ORIGINAL PAPER

Designing efficient surveys: spatial arrangement of sample points for detection of invasive species

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Abstract Effective surveillance is critical to managing biological invasions via early detection and eradication. The efficiency of surveillance systems may be affected by the spatial arrangement of sample locations. We investigate how the spatial arrangement of sample points, ranging from random to fixed grid arrangements, affects the probability of detecting a target population (survey sensitivity) and the overall cost of detecting and eradicating populations invading over time. For single period surveys, regular sampling patterns outperform the equivalent number of random samples at intermediate sample densities, but only when sample sensitivity is high. Otherwise, sample point arrangement has little effect on survey sensitivity, which can be modelled reasonably accurately using a Poisson approximation. For multiple period surveys, we find little difference in the costs of sample point arrangements for most combinations of parameters tested. However, the costs of different arrangements vary when sampling methods have higher sensitivity and trap densities are low, a situation representative of many real surveillance programs. In particular, our results suggest that dynamic trapping arrangements increase the efficiency of detection when traps are sparse relative to the size of target populations. Also, for the scenarios we considered managers may exercise some freedom in allocating sample point locations. Placing individual traps or samples in perceived higher probability sites at the local scale is unlikely to diminish the probability of detection at the broader scale.

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Introduction

Typical sampling programs in ecology aim to estimate a mean, or some other statistic, for a target population without focusing on how the population is spatially distributed (Albert et al. 2010). However, ecologists are increasingly addressing problems for which it is necessary to characterize spatial patterns of occupancy in populations. Such surveillance programs must carefully consider spatial locations in addition to the number of sample locations (Andrew and Mapstone 1987; Perry et al. 2002).

The challenge of detecting rare populations is central to many applied ecological problems such as confirming presence of an endangered species, detecting a patchily distributed exploitable resource, detecting a recently established invasive pest, or monitoring for the remnants of populations under eradication (Nicholson and Barry 1996; Venette et al. 2002; Chadès et al. 2008; Cacho et al. 2006; Regan et al. 2011). Examples abound of invasive species that escaped early detection and became so abundant and widespread that containment and eradication were no longer possible (Myers et al. 1998). Similar sampling problems exist for detecting establishment and spread of infections through a spatially dispersed population (Hoye et al. 2010) or spatial spread of chemical contamination in an aquifer seeded at several locations (Carpenter et al. 2012).

The efficiency of detecting rare targets may be affected by the spatial arrangement of sampling locations. When conducting point sampling, our focus here, previous work and conventional wisdom suggest that across areas of uniform risk grid designs are more effective at detecting patchy targets than other spatial designs (e.g., Barry and Nicholson 1993; Stevens and Olsen 2004). However, the superiority of a grid design may be compromised by at least three factors. First, previous studies that identified the superiority of grids assumed that a target patch is always detected whenever it is intersected by a sample point (perfect sample sensitivity; Barry and Nicholson 1993). However, this is often not the case. For example, when

target organisms are small, cryptic, and difficult to observe, the type II error rate (failure to detect when present) can be relatively high. Sampling mechanisms may also be imperfect, such as when trapping an organism depends on fortuitous animal behaviour. Alternatively, target patches may be ephemeral or only detectable during limited time periods, such as for calling birds.

Second, real-world constraints mean that a regular grid of sample points may not be practically attainable. For example, some sampling locations may be inaccessible because of physical conditions. Such constraints create uncertainty about whether imperfect grid designs compromise the effectiveness of entire surveillance programs.

Finally, Barry and Nicholson (1993) and others (e.g. Nicholson and Barry 1996, 2005) employed a one-time evaluation of survey sensitivity. However, many surveys extend over multiple time periods and the probability of detection may change over time. For example, invading populations may grow and spread so that their probability of detection increases over time. In addition, by considering multiple sampling periods, the probability of detecting target patches may be affected by locating sample points where these points were previously absent. Whether and to what extent this increases the efficiency of a surveillance program is currently unclear.

In this paper, we explore the effects of spatial arrangement of samples taken with imperfect sample sensitivity (probability of an individual sample detecting a target population when present at the sample point) on survey sensitivity (probability of detecting one or more target populations present within the survey area) for rare populations. Although we use detection of invasive insect pests via pheromone traps as a model system, our analysis applies more generally to the spatial design of surveillance systems.

We also evaluate effects of the spatial sample arrangement on overall costs of a long term program to detect and eradicate new incursions of an invasive pest species over time. Early detection is here a key determinant of the feasibility of its eradication (Liebhold and Tobin 2008; Tobin et al. 2014). However, exhaustive surveillance, such as inspection of all locations or by massive deployment of attractive traps, is seldom practical due to budget limitations and the vast number of potentially damaging species that require separate surveillance. In addition, there are

direct trade-offs between investments in surveillance and eradication costs (Mehta et al. 2007; Bogich et al. 2008; Epanchin-Niell et al. 2012, 2014). By deploying too few traps, newly invaded pest populations may remain undetected until they are large, leading to high eradication costs (Tobin et al. 2014). Conversely, deploying more traps than necessary leads to higher costs of surveillance, but only marginal increases in the pest detection probability and reductions in eradication costs.

Recently, there has been substantial progress in developing methods for balancing the costs of invasive species detection with costs of post-detection eradication. However, these studies have not addressed the spatial arrangement of trap locations; they have either quantified the detection costs and probabilities phenomenologically (Mehta et al. 2007; Hauser and McCarthy 2009; Regan et al. 2011) or assumed random trap location (Bogich et al. 2008; Epanchin-Niell et al. 2012, 2014). While these approaches capture the essence of the detection-eradication trade-off, it is important to evaluate the cost-effectiveness of spatial arrangements of sample points other than random placement, especially since the latter is rarely used in biosecurity operations (Marsh and Trenham 2008).

Design of efficient surveys for biosecurity surveillance programmes must allocate samples through time, in addition to stratifying samples through space. We address the problem of early detection of new invasions in a homogeneous region by evaluating the effects of spatial sample arrangement under two scenarios. In Problem 1 we compare various arrangements of sample points deployed over a single sampling period; in Problem 2 we consider a multi-temporal surveillance problem in which new populations establish, undetected populations grow, and sampling is stratified across time. In both cases, we assume that the location of the target population centre is static and that there is a uniform risk of population establishment across the entire spatial domain. As a practical illustration, we parameterise our models using data on invading populations of the gypsy moth *Lymantria dispar* (L.) in North America (Liebhold and Tobin 2006), noting that in practice gypsy moth surveillance traps are often deployed in square grids (Roberts and Ziegler 2007). However, we also conduct an extensive sensitivity analysis so as to cover a wide range of potential invasive species. We show that in most situations, spatial sample arrangement has

relatively little effect on survey sensitivity, and survey sensitivity can be modelled reasonably accurately using a Poisson approximation (Problem 1). Similarly, we find relatively little difference in the cost-efficiency of different trap arrangements for the specific application of detecting and eradicating invasions over multiple time periods; however, the costs of different arrangements vary when sampling methods have high sensitivity and trap densities are low (Problem 2).

Materials and methods

Problem 1: Effects of sample arrangement on survey sensitivity over a single sampling period

This model considers samples as discrete points in space that may detect a homogeneous population of a given radius; any sample that falls within the circular area occupied by the target population has some probability of detecting it. This framework was used in many previous studies (Barry and Nicholson 1993; Mehta et al. 2007; Bogich et al. 2008; Epanchin-Niell et al. 2012, 2014). However, our implementation differs in that we allow for imperfect sample sensitivity and investigate a variety of sample arrangements.

Formally, *n* samples (e.g. insect traps) are modelled as discrete points located within a square region of area *A*. The target population is modelled as a single circular, continuously occupied area of a radius *r* located at random completely within the region. Each sample that lies within the occupied area has a

Table 1 Parameters and variables for Problem 1

Symbol	Meaning
A	Total area sampled (square region)
r	Radius of the circular area occupied by the population
n	Total number of samples
d	Sample spacing (for regular grids only)
D	Relative sample density (expected number of randomly distributed samples intersecting the population) $= n\pi r^2/A$
s	Sample sensitivity (probability of a sample lying within the population area detecting the population)
P	Survey sensitivity (probability of detecting a population by at least one sample)

probability s of detecting the population (sample sensitivity), and we are interested in the survey sensitivity P, which is the probability that the population will be detected by at least one sample. These and other model parameters and variables are summarized in Table 1.

Stochastic simulations were conducted in Matlab (R2009b, The MathWorks, Inc.). Survey sensitivity was estimated as the proportion of 10,000 stochastic

equivalently at the centres of tessellated squares). For this arrangement, an analytical solution for survey sensitivity may be derived by geometry when sample sensitivity is $s = 1$ (Barry and Nicholson 1993). Denoting the nearest neighbour spacing between samples as d, the mean sample density is $n/A = 1/d^2$, the relative sample density (Table 1) is $D = \pi(r/d)^2$ and

$$
P = \begin{cases} D & 0 < \dfrac{r}{d} = \sqrt{\dfrac{D}{\pi}} \le \dfrac{1}{2} \\ D\left(1 - \dfrac{4}{\pi}\cos^{-1}\left(\sqrt{\dfrac{\pi}{4D}}\right)\right) + \sqrt{\dfrac{4D}{\pi} - 1} & \dfrac{1}{2} < \dfrac{r}{d} = \sqrt{\dfrac{D}{\pi}} \le \dfrac{1}{\sqrt{2}} \\ 1 & \dfrac{r}{d} = \sqrt{\dfrac{D}{\pi}} > \dfrac{1}{\sqrt{2}} \end{cases} \tag{2}
$$

simulations in which at least one sample detected the population. We also calculated the 95 % Wilson score confidence intervals for the estimated proportions. We ran these simulations for a range of parameter values and the following spatial arrangements of sample points. Where possible, we also calculated survey sensitivity analytically and compared the simulation and analytical results to validate the simulations.

Random sample arrangement

The probability that a randomly placed sample will lie within the population area is $\pi r^2/A$, so the probability that a random sample would detect the population is $s\pi r^2/A$. Given n such sample points, the probability of detecting the population by one or more samples is $P = 1 - (1 - s\pi r^2/A)^n$, which for large n and small $s\pi r^2/A$ can be approximated by the zero term of the Poisson distribution as

$$ P = 1 - \exp(-ns\pi r^2/A) = 1 - \exp(-sD) \tag{1} $$

where $D = n\pi r^2/A$ is the expected number of sample points intersecting the population.

Samples arranged as a square grid

Here we consider a *square grid*, with sample points located at the vertices of a tessellation of squares (or
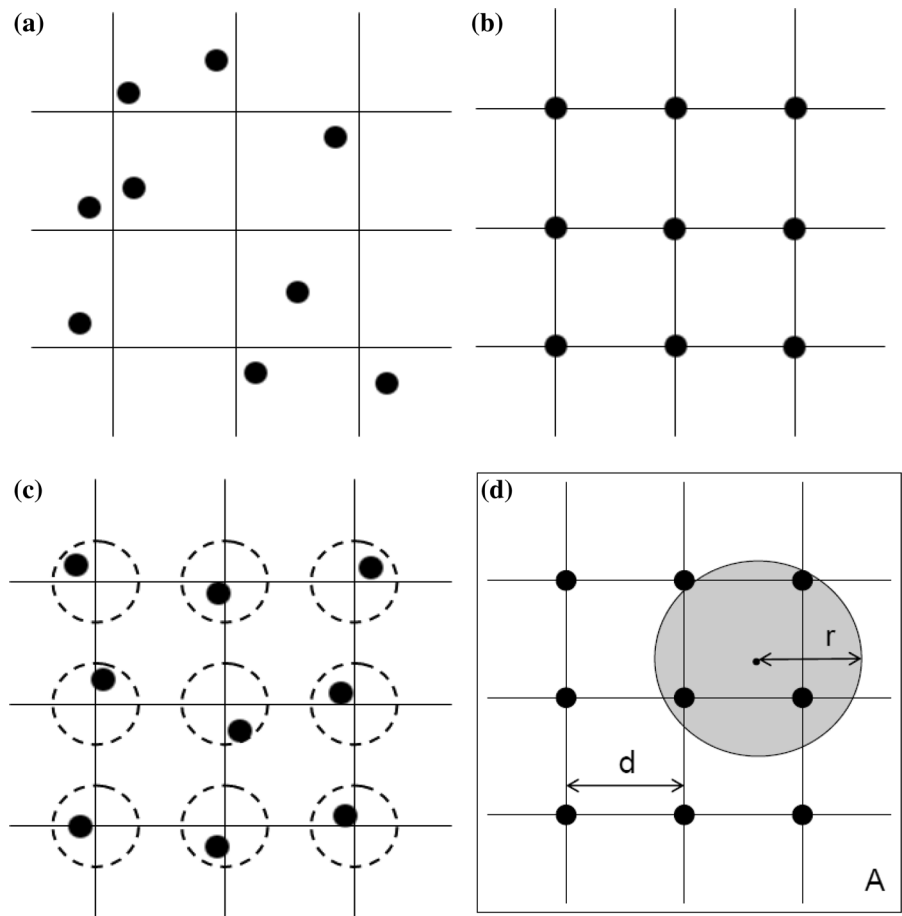
A sub-random sample arrangement

Samples may also be deployed in various sub-random arrangements, intermediate between random and grid arrangements. For example, in North American gypsy moth surveillance programs, placement of traps in certain locations, such as extremely steep, swampy, or densely vegetated areas may be impractical. Rather than using precise grid vertices, trappers may place traps anywhere within target circles around each vertex, with radius equal to 30 % of the inter-trap distance d (Roberts and Ziegler 2007). The target circles facilitate trap placement while maintaining integrity of the trapping grid. We modelled this strategy as a *fuzzy grid*: samples are placed randomly within distance equal to 0.3 × inter-sample distance of the sample locations specified with a square grid. The various configurations we consider here are depicted in Fig. 1.

Problem 2: Effects of sample arrangement on pest management costs over multiple sampling periods

Here we address a multi-temporal variant of the previous problem. Specifically, we evaluate the effects of trap arrangement on overall costs of a program to detect and eradicate an invasive pest species over an infinite time horizon. New local populations can

Fig. 1 Schematic representation of sample arrangements used in this study. The alternative arrangements are **a** random, **b** square grid, **c** fuzzy grid. *Filled dots* indicate example trap locations. In **d**, some variables used in Eqs. (1) and (2) and listed in Table 1 are visualized: the *shaded circle* represents a population of radius r, located in an arena of area A in which traps are arranged in a square grid of inter-node distance d

establish each year, detected populations are immediately eradicated, and undetected populations grow in each time period. Focusing on overall managements costs (including costs of eradication) as the measure of surveillance efficiency is more relevant here than a measure of detection probability.

For this we modified a generic, age-structured model of pest population dynamics (Epanchin-Niell et al. 2012). At the beginning of year t, any population can be in one of L age classes. During year t, these populations can be detected by traps spatially distributed over a square region of area A. We assume that populations are detected using the same logic as in Problem 1 and are eradicated immediately upon detection. Moreover, new populations can establish each year at the region-wide rate b, meaning that the actual number of new populations that establish during year t is Poisson distributed with mean and variance b. We assume that b is independent of the size and

number of infestations already present in the region; this is the most likely scenario when an originally unaffected area is repeatedly invaded by an alien species and we aim to detect and eradicate such species as soon as possible. The parameter b thus represents immigration rate and we use $b = 1$ as our baseline value. Centres of these new populations are located randomly in space. We do not impose any specific rules if a centre falls within the area of an existing population, very close to an existing population, or close to the edge of the study area, since A was sufficiently large that these events were extremely rare and did not affect our results.

If a population stays undetected during year t, it continues to grow. Here we distinguish two different scenarios. First, we model a species that demonstrates a strong demographic Allee effect so that the radial growth rate of such populations accelerates until reaching an asymptotic radial growth rate (Veit and

Lewis [1996]). Therefore, the annual change in the radius of a circular population range is a sigmoid function:

$$r(j+1) = r(j) + \frac{gj^m}{h^m + j^m} \qquad (3)$$

where $r(j)$ is the radius of a j-year-old population, g is the asymptotic radial growth rate, h is the population age at which half that asymptotic rate is reached, and m is a shape parameter. We assume that $r(0) = 0$, so that newly established populations have negligible spatial extent. Equation (3) implies that the population radius grows slowly at first, then accelerates around the age of h and approaches an asymptotic rate of spread g in older populations. We initially use $g = 1.5$, $h = 5$, and $m = 5$, as it reflects the radial growth rate of the invasive gypsy moth populations (Epanchin-Niell et al. [2012]), which demonstrate a strong Allee effect (Tobin et al. [2009]). For species not subject to strong demographic Allee effects we assume that the population radius grows at a constant rate by assuming $m = 0$ in Eq. (3) and doubling the value of g to get the same asymptotic rate for both scenarios. We believe that these models capture the early spread patterns of a wide range of potentially invading species; this generality is further enhanced by the sensitivity analysis described later in this section.

Using Matlab (R2009b, The MathWorks, Inc.), we simulated our age-structured model across a region of area $A = 100$ km $\times$ 100 km. We used a variety of spatial trap arrangements, including random trap placement and several variants of the square grid design. For the latter, the region was divided into equal-sized squares, with one trap positioned in each square as follows:

- *Fixed grid*—one trap located at the centre of each square,
- *Fuzzy grid*—traps placed randomly within distance equal to 0.3 × inter-trap distance of the trap locations specified with the square grid,
- *Alternating grid*—traps placed as with the square grid but shifted by half the distance of the side of the grid square in both directions and back in alternating years,
- *Wobbling grid*—traps placed as with the square grid but the whole grid shifted at random within the

region in each year (ensuring that all traps remain located within the region).

While the first two grid-like patterns were also used in Problem 1, the latter two are only applicable for multi-period sampling. The potential advantage of their dynamic character is that the change in sample locations between sampling periods may increase the chance of intersecting a growing local population. We note that the random arrangement is actually also dynamic because traps are re-randomized each year. For all grid-like arrangements, the number of equal-sized squares was calculated as $[\sqrt{n}]^2$ where n is the number of traps to be deployed and $[X]$ denotes the whole part of a real number X; the remaining $n - [\sqrt{n}]^2$ traps were placed randomly within the region.

The efficiency of a surveillance method (trap number plus trap arrangement) is based on the total costs of detecting (surveillance cost) and removing (eradication cost) populations (Epanchin-Niell et al. [2012]). Letting c_s be the trapping cost (USD per trap), the annual surveillance cost is $c_s n$. Letting c_e be the constant marginal cost of eradicating a detected population (USD km^{-2}), the cost of removing a population of age j with area $a(j) = \pi \, r(j)^2$ is $c_e a(j)$ and the cost of eradicating populations detected in year t is $\sum_{j=1}^{L} c_e a(j) w_j(t)$, where $w_j(t)$ is the number of populations of age j detected in year t. For the gypsy moth, Epanchin-Niell et al. ([2012]) estimated $c_s = \$47.78$ USD per trap and $c_e = \$29,357$ USD per km^2, so we use $c_s = \$50$ USD per trap and $c_e = \$30,000$ USD per km^2 as our initial values, and vary them in our sensitivity analysis.

We also consider the 'penalty cost' of $c_{fail} = \$60,000,000$ USD for all populations which are not detected by L years of age (Epanchin-Niell et al. [2012]). This value roughly corresponds to the cost of eradicating a population of age L growing at a constant radial rate, and twice the cost of eradicating a population of age L growing at a sigmoid radial rate. However, as we will show, the precise value of c_{fail} has little effect on the efficiency of different surveillance methods, so long as it is sufficiently large (as is expected to be the case). Once the penalty cost is incurred for a population of age L, that population is formally removed from the region so that we do not count the penalty cost repeatedly. Every year, the sum

Table 2 Parameters and variables for Problem 2

Symbol	Meaning	Baseline value and unit
$w_j(t)$	Number of local populations of age class j detected and eradicated during year t	
L	Maximum age class	17 years
s	Trap sensitivity	
$a(j)$	Area occupied by j-year-old local population	km^2
g	Asymptotic radial growth rate	1.5 km/year^{-1}
h	Population age at which half the asymptotic radial growth rate is reached	5 years
m	Shape parameter of the asymptotic radial growth rate	5
A	Area of the considered region	100 km × 100 km
n	Total number of traps deployed each year	
B	Fixed annual monitoring budget	USD
b	Time-independent establishment rate of local populations	1 year^{-1}
c_s	Trapping cost	$50 USD per trap
c_e	Marginal cost of eradicating a detected local population	$30,000 USD per km^2
c_{fail}	Cost associated with failing to detect and eradicate a local population within time L following establishment	$60,000,000 USD

of the cost of eradicating detected populations and the penalty cost is referred to as the (total) eradication cost, and the sum of the surveillance and eradication costs as the (total) management cost.

We assume that an equal number of traps is deployed each year according to a fixed annual surveillance budget B so that $n = [B/c_s]$ traps are deployed annually. While we assume a fixed value of B, eradication expenditures were incurred as required. This is common for many budgeting situations, because surveillance is typically an ongoing activity while eradication costs are incurred only sporadically on detection. In addition, funds for surveillance frequently come from budget sources that are different from those used for eradication (Monke 2004). Model parameters and variables pertinent to Problem 2 are summarized in Table 2.

After some time, system dynamics reach a (stochastic) equilibrium state. We evaluate how the average annual eradication and management costs for the equilibrium state change with surveillance budget, trap arrangement and trap sensitivity. For each sampling scenario, we run the system for 600 years, exclude the initial 100 years to avoid any transients, and calculate the mean and the associated 95 % confidence interval of the annual eradication and management costs over the remaining 500 years. The system is ergodic, such that all simulations are equally representative of the true distribution. Thus, we do not need to carry out replicate simulations. Also, because our evaluation is based upon equilibrium dynamics, it is not necessary to discount costs to a common point in time.

Results

Problem 1

Figure 2 shows the survey sensitivity for varying sample densities for perfect sample sensitivity ($s = 1$; Fig. 2a) and for low sample sensitivity ($s = 0.2$; Fig. 2b). The grid arrangements resulted in higher probabilities of detecting the population (i.e. greater survey sensitivities) than the random arrangement (Fig. 2). The fuzzy grid sampling resulted in survey sensitivities intermediate between random and fixed grid samplings (Fig. 2). The effect of sample arrangement was greatest at high sample sensitivities s and intermediate relative sample densities D (Fig. 2a). However, when the sample sensitivity s was low or the relative sample density D was low or high, sample arrangement had minimal effect on the results, with all cases being closely predicted by the Poisson formula (Fig. 2). Specifically, for $s = 1$ the maximum distance between the Poisson approximation and the results for the fixed grid arrangement was about 0.27 for our parameter values, whereas it was less than 0.1 for $s < 0.5$ and less than 0.05 for $s < 0.2$.

Problem 2

We start by presenting the results for the baseline parameter values specified in Table 2, for populations whose annual change in range radius is either constant or grows sigmoidally with age. We then conduct a
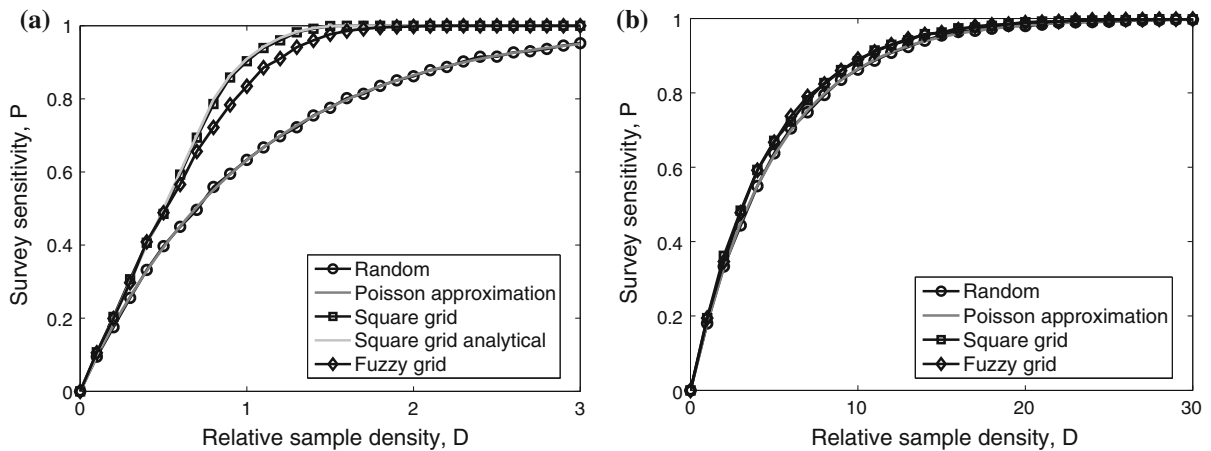
Fig. 2 Results for Problem 1. Sample sensitivity is set to **a** s = 1 and **b** s = 0.2. *Each point* represents survey sensitivity obtained from 10,000 simulations. For random sampling, results are shown for both the analytical Poisson approximation (Eq. 1)

and simulations (random). For the square grid sample arrangement with perfect sample sensitivity (s = 1) both the simulated and analytical (Eq. 2) results are presented. For each simulated scenario the 95 % Wilson score CI is <0.01

sensitivity analysis of the impacts of varying certain model parameters.

To ensure 100 % detection of all 1-year-old populations governed by the baseline parameter values (with radius of about 0.5 m) with a square grid and 100 % trap sensitivity ($s = 1$), traps would need to be deployed so that the inter-trap distance is close to 0.7 m. This actually follows from Eq. 2: for 100 % detection when sample sensitivity is perfect, trap spacing should be $\sqrt{2}$ times the population radius. For a 100 km × 100 km region this corresponds to nearly 22×10^9 traps and surveillance cost of about 10^{12} USD every year. This level of monitoring effort is obviously unrealistic. Fortunately, a strong demographic Allee effect exists in this system that limits initial population growth, such that costs increase relatively slowly with delay in colony detection. For comparison, to ensure 100 % detection of all 5-year-old populations (with a predicted radius of about 1.25 km) with a square grid and perfect trap sensitivity ($s = 1$), traps would need to be deployed so that the inter-trap distance is about 1.8 km. For a 100 km × 100 km region this corresponds to 3,136 traps and surveillance cost of $156,800 USD every year, a much more realistic investment.

To explore the effect of annual surveillance budget around this level, we consider $B = \$10,000$ USD, $\$100,000$ USD and $\$1,000,000$ USD. Based on the trapping cost $c_s = \$50$ USD these budgets correspond

to deploying 200, 2,000 and 20,000 traps, respectively, at densities 0.02, 0.2 and 2 traps per km². respectively. As expected, the annual eradication cost was affected by the surveillance budget B and trap sensitivity s. In particular, the annual eradication cost decreased with increasing trap sensitivity (Fig. 3) and increasing surveillance budget (Fig. 4). Somewhat surprisingly, trap arrangement played only a negligible role. Technically, the random trap arrangement was the most costly and the alternating grid arrangement appeared to be the least costly, but the differences between these two trap arrangements were minor, though greatest at high trap sensitivities (Fig. 3) and low surveillance budgets (Fig. 4). In addition, any small differences in the annual eradication cost between trap arrangements declined with decreasing trap sensitivity (Fig. 3) and increasing surveillance budget (Fig. 4). The results were unaffected by the way the population radius grows; that is, the results are robust to whether the species is subject to a strong demographic Allee effect ($m = 5$) or not ($m = 0$). Overall, for the baseline parameter values, our model suggests that the choice of trap arrangement, among those considered here, has little to no influence on the costs of a long term management program for early detection and eradication of invasive species incursions.

However, our sensitivity analysis suggests that this is not universally so (Electronic Supplementary
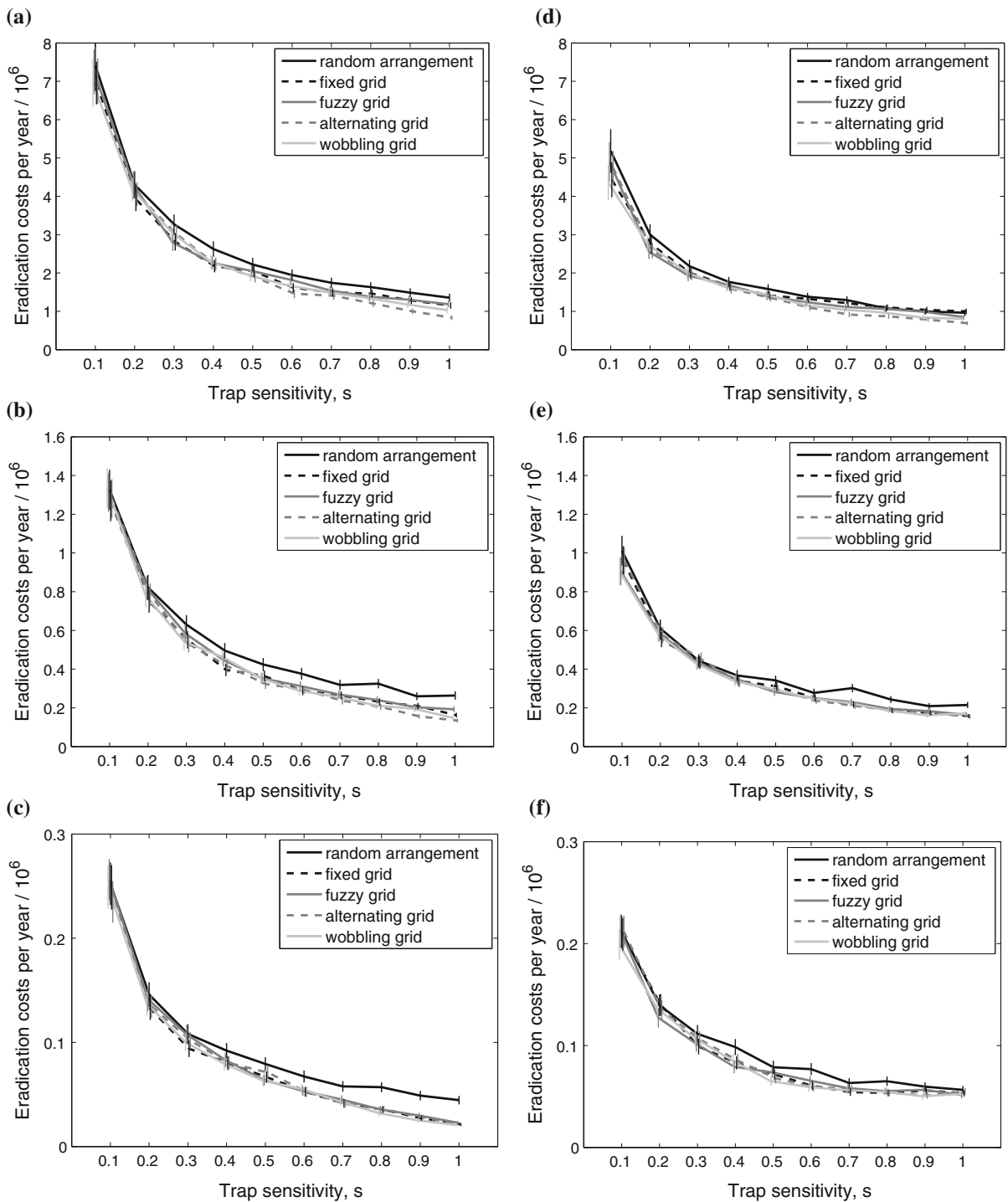
(a)

(d)

(b)

(e)

(c)

(f)

Fig. 3 Annual eradication costs (including penalty costs) as a function of the surveillance budget, trap location arrangement, trap sensitivity, and the presence (**a–c**, $m = 5$) or absence (**d–f**, $m = 0$) of an Allee effect. The alternative surveillance budget values are **a**, **d** B = $10,000 USD, **b**, **e** B = $100,000 USD, **c**, **f** B = $1,000,000 USD. The various curves are plotted with a horizontal offset with respect to each other, so that *vertical bars* corresponding to each curve are more easily seen; the curves represent means, the vertical bars represent 95 % CI for the means. Results are based on 500 simulated years. Note different scales for y-axes of different panels. Other parameters are as in Table 2
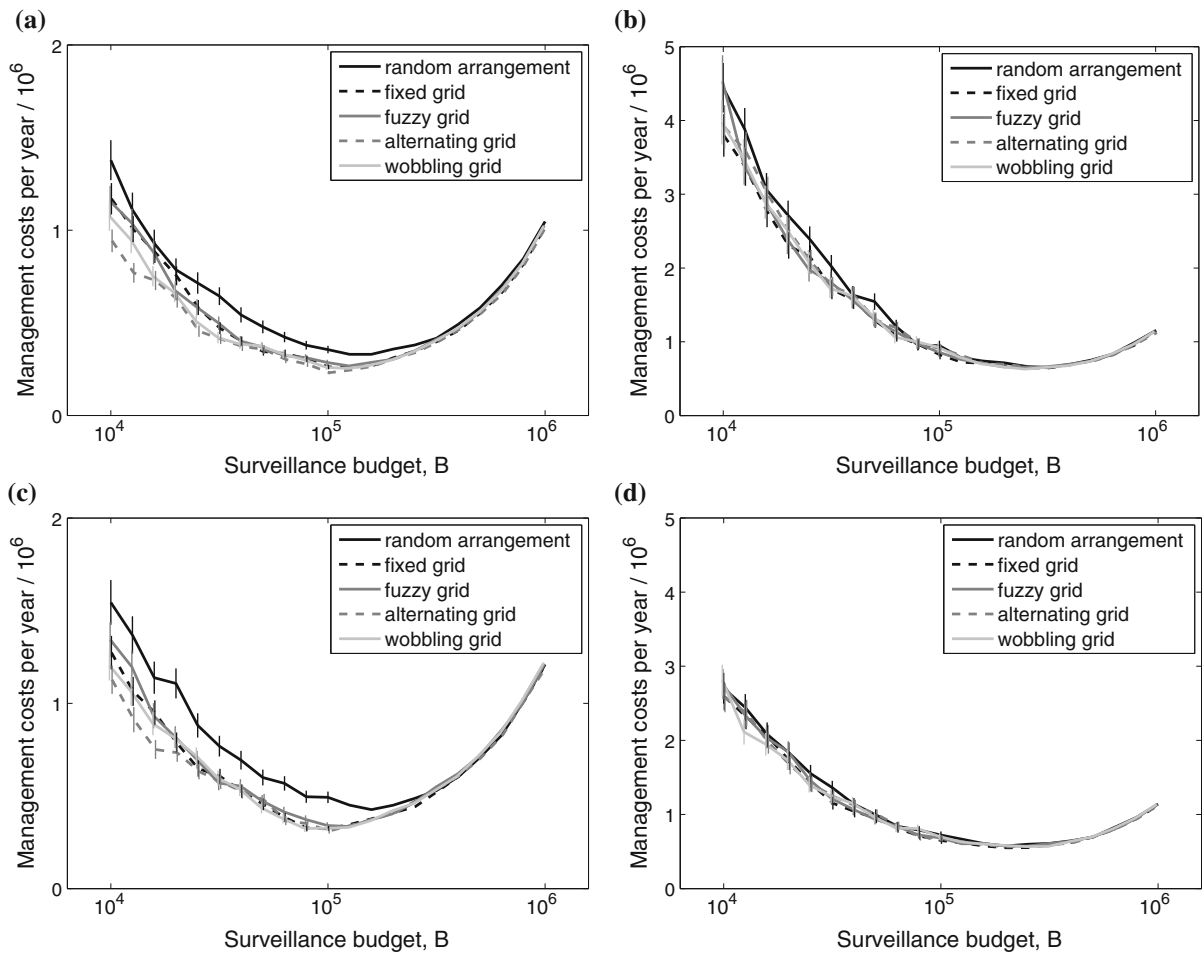
(a)

(b)

(c)

(d)

Fig. 4 Annual overall management costs as a function of the surveillance budget, trap location arrangement, trap sensitivity ($s = 1$ in **a** and **c**, and $s = 0.2$ in **b** and **d**), and the presence (**a**, **b**, $m = 5$) or absence (**c**, **d**, $m = 0$) of an Allee effect. The various curves are plotted with horizontal offsets with respect to each other, so that *vertical bars* corresponding to each curve are more easily seen; the curves represent means, the *vertical bars* represent 95 % CI for the means. Results are based on 500 simulated years. Note different scales for y-axes of different panels. Other parameters are as in Table 2

Material). The effect of the asymptotic radial spread rate g is perhaps the most interesting. With high spread rate the random trap arrangement is by far the least efficient, even for relatively high surveillance budgets; the other trap arrangements are comparable in performance. At intermediate spread rates and even at relatively low surveillance budgets all trap arrangements behave roughly equally, with the alternating grid apparently the most efficient. Finally, for low spread rates and relatively low surveillance budgets the fixed grid trap arrangement is by far the least efficient, while the random trap arrangement is among the most efficient ones,

especially at high trapping cost c_s. Indeed, for the lowest spread rates examined, the fixed grid arrangement deviates much more from the other arrangements for $c_s = 200$ than for $c_s = 50$, which corresponds to one fourth the trap density. Otherwise, the effect of the trapping cost c_s is largely quantitative, with differences in management costs among trap arrangements tending to increase with higher trapping cost and lower surveillance budget (which both correspond to lower trap densities). The other tested parameters, the population establishment rate b and the eradication costs c_e and c_{fail} appear to influence only the magnitude of

Table 3 The optimal numbers of traps for scenarios with the Allee effect ($m = 5$) and trapping cost $c_s = \$50$ USD

	$g = 0.5$	$g = 1.5$	$g = 3$	$g = 5$
$b = 0.5$	1,003	1,589	3,170	3,170
	1,589	2,000	2,518	2,000
	1,262	2,000	3,170	2,000
	1,262	2,000	3,170	1,589
	1,003	2,000	3,170	2,000
$b = 1$	2,518	3,170	3,991	3,991
	2,000	2,518	3,170	2,000
	1,589	2,518	3,991	2,000
	1,589	2,000	3,170	1,589
	2,000	2,518	3,170	2,000
$b = 2$	3,170	3,991	6,325	5,024
	2,518	2,518	3,991	2,000
	2,518	3,170	5,024	2,518
	2,000	2,000	3,991	1,589
	2,518	2,518	3,991	2,000

The numbers in each cell from top to bottom correspond to random arrangement, fixed grid, fuzzy grid, alternating grid, and wobbling grid. The respective optimal budget for surveillance B is simply c_s times the optimal number of traps. The other parameters are as in Table 2. Full results for these scenarios are plotted if Fig. 1 of the Electronic Supplementary Material

Table 4 The optimal numbers of traps for scenarios with no Allee effect ($m = 0$) and trapping cost $c_s = \$50$ USD

	$g = 1$	$g = 3$	$g = 6$	$g = 10$
$b = 0.5$	1,262	2,000	1,589	1,262
	1,262	2,000	633	797
	1,262	1,589	633	317
	1,003	1,589	633	252
	1,589	2,000	797	797
$b = 1$	1,589	3,170	2,000	1,003
	2,518	2,000	1,262	503
	2,000	2,518	633	503
	2,518	2,000	1,003	503
	2,000	1,589	797	400
$b = 2$	3,170	3,991	2,518	2,000
	3,170	2,000	1,262	797
	2,518	2,518	1,262	1,003
	2,518	2,000	1,003	797
	2,518	2,518	1,589	503

The numbers in each cell from top to bottom correspond to random arrangement, fixed grid, fuzzy grid, alternating grid, and wobbling grid. The respective optimal budget for surveillance B is simply c_s times the optimal number of traps. The other parameters are as in Table 2. Full results for these scenarios are plotted if Fig. 3 of the Electronic Supplementary Material

management costs but not the efficiency ranking of the examined trap arrangement patterns.

As trap sensitivity increased, the optimal surveillance budget (hence, divided by c_s, the optimal trap density) decreased (Fig. 4). In addition, the optimal surveillance budget was (nearly) identical for the random and grid-like trap arrangements. Interestingly and perhaps most importantly from the practical point of view, all curves are relatively shallow around the optimal surveillance budgets, such that the annual management costs do not increase markedly with small deviations from the optimal surveillance budget and the corresponding optimal surveillance costs vary little among the considered trap arrangements. For example, for trap sensitivity $s = 0.2$, surveillance budget can range between 100,000 USD and 1,000,000 USD without substantially affecting the average annual management costs (Fig. 4). Tables 3 and 4 show the optimal numbers of traps corresponding to the minimal average management costs, for the trapping cost $c_s = \$50$ USD and for an Allee effect (sigmoid radial growth rate, $m = 5$) and no Allee

effect (constant radial growth rate, $m = 0$), respectively. These optimal numbers get more variable among the examined trap arrangements as both the population establishment rate b and the asymptotic radial growth rate g increase. Also, for relatively high values of g we apparently need much less traps when no Allee effect is present; for relatively low values of g the optimal numbers of traps are comparable for an Allee effect and for no Allee effect. However, we emphasize again that generally the annual management costs do not increase markedly with small deviations from the optimal surveillance budget and the corresponding optimal surveillance costs vary little among the considered trap arrangements (Electronic Supplementary Material).

Discussion

Survey design for detecting rare target organisms or populations applies across a diversity of ecological contexts. In our focus, surveillance plays a critical role

in efforts to manage biological invasions via early detection and eradication (Liebhold and Tobin 2008; Jarrad et al. 2011). The optimization of surveillance effort is a subject for which several very useful quantitative approaches have been developed for increasing the efficiency of biosecurity activities (e.g., Mehta et al. 2007; Bogich et al. 2008; Hauser and McCarthy 2009; Epanchin-Niell et al. 2012, 2014). Despite these successes, there has been little consideration of spatial arrangement of sample points; most studies simply assumed random sample distribution. In this study, we explicitly model several non-random spatial sample arrangements and examine their effectiveness in various surveillance scenarios. While regular sampling grids generally are thought to be superior to other sample arrangements (e.g., Barry and Nicholson 1993; Stevens and Olsen 2004), we found that the difference in efficiency of spatial sample arrangements was in many cases small, especially when employing a sampling method that was not highly sensitive (e.g. visual surveys for a cryptic species or traps with poor attractants) or when having sufficient budget for detailed, multi-period surveillance for eradicating invasions over time.

When sampling is conducted within a single period (Problem 1), regular sampling patterns may outperform the equivalent number of randomly placed sample points in some limited situations—specifically at intermediate sample densities (Fig. 2), but only when sample sensitivity is high. In most other situations, spatial arrangement of sample points has relatively little effect on survey sensitivity, and survey sensitivity can be modelled reasonably accurately using a Poisson approximation.

In our analysis of invasive species detection over time (Problem 2), eradication costs always decrease with increasing trap sensitivity and increasing surveillance budget. However, total management costs decrease and then increase with increasing trap density. We found that trap density (correlated to the annual surveillance budget) has a much greater effect on survey sensitivity than spatial arrangement. Indeed, in many situations we found relatively little difference in the cost-efficiency of different arrangements for the specific application to detecting and eradicating invasions over multiple time periods. For example, our analysis indicated that there is surprisingly little benefit to varying sampling positions by shifting sample grids through time in most situations; the

benefits are greatest when sampling densities are low. These results suggest that dynamic trapping arrangements increase the efficiency of detection when traps are sparse relative to the size of target populations in multi-period sampling.

When employing sampling methods with high sensitivity, the asymptotic radial growth rate g of populations also is important for affecting trap arrangement efficiency: relatively high values of g lead to the least efficient performance of the random trap arrangement and comparable efficiency amongst the other considered arrangements, moderate g's give equal efficiency for all arrangements, and low g's lead to the least efficient performance of the fixed grid and comparable efficiency amongst the other arrangements. A possible explanation here is that fast growing populations will reach a size large enough to likely intersect traps in a regular grid within a short time, whereas a random grid has potentially larger unsampled spaces that may allow for longer times to detection. With a low growth rate the effect may be just the opposite as populations may take a long time to grow to reach a distant fixed sample, but could be intersected sooner by the random traps, since trap locations in this arrangement change from year to year.

The cost-efficiency of surveillance and subsequent eradication is especially sensitive to the choice of spatial trap arrangement when the annual surveillance budget B is low and the trapping cost c_s is high, since then trap densities are quite low. Unfortunately, and quite importantly, this is the case for many invasions due to limited funds and competing demands. When population growth rates are particularly small, low trap densities make the fixed grid arrangement the least efficient. Given that fixed grids are widely used in actual surveillance programs, care must be taken in such cases: adopting a dynamic grid arrangement, including the random arrangement, is preferable. The equal performance of the dynamic grid arrangements and the random arrangement appears here as slightly counter-intuitive, since if there are large gaps in the surveillance network under the random arrangement pattern, there would be significant advantages in shifting traps from year to year to locations that were not searched in the previous year. But note that the random arrangement of traps is also assumed to vary from year to year, albeit in an unpredictable manner. Thus, while this dynamic random pattern is inefficient

if growth rates are sufficiently high, when growth rates and trap densities are low it is among the most efficient surveillance strategies.

The fixed grid trap arrangement (including fuzzy grids) has been the default standard for several large scale insect surveillance programs (gypsy moth: Roberts and Ziegler 2007; fruit flies: Quilici and Donner 2012) and our results support the efficiency of this arrangement under a range of circumstances. In addition, our findings suggest that deviations from the ideal grid, which cannot be practically avoided, do not appear to substantially reduce the overall efficiency of the program. The pheromone-baited traps for detecting gypsy moth populations that were considered in our baseline application are quite sensitive (Schwalbe 1981), but sample sensitivity may be lower for other target species or for sampling methods that are based on weaker attractants or visual surveys. In these cases, adhering to a strict grid arrangement is even less important.

Obviously, higher trap sensitivity reduces management costs, regardless of the actual trap arrangement. A straightforward implication of this is that expenditure on research and production of sampling devices (e.g. traps) with high sensitivity may be beneficial, but once sample sensitivity is sufficiently high, the choice of sample arrangement may be more important. In addition, for systems in which it is possible to invest resources to either increase sample sensitivity (e.g., spending more time on each local visual survey) or to increase sample density, exploring this trade-off may be worthwhile.

Despite providing a quite detailed model formulation for Problem 2, several features of real management programs have not been fully incorporated. For example, we assume that our spatial region is homogeneous in risk of arrival and establishment whereas in many cases arrival rates or chance of establishment may vary across space. In this case, we would expect that our basic findings with respect to sample arrangements would hold, but that the optimal sample density would vary based on these differences, as found by Epanchin-Niell et al. (2012, 2014). In such situations it may be possible to divide the environment into areas of approximately homogeneous introduction risk or habitat preferences, and optimise the allocation of samples between such areas (Martin et al. 2007); the current models would apply to sample arrangement within each such area.

We also assumed constant marginal trapping cost, but this cost is likely to decrease with increasing trap density because of decreased per-trap travel costs. It is also likely to vary among trap arrangement patterns and to depend on topography and road access to sites. For example, in the Midwestern US, roads are mostly configured on a rectangular grid and grid-like trapping arrangements may impose particularly low costs in these situations. Similarly, trapping arrangements that allow for trap placement flexibility based on local conditions (e.g. fuzzy grids) are likely to be less costly than inflexible trap locations.

Finally, we modelled appearance of new populations in the target region as immigration (at a constant rate) from outside source populations. This situation is representative of the recurrent gypsy moth invasions to California (Epanchin-Niell et al. 2012), and we believe it is generally the most likely scenario when the primary aim is to survey an originally unaffected area to detect and eradicate a repeatedly invading alien species at minimal cost. One may argue that our model is not representative of a scenario where establishment of new populations results from short-to-medium distance dispersal from established populations within the target region. However, we see such short or mid-range dispersal as drivers of range expansion in our model, which would accelerate local population growth making it more important to detect and remove established populations early. Our model could also apply to detecting satellite populations establishing into uninvaded areas via dispersal from known, established populations, by allowing the optimal density (rather than arrangement) of traps to vary across a gradient of establishment rate extending away from the source population. Given that our results regarding trap arrangement are unaffected by the way the population radius grows, that is, they are robust to whether the species is subject to a strong demographic Allee effect ($m = 5$) or not ($m = 0$), our results are probably valid for a wide range of potential invaders.

Here we consider strategies for long term surveillance design for early detection of new invasive species incursion via traps or point samples. Alternative strategies or spatial arrangements may be applicable for detecting species that lend themselves to more continuous sampling, such as transects using visual surveys. For example, Cacho et al. (2006) employed search theory to evaluate the eradicability of known weed populations in cases where surveyors use

visual searches, e.g. transects, to find individual plants to control. They showed that searching in equidistant parallel tracks performed better than random (wandering) searches. In later studies, they also considered passive and active surveillance for controlling a spreading plant invasion and showed how surveillance intensity should vary across the landscape to efficiently control the invasion, using search theory to model search behavior and sensitivity at individual locations (Cacho et al. 2010; Cacho and Hester 2011; Hester and Cacho 2012). In contrast, our focus on spatial arrangement of samples applies to the diverse range of species or situations that employ traps or other point sampling methods to survey an area. The optimal, landscape-wide surveillance strategy for these situations thus depends on both the optimal spatial arrangement of samples and the intensity of surveillance, e.g. density of samples across the landscape.

In conclusion, we addressed the issue of whether different sample point arrangements might result in either significantly different survey sensitivities over single sampling periods (Problem 1) or markedly different costs of detecting and eradicating steadily invading populations (Problem 2). For the scenarios we considered we showed that under most circumstances there was generally little benefit from pedantically adhering to a specific pattern in sample point locations. This is good news for natural resource managers deploying traps for surveillance of invasive pests or depending on volunteers for sample placement. Indeed, managers can exploit the freedom to place individual traps or samples into preferred locations to maximize the probability of detection at a local scale, secure in the knowledge that this is unlikely to diminish the probability of detection at the broader scale. On the other hand, if the annual surveillance budget is limited and surveillance costs are high, which is the case in many real surveillance programs, a particular strategy might underperform others and some care then needs to be taken. In any case, modelling studies such as ours can provide a rigorous basis for optimizing surveillance and eradication programs against an increasing number of invasive pests.

References

Albert CH, Yoccoz NG, Edwards TC Jr, Graham CH, Zimmermann NE, Thuiller W (2010) Sampling in ecology and evolution—bridging the gap between theory and practice. Ecography 33:1028–1037

Andrew NL, Mapstone BD (1987) Sampling and the description of spatial pattern in marine ecology. Oceanogr Mar Biol Annu Rev 25:39–90

Barry J, Nicholson M (1993) Measuring the probability of patch detection for four spatial sampling designs. J Appl Stat 20:353–362

Bogich TL, Liebhold AM, Shea K (2008) To sample or eradicate? A cost minimization model for monitoring and managing an invasive species. J Appl Ecol 45:1134–1142

Cacho OJ, Hester SM (2011) Deriving efficient frontiers for effort allocation in the management of invasive species. Aust J Agric Resour Econ 55:72–89

Cacho JO, Spring D, Pheloung P, Hester S (2006) Evaluating the feasibility of eradicating an invasion. Biol Invasions 8:903–917

Cacho OJ, Spring D, Hester S, Mac Nally R (2010) Allocating surveillance effort in the management of invasive species: a spatially-explicit model. Environ Model Softw 25:444–454

Carpenter PJ, Ding A, Cheng L (2012) Identifying groundwater contamination using resistivity surveys at a landfill near Maoming, China. Nat Educ Knowl 3(7):20

Chadès I, McDonald-Madden E, McCarthy MA, Wintle B, Linkie M, Possingham HP (2008) When to stop managing or surveying cryptic threatened species. Proc Natl Acad Sci 105:13936–13940

Epanchin-Niell RS, Haight RG, Berec L, Kean JM, Liebhold AM (2012) Optimal surveillance and eradication of invasive species in heterogeneous landscapes. Ecol Lett 15:803–812

Epanchin-Niell R, Brockerhoff E, Kean J, Turner J (2014) Designing cost-efficient surveillance for early-detection and control of multiple invading species. Ecol Appl. doi:10.1890/13-1331.1

Hauser CE, McCarthy MA (2009) Streamlining 'search and destroy': cost-effective surveillance for invasive species management. Ecol Lett 12:683–692

Hester S, Cacho O (2012) Optimization of search strategies in managing biological invasions: a simulation approach. Hum Ecol Risk Assess: Int J 18:181–199

Hoye BJ, Munster VJ, Nishiura H, Klaassen M, Fouchier RAM (2010) Surveillance of wild birds for avian influenza virus. Emerg Infect Dis 16(12)

Jarrad FC, Barrett S, Murray J, Stoklosa R, Whittle P, Mengersen K (2011) Ecological aspects of biosecurity surveillance design for the detection of multiple invasive animal species. Biol Invasions 13:803–818

Liebhold AM, Tobin PC (2006) Growth of newly established alien populations: comparison of North American gypsy moth colonies with invasion theory. Popul Ecol 48:253–262

Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management. Annu Rev Entomol 53:387–408

Marsh DM, Trenham PC (2008) Current trends in plant and animal population monitoring. Conserv Biol 22:647–655

Martin PAJ, Cameron AR, Greiner M (2007) Demonstrating freedom from disease using multiple complex data sources 1: a new methodology based on scenario trees. Prev Vet Med 79:71–97

Mehta SV, Haight RG, Homans FR, Polasky S, Venette RC (2007) Optimal detection and control strategies for invasive species management. Ecol Econ 61:237–245

Monke J (2004). Funding plant and animal health emergencies: transfers from the Commodity Credit Corporation. US Congressional Information Service, Library of Congress. CRS Report RL32504. 13 pp. (available at http://research.policyarchive.org/2146.pdf)

Myers JH, Savoie A, Van Randen E (1998) Eradication and pest management. Annu Rev Entomol 43:471–491

Nicholson M, Barry J (1996) Survey design for detecting patches. J Appl Stat 23:361–368

Nicholson M, Barry J (2005) Target detection from a classical and a Bayesian viewpoint. J Appl Stat 32:475–482

Perry JN, Liebhold AM, Rosenberg MS, Dungan J, Miriti M, Jakomulska A, Citron-Pousty S (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. Ecography 25:578–600

Quilici S, Donner P (2012) Analysis of exotic fruit fly trapping networks. EPPO Bull 42:102–108

Regan TJ, Chadès I, Possingham HP (2011) Optimally managing under imperfect detection: a method for plant invasions. J Appl Ecol 48:76–85

Roberts EA, Ziegler A (2007) Gypsy moth population monitoring and data collection. In: Tobin PC, Blackburn LM (eds) Slow the spread: a national program to manage the gypsy moth. General Technical Report NRS-6, US Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp 33–46

Schwalbe CP (1981) Disparlure-baited traps for survey and detection. In: Doane CC, McManus ML (eds) The gypsy moth: research toward integrated pest management. USDA Technical Bulletin 1584, pp 542–548

Stevens DL Jr, Olsen AR (2004) Spatially balanced sampling of natural resources. J Am Stat Assoc 99:262–278

Tobin PC, Robinet C, Johnson DM, Whitmire SL, Bjørnstad ON, Liebhold AM (2009) The role of Allee effects in gypsy moth, Lymantria dispar (L.), invasions. Popul Ecol 51:373–384

Tobin PC, Kean JM, Suckling DM, McCullough DG, Herms DA, Stringer LD (2014) Determinants of successful arthropod eradication programs. Biol Invasions 16:401–414

Veit RR, Lewis MA (1996) Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. Am Nat 148:255–274

Venette RC, Moon RD, Hutchison WD (2002) Strategies and statistics of sampling for rare individuals. Annu Rev Entomol 47:143–174