate an application by designing an optimal surveillance program for gypsy moth (*Lymantria dispar*) in California, USA.

PROBABILISTIC SIZE CLASS MODEL OF POPULATION DYNAMICS

Consider a large region in which new populations of a non-native pest are establishing from an outside source. The region-wide rate at which new, isolated populations establish is known and consistent, but the actual arrival of new populations is random in both space and time, such that the number, size, and location of populations on the landscape at any point in time are unknown. We assume that each population occupies a circular area that grows radially at a known rate. To find populations, surveys are conducted at regular (e.g. annual) intervals. Each survey consists of a number of samples (e.g. visual assessments or traps) distributed at random over the surveyed region and at a cost dependent on sampling intensity (e.g. hours of field work or number of traps deployed). For each sample that intercepts a circular population, the population is detected with a probability that depends on the sensitivity of the sampling method. When a population is detected, we assume it is successfully eradicated, at a cost dependent on the population's area. If no samples intercept a particular population or if all intercepting samples fail to detect it, that population continues to grow. Knowledge of the rates of population establishment and spread, and the probability of detecting a population when intercepted by a sample, allows calculation of the steady-state probability distribution of population sizes and numbers for any potential long-term sample den-

sity. Thus, we can determine the constant, long-term sample density that minimises the total expected costs of surveillance, eradication, and damages over time. This approach simplifies a complex dynamic problem by solving for its optimum equilibrium solution.

We define S as the set of potential population size (or age) classes, $S = \{1, 2, \dots, S_{\max}\}$, where $a(s)$ is the area occupied by a population of size class s . The area $a(s)$ can be modeled by an appropriately parameterised growth function. For practical applications, this may be the most difficult factor to estimate accurately, as most invasive species populations are controlled following discovery and their age is rarely known. The maximum size class, S_{\max} , should be chosen to represent the maximum acceptable size for a population to achieve before detection, based on factors such as the likelihood of eradication success or likelihood of propagating new populations. We define G as the set of possible numbers of populations of each size class, $G = \{0, 1, 2, \dots, G_{\max}\}$, where G_{\max} is greater than the highest number of populations likely to ever establish in a single time period. We then define x_i^s as the probability of there being $i \in G$ populations of size $s \in S$ on the landscape, X^s as a row vector of the probabilities x_i^s .

We assume that establishment of new populations is stochastic with an average rate b , such that the probability distribution of the number of new populations (of size class $s = 1$) can be described by a Poisson distribution with mean and variance b :

$$x_i^1 = \frac{b^i}{i!} e^{-b} \quad \forall i < G_{\max} \quad (1)$$

$$x_i^1 = 1 - e^{-b} \sum_{k=0}^{G_{\max}-1} \frac{b^k}{k!} \quad i = G_{\max} \quad (2)$$

We assume implicitly that the establishment rate b is determined by a combination of site conditions and propagule pressure from outside the survey area. This rate may be estimated based on observed historical establishments or knowledge of introduction pathways and success likelihoods (e.g. Work *et al.* 2005).

We define $p_{i,j}^s(d)$ ($i, j \in G$) as the probability of transitioning from i populations of size class s to j populations of size class $s + 1$ in the following time period, and $\mathbf{P}^s(d)$ is a matrix of transition probabilities $p_{i,j}^s(d)$. These transition probabilities are functions of sample density, d . In the absence of detection, all populations of size class s transition to size class $s + 1$ in the following time period. However, with sampling effort, some populations may be detected and controlled in each time period. Our model assumes that all populations are eradicated following detection, as this is the primary objective of most surveillance programs; surveillance provides few benefits if control methods are not available for the target species.

The probability of detecting each population on the landscape depends on sample density d , population size $a(s)$ and sample sensitivity y . We define sample sensitivity as the probability that a sample detects a population when placed within the population's boundaries, which can depend on sampling technology or methods, characteristics of the species (e.g. its crypticness or population density) and characteristics of the landscape (e.g. grassland or shrub; Hauser & McCarthy 2009). Because we assume that both sample placement and population establishment are random in space, the probability that at least one sample will fall within the range of an isolated population and detect that population equals $1 - \exp[-da(s)y]$. Thus,

in common with past studies (e.g. Mehta *et al.* 2007; Hauser & McCarthy 2009), the probability of failing to detect an invading population declines exponentially with sampling effort and sample sensitivity. Here, it also declines with population size (e.g. Bogich *et al.* 2008). This pattern is consistent with empirical data (Moore *et al.* 2011).

For a given trap density d , detection of each population of size class s can be viewed as a Bernoulli trial with probability $1 - \exp[-da(s)y]$ of success. Thus, the probability $p_{i,j}^s(d)$ of transitioning from i populations of size class s to j populations of size class $s + 1$, which equals the probability of detecting $i-j$ of i populations, is specified as

$$p_{i,j}^s(d) = \binom{i}{i-j} (1 - e^{-a(s)d})^{(i-j)} (e^{-a(s)d})^j \quad \forall j \leq i, \forall s < S_{\max} \tag{3}$$

$$p_{i,j}^s(d) = 0 \quad \forall j > i, \forall s < S_{\max} \tag{4}$$

We construct the matrix $\mathbf{P}^s(d)$ from these probabilities for each $s < S_{\max}$.

The invasion and detection process described above is a Markov process: the probability of being in a given state in one time period depends only on the probability of each state in the previous time period and the choice of control. The row vector X^s of state probabilities x_i^s (for any state $s > 1$) is thus calculated as

$$X^s = X^1 \prod_{k=1}^{s-1} P^k(d) \quad \forall s > 1 \tag{5}$$

and defines the equilibrium probability distribution of the number of populations of size class s under constant sampling density d .

DETERMINING OPTIMAL SAMPLE DENSITIES

We consider four component costs in calculating total invasion management costs: costs of sampling for populations, costs of eradicating populations, damages associated with established populations and costs associated with failing to detect and eradicate a population prior to it achieving size class S_{\max} . We define $C_s(d, A)$ as the surveillance (or sampling) cost associated with sample density d applied over the surveyed region of area A . We define $C_e(a(s))$ to be the cost of eradicating a population of size $a(s)$. This includes all expected costs associated with eradication, including delimitation, treatment, monitoring, quarantine, public relations and follow-up costs. In a given time period, the probability of detecting (and eradicating) k populations of size class s equals $\sum_{i=k}^{G_{\max}} x_i^s p_{i,i-k}^s(d)$. The total expected number of eradicated populations of size s thus equals $\sum_{k=0}^{G_{\max}} k \sum_{i=k}^{G_{\max}} x_i^s p_{i,i-k}^s(d)$. Across all size classes, the total expected costs of eradication in a given time period are

$$E(TC_{erad}) = \sum_{s=1}^{S_{\max}-1} C_e(a(s)) \sum_{k=0}^{G_{\max}} k \sum_{i=k}^{G_{\max}} x_i^s p_{i,i-k}^s(d) \tag{6}$$

We define $C_d(a(s))$ to be the expected damage costs caused by a population of size $a(s)$. In a given time period, the total expected damages across all size classes equal

$$E(TC_{damage}) = \sum_{s=1}^{S_{\max}-1} C_d(a(s)) \sum_{k=0}^{G_{\max}} k x_k^s \tag{7}$$

Our model also includes a penalty cost, c_{fail} , associated with failing to detect and eradicate a population prior to its reaching the maximum size class (S_{\max}). This penalty cost is designed to encompass the range of costs associated with large populations, which may have greater probabilities of spawning new populations, being ineradicable, incurring trade bans or causing large damages. This cost also includes the potentially very high cost of eradication efforts when the population eventually is detected. This cost should be set large enough to ensure a high probability of eradicating populations prior to achieving size class S_{\max} , as S_{\max} is defined as the largest acceptable size class for a population to reach prior to detection and control. The total expected penalty cost associated with large populations is

$$E(TC_{penalty}) = c_{fail} \sum_{k=0}^{G_{\max}} k x_k^{S_{\max}} \tag{8}$$

Having accounted for the costs associated with large populations, we assume perfect detection and removal of populations of size class S_{\max} to avoid double counting of eradication or damage costs:

$$p_{i,j}^{S_{\max}}(d) = 1 \tag{9}$$

$$p_{i,j}^{S_{\max}}(d) = 0 \quad \forall j > 0 \tag{10}$$

The objective is to choose the sample density (d^*) that minimises the sum of expected surveillance costs, eradication costs, damage costs and the penalty costs associated with failing to detect and eradicate large populations:

$$TC(d) = C_s(A, d) + \sum_{s=1}^{S_{\max}-1} C_e(a(s)) \sum_{k=0}^{G_{\max}} k \sum_{i=k}^{G_{\max}} x_i^s p_{i,i-k}^s(d) + \sum_{s=1}^{S_{\max}-1} C_d(a(s)) \sum_{k=0}^{G_{\max}} k x_k^s + c_{fail} \sum_{k=0}^{G_{\max}} k x_k^{S_{\max}} \tag{11}$$

We do not need to choose a discount rate because we focus on equilibrium dynamics.

Application of this framework to a single region implicitly assumes that the invasion processes and costs are homogeneous across the survey area. However, invasion processes and costs may vary in space. Such heterogeneities can be accounted for by optimising surveillance across subregions, defined as discrete areas that represent similar population establishment and growth rates, costs, damages and sampling sensitivity. Our framework does not require that subregions are equally sized, but they should be substantially larger than the largest acceptable population size, S_{\max} .

Consider a survey area composed of N subregions, with each subregion indexed by $n \in \{1, 2, \dots, N\}$. We then choose the optimal sample density d_n^* for each subregion to minimise the total management costs across all subregions:

$$\min_{d_n} \sum_{n \in \{1, 2, \dots, N\}} TC_n(d_n) \tag{12}$$

where all parameters are indexed by subregion n . If a budget constrains surveillance efforts, the following constraint is imposed:

$$\sum_{n \in \{1,2,\dots,N\}} C_{s_n}(d_n, A_n) \leq B \quad (13)$$

where B is the total region-wide annual surveillance budget.

Model complexity prevents derivation of analytical solutions to this optimisation problem, so we solve for optimal sample densities numerically as a constrained optimisation using the 'fmincon' solver in Matlab R2010b (The MathWorks, Inc.) with an interior point algorithm.

MODEL BEHAVIOUR

To apply this model, functional forms and parameter values must be defined to represent the specific system being modeled. To illustrate the general behaviour of the model we define arbitrary, albeit reasonable, functional forms and baseline parameter scenarios. We assume that total sampling costs increase in proportion to sampling density, eradication costs and population damages increase proportionately with population size and populations grow radially with a constant radial rate (Table 1).

Figure 1 shows how total and component management costs vary with sampling density for each of twelve baseline scenarios. Surveillance costs increase with sampling density, as per definition. Total expected penalty costs, eradication costs and damage costs decrease with increasing sampling density, because earlier detection reduces these costs. The convex shape of the total cost curve, which is the sum of the four component costs, reflects the trade-off between

surveillance expenditures and invasion costs. Optimal sampling density occurs at the minimum of the total cost curve.

Understanding how each component total cost function depends on model parameters facilitates intuition for how total cost and optimal sample density depend on invasion and economic characteristics. Total damage and eradication cost lines (1) increase with population growth rate (row 1 vs. 2) because costs accrue faster, (2) may increase with S_{\max} (row 2 vs. 3) because costs can accrue for longer, (3) increase with establishment rate (columns 1 vs. 2, 3 vs. 4) because more populations are on the landscape and (4) are unaffected by sample costs (columns 1 vs. 3, 2 vs. 4) as by definition (Fig 1). For any given sample density, total expected penalty costs (1) decrease with growth rate (row 1 vs. 2) because populations that grow quickly are more likely to be detected prior to achieving size class S_{\max} , (2) decrease with S_{\max} (row 2 vs. 3) because there are more opportunities for detecting each population prior to reaching size class S_{\max} , (3) increase with establishment rate (columns 1 vs. 2, 3 vs. 4) because there are more populations and (4) are unaffected by sample costs (columns 1 vs. 3, 2 vs. 4).

Because total management costs are the sum of the four component costs, this cost line increases with establishment rate (columns 1 vs. 2, 3 vs. 4) and with marginal eradication, damage, penalty and sample costs (columns 1 vs. 3, 2 vs. 4), and decreases with increasing sample sensitivity and maximum size class (row 2 vs. 3). The relationship between total cost and growth rate is variable (row 1 vs. 2) because population growth rate affects eradication and damage costs positively and penalty costs negatively.

Table 1 Model parameters used in the generalised analysis and in optimisation of surveillance for the gypsy moth in California, USA

Model function	Notation	Units	Baseline assumptions	Case study assumptions
Population size (area)	$a(s)$	km ²	$a(s) = \pi(g s)^2$	$a(s) = \pi \left(\sum_{i=1}^s \frac{g i^m}{b^m + i^m} \right)^2$
Eradication costs	$C_e(a(s))$	\$/population	$C_e(a(s)) = c_e a(s)$	$C_e(a(s)) = c_e a(s)$
Damage costs	$C_d(a(s))$	\$/population	$C_d(a(s)) = c_d a(s)$	$C_d(a(s)) = c_d a(s)$
Sampling costs	$C_s(d, A)$	\$	$C_s(d, A) = c_s d A$	$C_s(d, A) = c_s d A$

Model parameter	Symbol	Units	Baseline scenario values [†]	Case study values	
				Statewide	County-level [‡]
Sample density	d	samples/km ²	Optimised	Optimised	Optimised
Establishment rate	b	populations/year*	0.1, 1 [0.55]	0.862	0.142 (0.657) [§]
Sample sensitivity	y	—	1	0.95	0.95
Maximum population size class	S_{\max}	—	10, 100 [10]	17	17
Population growth rate	g	km/year*	0.3, 3 [1.65]	1.5	1.5
Marginal eradication costs	c_e	\$/km ²	5000	29 357	29 357
Half time for reaching asymptotic growth rate	b	year*	—	5	5
Growth function shape parameter	m	—	—	5	5
Marginal damage costs	c_d	\$/km ²	1000	0	0
Marginal sampling costs	c_s	\$/sample	50, 250 [150]	47.78	43.15 (68.74)
Penalty cost	c_{fail}	\$/population	100 000 000	61 403 248	61 403 248
Region area	A	km ²	10 000	414 633	7149 (8187)
Max. no. populations in a size class	G_{\max}	—	100	100	50

*Year or other choice of inter-survey period.

†The parameter values in brackets are those used as the baseline in Fig. 2.

‡Mean and standard deviation (in parentheses) for parameters that vary across counties.

§Values shown as populations/10 000 km²/year for comparison across different-sized counties; simple, unweighted mean.

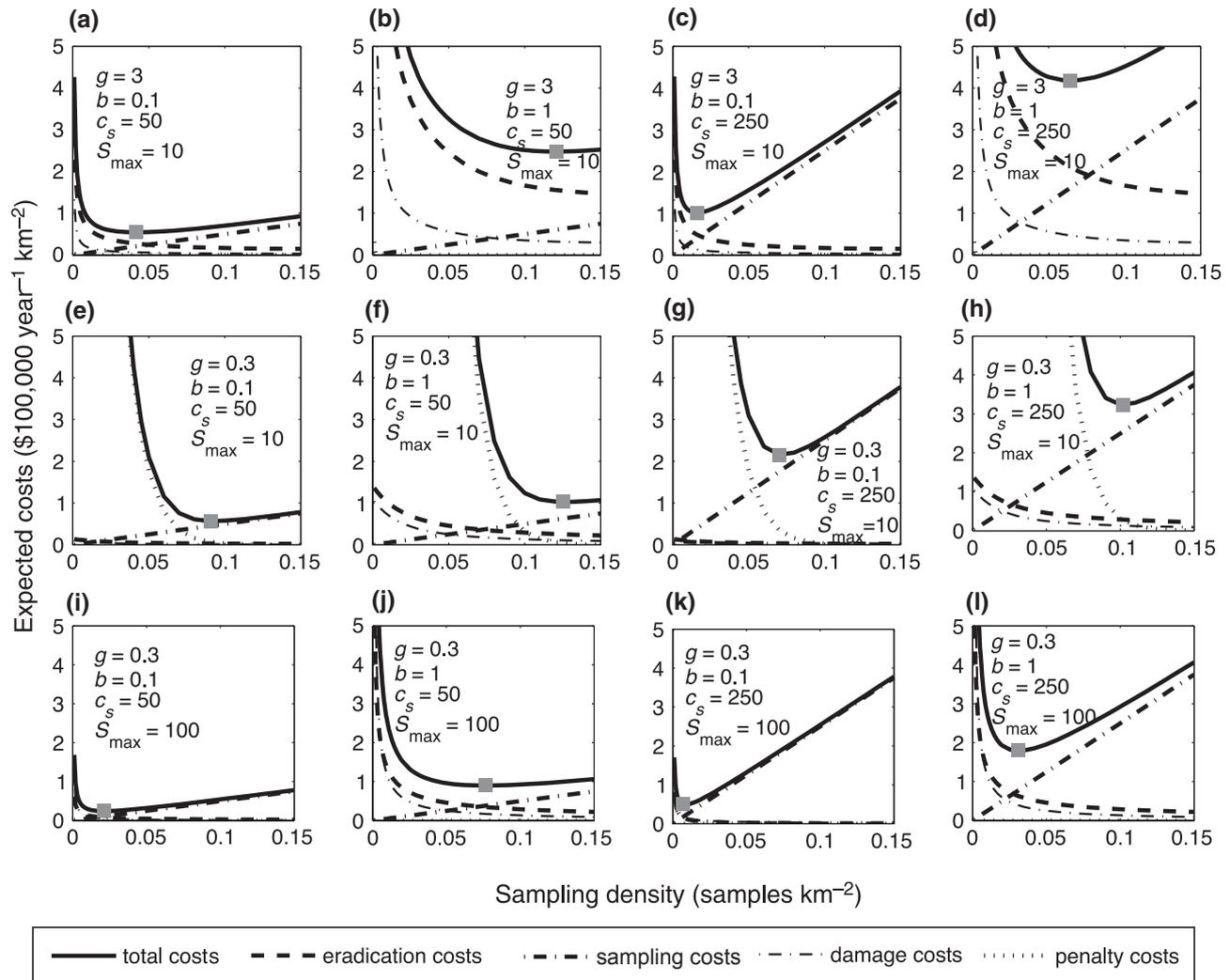


Figure 1 Total and component costs for 12 baseline scenarios. Dashed lines show surveillance costs and expected eradication, damage, and penalty costs. Solid lines show total expected management costs. Square marks optimum. The top row represents species with a high growth rate ($g = 3$) and short time horizon for detection prior to incurring a penalty cost ($S_{\max} = 10$); the middle row represents low growth rate ($g = 0.3$) and short time horizon ($S_{\max} = 10$); the bottom row represents low growth rate ($g = 0.3$) and long time horizon ($S_{\max} = 100$). The left and right columns show low sample costs ($c_s = \$50/\text{sample}$) and high sample costs ($c_s = \$250/\text{sample}$), respectively. The first and third column represent low establishment rates ($b = 0.1$), and the second and fourth columns represent high establishment rates ($b = 1$).

While optimal sampling density leads to minimum total management costs, the sensitivity of total costs to deviations from optimal sampling effort is determined by the slope of the total cost function around its minimum. For the baseline scenarios (Fig. 1), this sensitivity is higher for higher sample cost, as indicated by the steeper slope near the minimum (columns 1 vs. 3, 2 vs. 4).

Figure 2 shows how optimal surveillance effort and total expected management costs vary in response to changes in model parameters. We vary each parameter one at a time, over a broad range of potential values, holding all others at their average baseline value (Table 1). We also consider a joint change in growth rate and maximum size class, which specifies the maximum acceptable size of a population. Under the average baseline parameterisation and optimal management, at any given point in time the expected numbers of populations 1, 2, 3 and 4 years old are 0.550, 0.366, 0.072 and 0.002, respectively, with no populations (i.e. <0.00001) >4 years old.

We find that optimal sample density and total expected management costs increase with increasing population establishment rate,

marginal damages and marginal eradication costs (Fig. 2a,b and c); decrease with increasing sample sensitivity and maximum size class S_{\max} (Fig. 2d and g); and are insensitive to the choice of penalty cost (Fig. 2e). As sample costs increase, optimal sample density decreases and total management costs increase (Fig. 2f). Optimal sample density and management costs change non-monotonically with changes in population growth rate, because population size affects the costs and detectability of populations in ways that have antagonistic effects on optimal management and costs (Fig. 2h). At very low growth rates, the role of detectability dominates, such that very high sampling densities are needed to reduce expected penalty costs from failing to detect populations before they reach size class S_{\max} . As population growth rate increases, detectability increases which decreases optimal sampling density. At higher population growth rates, damage and eradication costs of populations become larger, increasing the optimal sample density and total expected costs. Again, at very high growth rates, increased detectability reduces optimal sample density, but total costs continue to increase.

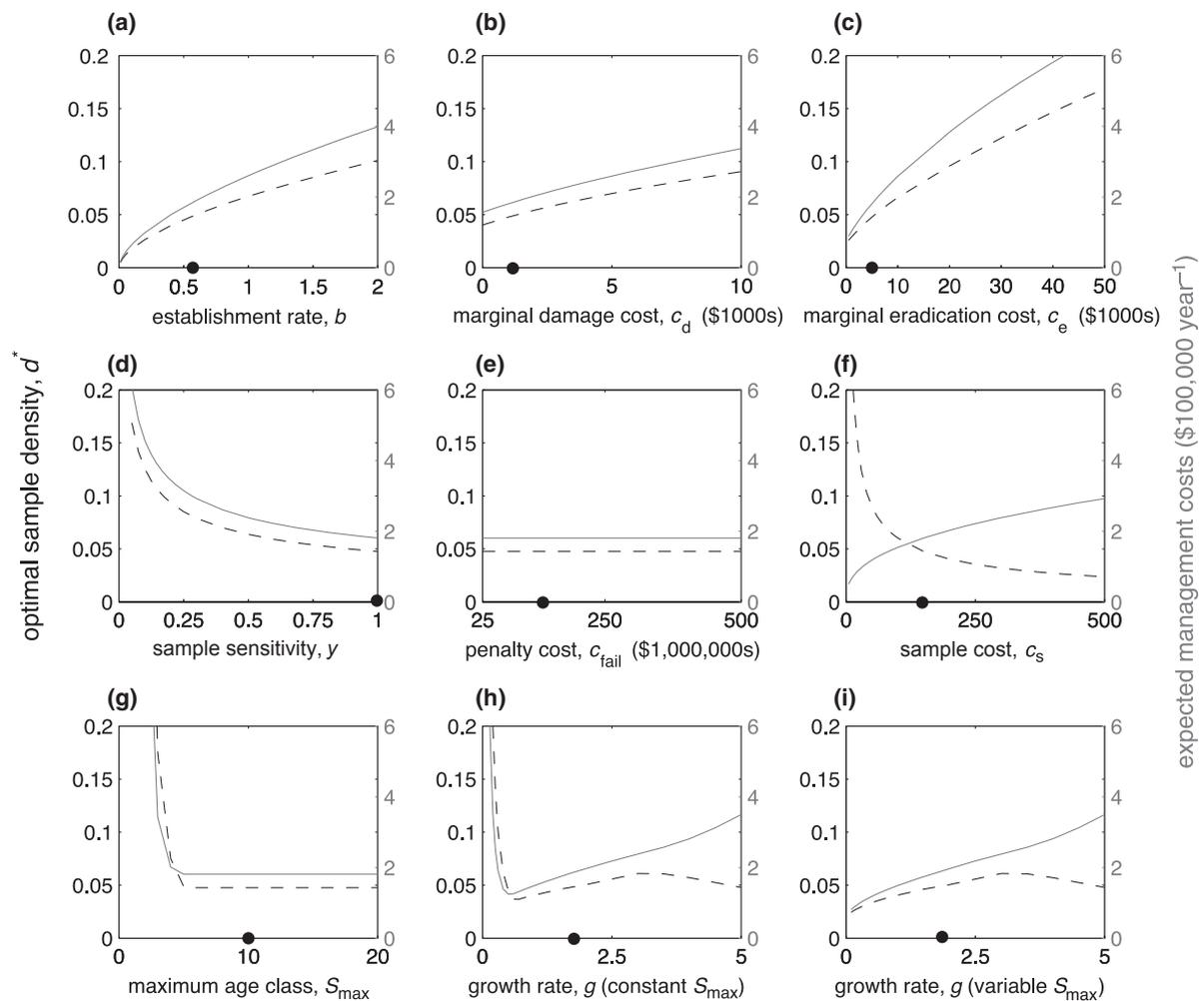


Figure 2 Sensitivity of optimal sample density (dashed line) and expected management costs (solid line) to model parameters. The circle on the x-axis shows the baseline parameterisation (Table 1).

A different relationship occurs when growth rate and the maximum size class, S_{\max} , vary simultaneously such that the area of largest size class, $a(S_{\max})$, remains similar and slow growing populations have more time available for detection to avoid a penalty cost (Fig. 2i).

Specifically, we chose $S_{\max} = \text{round}\left(\frac{\sqrt{A/3}}{g\sqrt{\pi}}\right)$, where we rounded

down and g is the population growth rate, so that the maximum sized population is no larger than one third of the survey area A . Here, total management costs increase monotonically with growth rate, while optimal sampling density increases initially with growth rate, reflecting the effects of increasing damage and eradication costs, but decreases at very high growth rates when detectability is high.

CASE STUDY: OPTIMAL MANAGEMENT OF GYPSY MOTH IN CALIFORNIA, USA

We apply our model to the problem of detecting and eradicating isolated gypsy moth (*Lymantria dispar*) populations in California, USA. The gypsy moth, a native of temperate Europe, Asia and North Africa, is now established throughout the northeastern United States and is one of the country's most devastating forest pests

(Liebhold *et al.* 1995). It is capable of establishing and becoming a pest throughout North America (Morin *et al.* 2004) in natural and urban landscapes. Nearly every year, isolated gypsy moth populations establish outside the species' current introduced range through human-assisted dispersal (e.g. on vehicles, firewood, cargo ships). Networks of pheromone traps are used to detect these populations so that they can be eradicated (Liebhold & Bascompte 2003; Hajek & Tobin 2011).

We demonstrate the use of our model to optimise surveillance for gypsy moth across California, with and without a state-wide budget constraint. We parameterised the model for California as a whole and separately for each of its 58 counties, the scale at which trapping information and establishment history are available. The parameter values and functional forms are based on a combination of empirical data, estimates from the literature and expert opinion (see Table 1 and Supporting Information). Population growth is modeled by a sigmoid function, representing initially accelerating radial population growth that eventually asymptotes at a rate g such dynamics are characteristic of species that are subject to strong Allee effects (Vercken *et al.* 2011). Damages are assumed to be zero because gypsy moths cause minimal damage in populations smaller

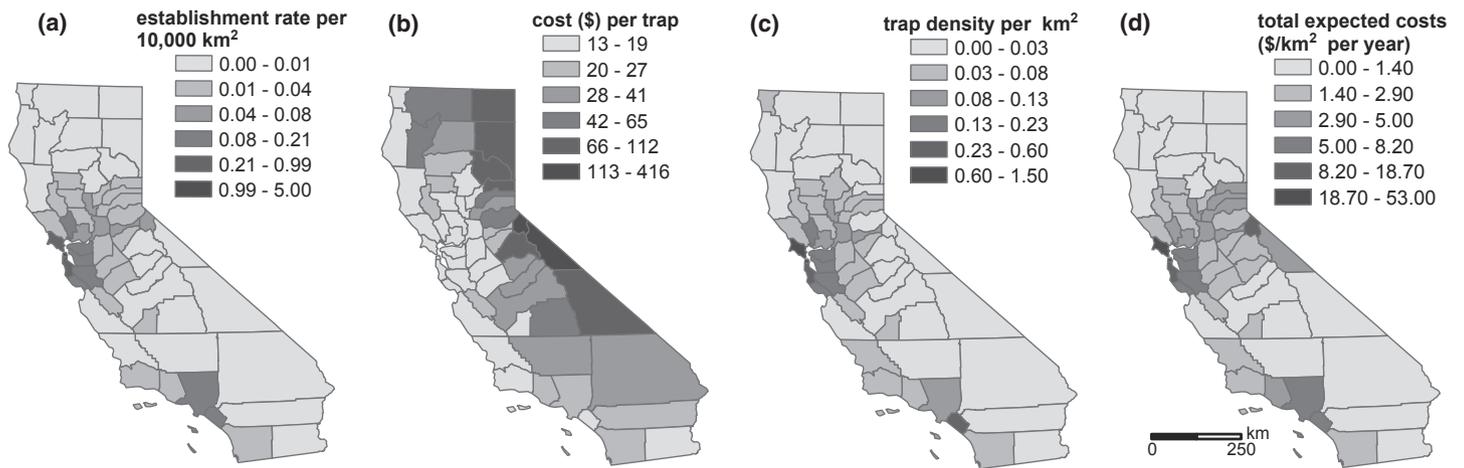


Figure 3 Parameterisation of (a) establishment rate (populations/10 000 km²/year) and (b) sample costs (\$/trap) across California counties. Subregional optimisation results showing (c) optimal trap densities (traps/km²) and (d) expected management costs (\$/km²/year) across California counties.

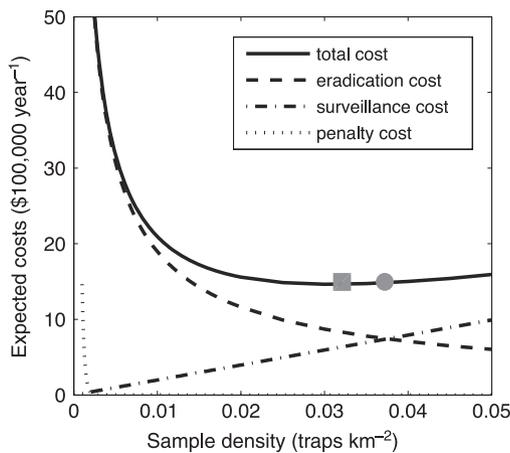


Figure 4 Expected management costs as a function of trap density. The square represents the optimal trap density (0.031 traps/km²) and the total annual expected management costs associated with that density (\$1 464 200/year). The circle represents the actual average statewide trap density (0.037 traps/km²) for California.

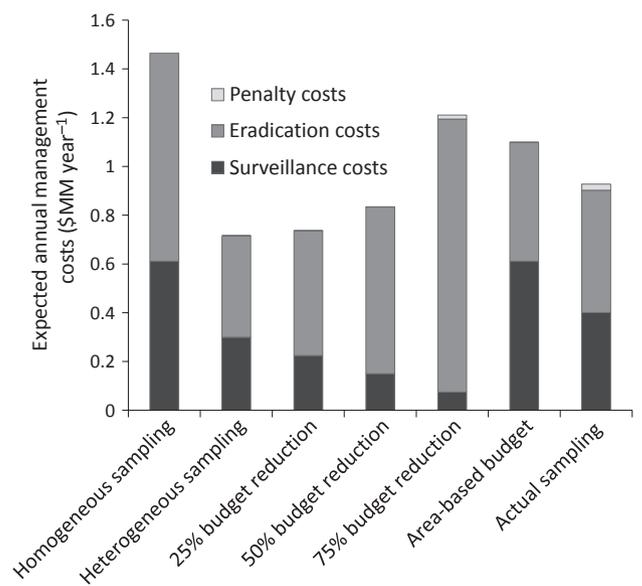


Figure 5 Comparison of total costs (including surveillance costs, eradication costs, and penalty costs from failed detection) under optimal management for various budget and sampling allocations and actual trapping densities in California (Table S2).

than the maximum acceptable size class S_{max} (Appendix S1). Sampling costs and establishment rates are heterogeneous across the region and have been parameterised at the county level (Fig. 3a and b). Sampling uses pheromone traps, so surveillance effort is measured as trap density (traps/km²). The statewide establishment rate and sample cost parameters are calculated as the sum and area-weighted average, respectively, of their county-level values.

We first used the model to optimise homogeneous sampling density for the state of California as a whole. The optimal solution is 0.031 traps/km², corresponding to a total annual expected management cost of \$1.46 million (Fig. 4), and is similar to 0.037 traps/km², the actual statewide sampling density for California in 2010 (Kevin Hoffman, California Department of Food and Agriculture, personal communication). The model suggests that there is little dif-

ference in the expected management costs at these sampling densities. Total management costs drop steeply with initial investments in sampling, but are less sensitive to changes in sampling density between *c.* 0.02 and 0.05 traps/km² (Fig. 4). Nonetheless, there is significant variation in total sampling and total eradication costs across sampling densities. The expected equilibrium number of populations in each size class is shown in Table S3.

Next, we optimised heterogeneous surveillance effort between the 58 counties of California based on data for establishment rates and sampling costs for each county. Here, the optimal number of traps deployed in total is nearly the same as for the previous analysis

(12 794 vs. 12 832) but the optimal distribution of samples across counties differs dramatically (Fig. 3c; Table S1), ranging from 0.002 to 1.434 traps/km² with a mean of 0.093 and standard deviation 0.207 traps/km².

Heterogeneous trapping in response to county differences in establishment rate and sampling costs dramatically reduces the expected statewide management expenditures (Fig. 5; Table S2): eradication costs and surveillance costs are reduced by about half (\$748 416/year), while penalty costs are negligible under both strategies. The expected annual county-level management costs are shown in Fig. 3d.

If county-specific establishment rates were not known, then a suitable strategy for heterogeneously allocating surveillance effort might be to divide the total optimal surveillance budget under homogeneous management (\$611,294/year) across counties in proportion to their area. If we assume that counties deploy as many traps as their sampling budget allows using the county-specific trapping costs, then nearly twice as many traps (21 803 vs. 12 793) are deployed across the state, which reduces total expected statewide management costs by 25% (Fig. 5; Table S2). By allowing sample density to vary based on sampling costs, surveillance is more intense in counties that have lower average sampling costs, which reflects the optimal response of sampling effort to cost differences. Thus, even a relatively naïve heterogeneous sampling plan may result in substantial savings in comparison to a homogeneous approach.

Finally, we applied our methods to predict the effect of region-wide sampling budget reductions of 25, 50 and 75% relative to sampling expenditures needed for optimal heterogeneous sampling effort (\$299 465). The model suggests that by re-optimising surveillance effort between counties, a 25% reduction in the sampling budget leads to about a 3% increase in total management costs; expenditures on surveillance are reduced, but increases in eradication costs almost exactly offset this reduction (Fig. 5; Table S2). A sampling budget reduction of 50% causes a 16.6% increase in total expenditures and a 75% sampling budget reduction increases total management costs by almost 70%. Such large sampling budget reductions would induce significant shifts in expenditure from surveillance to eradication and increase the risk of failing to detect populations before they become ineradicable.

California's 2010 county-level trapping densities (Kevin Hoffman, personal communication) correspond closely to the optimal heterogeneous trapping policy derived from the model. Overall, we estimate that the expected costs state-wide are 29% greater than under optimal heterogeneous management (Fig. 5; Table S2). Although California's current trapping policies have not been derived from a formal analysis of expected management costs, as performed here, the distribution of traps among counties reflects historical tendencies of new gypsy moth populations to establish in areas with higher human populations (Lippitt *et al.* 2008) and guidelines recommending varying densities of traps based on local habitat features that affect establishment risk (U.S. Department of Agriculture 2009). When we compared the expected management costs for each county based on reported trap density with the costs expected under optimal trap density (Figure S1), we found that suboptimality in the trap densities of just three counties caused 50% of the difference in state-wide costs. These results suggest that adjusting the sampling effort in just three counties might provide significant long-term gains in cost efficiency (unless those counties are basing their management on important additional information not considered here).

DISCUSSION

Our analyses suggest that greater surveillance effort is warranted for invasive species that have higher establishment rates, cause higher damages, that are more costly to eradicate or for which sampling is less costly. These results corroborate previous findings that optimal surveillance effort increases with the number of local populations on the landscape (Bogich *et al.* 2008; Homans & Horie 2011), the probability of species presence (Hauser & McCarthy 2009), the cost of damages (Homans & Horie 2011), eradication costs (Bogich *et al.* 2008), and decreasing surveillance costs (Bogich *et al.* 2008; Homans & Horie 2011). In contrast to our results, Homans & Horie (2011) concluded that optimal surveillance decreases with control costs, because they did not require populations to be eradicated upon detection and damages only accrued for a finite time horizon.

Our approach assumes the probability of detecting a population depends on population size, surveillance effort (measured as sample density), and sample sensitivity (i.e. the probability of detecting a population if a sample is located within it). In contrast, Bogich *et al.* (2008) assumed perfect sample sensitivity, and Homans & Horie (2011), Hauser & McCarthy (2009), and Mehta *et al.* (2007) did not consider changes in detectability with increasing population size. While we find that optimal surveillance effort declines with sample sensitivity, Homans & Horie (2011) found increases with detectability, which may reflect a decrease in effective sampling cost. Hauser & McCarthy (2009) found that a highly ineffective surveillance method should not be used at all and moderately effective methods warrant greater investment than more effective methods.

We find that optimal surveillance effort depends non-monotonically on population growth rate, a finding that parallels that of Bogich *et al.* (2008) who also accounted for changes in detectability with population size. Optimal sample densities are lowest for species with very low growth rates (and long time horizons for detection), because they remain small longer and are less expensive to eradicate. Optimal surveillance effort is highest for infestations with moderate growth rates because their costs of damages and eradication grow quickly but they may not be easy to detect. Species with very high growth rates warrant less surveillance effort because they are easier to detect. In contrast, Homans & Horie (2011) found a strictly increasing relationship by considering the effect of growth rate only on future costs and not on detection probability.

We show that substantial long-term savings may be achieved by accounting for spatial heterogeneity of invasion risk and surveillance costs. Only Hauser & McCarthy (2009) have previously considered optimal allocation of resources across multiple sites. In our example, we found that accounting for differences in surveillance costs and establishment rates across counties in California reduces expected annual management costs for gypsy moths by half. We expect that stratifying the management region (i.e. California) based on physiography and human geography instead of political boundaries (i.e. counties) would likely increase potential savings. Furthermore, stratifying based on additional features, such as surveillance costs, damages, and eradication costs, also could improve allocation of resources across space. Our method can accommodate this information and be used to optimise surveillance accordingly.

Our dynamic approach allows intuitive and mechanistic inclusion of future consequences of populations remaining undetected during a survey period. We simplify the solution and specification of this

dynamic problem by solving for the optimal long-term equilibrium surveillance effort. This approach requires several simplifying assumptions.

First, while we allow for interannual variation in the number of local populations established, our equilibrium analysis imposes the requirement that the average rate of establishment is constant. However, establishment rates may depend on the (changing) distribution of local populations in the survey area or may change in response to trade patterns, quarantine efforts, and control of source populations. While the former could be accounted for by specifying the establishment rate as a function of the size and number of other populations, the latter defies equilibrium analysis. Our approach may still be useful for guiding surveillance efforts in the context of an exogenously changing establishment rate, if strategies are updated over time as rates change. Furthermore, surveillance can provide valuable information for updating or improving estimates of establishment rates. Equilibrium analysis also is inappropriate for determining one-time surveillance efforts, an application for which Hauser & McCarthy's (2009) approach would be more appropriate, or for optimising surveillance if many local populations are thought to have established prior to the initiation of a surveillance program. In the latter case, higher surveillance effort may initially be optimal, prior to implementing the long-term surveillance effort identified by our model.

Our analysis also assumes that populations are successfully eradicated following detection. If, during surveillance implementation, a population were discovered that was not eradicated, rates of local population establishment would likely increase because of the additional propagule source. We do not believe that this assumption markedly limits the applicability of this approach, as most surveillance programs are established with the objective of early detection and eradication. Furthermore, our approach can account for the anticipated costs of a population becoming ineradicable through inclusion of this value in the penalty cost. In this way our model can help balance the risk of potential long term population establishment with the costs of surveillance.

As with any model of invasive species management, a challenge to applying our model is that many of the parameters will not be known with certainty. In such cases, 'value of information' methods can help determine how much it is worth to reduce uncertainty in model parameters (e.g. Runge *et al.* 2011). When model parameters are uncertain, the expected value of perfect information (EVPI) is the difference between the expected value of an optimal action after the new information has been collected and the expected value of an optimal action before the new information has been collected. EVPI can be interpreted as the maximum amount a decision-maker is willing to pay to acquire the information. Our methods can be extended to evaluate the value of information leading to the elimination of different subsets of uncertainty, which can help prioritise the direction of information gathering efforts. Undertaking a thorough analysis would require estimating the distribution of model uncertainty, and we leave that to future work.

Efficient allocation of resources to managing invasive species is needed to reduce their ecological and economic harm. We believe that our new model for optimising invasive species surveillance has general applicability to a wide range of unwanted plant, animal, and pathogen species. With minimal conceptual adjustment it may also be applicable to problems of environmental monitoring (e.g. detecting pollution of groundwater) and food quality (e.g.

shellfish toxicity). When adequate data are available on invasion biology, surveillance efficiency and management costs, our methodology can be applied in diverse management settings to identify the most efficient surveillance strategy for managing invading species over large and heterogeneous landscapes.

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AUTHORSHIP

RE-N, RH, LB, JK and AL designed the research. RE-N, LB, JK and AL performed the research, and RE-N, RH, LB, JK and AL wrote the paper.

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