

# When managers forage for pests: Implementing the functional response in pest management

Melodie Kunegel-Lion<sup>a,\*</sup>, Devin W. Goodsman<sup>b</sup>, Mark A. Lewis<sup>a,c</sup>

<sup>a</sup>*Department of Biological Sciences, University of Alberta, CW 405 Biological Sciences Bldg, Edmonton, AB T6G 2E9, Canada.*

<sup>b</sup>*Earth and Environmental Science Division, Los Alamos National Laboratory, Los Alamos, New Mexico, 87545, USA. dgoodsman@lanl.gov*

<sup>c</sup>*Department of Mathematical and Statistical Sciences, University of Alberta, 632 CAB, Edmonton, AB T6G 2G1, Canada. mark.lewis@ualberta.ca*

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## Abstract

In this study, we explore how the functional response framework can be implemented in pest management. Here, managers take the role of predators foraging on pests and facing monetary costs for survey and control in a spatial domain where the pest distribution and control strategy do not have to be random. To investigate this framework quantitatively, we simulated various management processes on different pest spatial distributions using a spatially-explicit individual-based model and Monte-Carlo simulations, and also confirmed some of the results analytically. By graphing the number of pests controlled versus pest density, we obtained management functional response curves. Whether the management functional response was shaped like a type I, type II or type III functional response depended on the management costs and the search area. However, the management spatial strategy and the pest spatial distribution had little effect on the functional response. We applied our model to the management of mountain pine beetle epidemic in Cypress Hills, Saskatchewan, Canada, with simulations matching the real number of attacked trees controlled by managers. We showed how to make an analogy between functional responses in predator-prey interactions and in human-pest interactions and thereby, apply insights from the functional response framework to pest management.

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\*Corresponding author, kunegel@ualberta.ca

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## 1. Introduction

The functional response framework characterizes predator-prey interactions by the relationship between prey density and the number of prey captured by a predator (Holling 1959a). In this well-defined framework, time acts as a limitation: authors typically consider temporal costs, such as handling time, which, when large, decreases the number of occasions for prey capture. In the functional response literature, researchers usually study pest management in two ways. First, in the context of biological control, a predator is a means of management (*e.g.* Mills and Getz 1996; Van Den Berg et al. 1997). Functional responses are then used in the usual way to describe a biocontrol response to the pest level. Second, management is added to a predator-prey system by removing either predator or prey at a given rate. When management is added to models in this way, the functional response usually does not vary except if the control method affects predators or prey behaviour or if the ratio between prey and predator abundance affects the number of prey captured (*e.g.* Liu et al. 2006; He et al. 2012).

An alternate way to model the direct influence of management on pests using functional responses would be to consider managers physically removing or controlling a pest as predators. Although they deal with a resource and not a pest, fisheries models, using harvesting effort or harvest rate, are a first step into describing the effect of management on a resource using a linear relationship (Sutherland 2001). However, to our knowledge, the theory of manager functional responses displaying various shapes has not been previously proposed or tested. Applying functional response literature to human-pest systems would be powerful as there is an extensive functional response theoretical background.

Could human-pest interactions be treated as predator-prey interactions in a functional response framework? Managers and predators tend to have similar

behaviours in this context: both wish to remove the maximum possible number of prey/pests; both have limitations, whether temporal or monetary, preventing them from maximizing the number of prey/pests they capture (Hassell 1978); both face complex spatial distribution of prey/pest population; and both may employ a variety of search strategies. In this study, we will explore the functional response types obtained under the assumption that managers take the role of predators, pests take the role of prey, and monetary costs constrain managers in a similar way that temporal costs constrain predators. For example, the pest handling cost for a manager can be shown to be equivalent to the prey handling time for a predator in the functional response formulation. Although time plays a major role in management, we argue that, at the scale of a management season, monetary costs are the most important limiters of management success; mostly because the time allotted to management directly depends on budget.

Although functional response theory usually concerns a random search in an homogeneous domain, spatial heterogeneity is usually considered as a norm in the environment (Levin 1992; Gustafson 1998) and should be studied for realism. Spatial patterns are usually classified as regular, random or clustered (Hopkins and Skellam 1954). A regular spatial pattern would look like points on a grid whereas a clustered, or aggregated, spatial pattern would feature isolated groups of points in space. In each case, the observed pattern depends on the scale of the study. Indeed, a population could appear randomly distributed when viewed on a small scale, but clustered on a large scale. Depending on the spatial distribution of resources the species depends on, observed patterns could also change from one area to another. Not taking into account realistic pest spatial distribution in functional response studies may include bias and lead to inaccurate determination of the functional response shape (Ives et al. 1999; Hochberg and Holt 1999). In this study, we examine the impact of random, clustered and regular pest spatial patterns.

The predator/manager searching strategy could also have an impact on the type of functional response observed. Functional response studies usually assume a

random search but other strategies are possible. The adaptive cluster sampling strategy is an established alternative to random searching (Thompson 1990).  
60 In this case, after the random sample of a first set of locations, if the variable of interest in any location is bigger than zero, additional nearby locations are added to the survey. When the pest population is clustered, the adaptive  
63 cluster sampling will efficiently find most of the individuals in a given cluster. Maxwell et al. (2012) compared adaptive cluster sampling to traditional transect designs and found out that the former was more efficient than the latter  
66 when the purpose is to survey as many individuals as possible in well-established populations away from roads in the shortest amount of time. This was found to be especially true for clustered populations. The adaptive cluster sampling  
69 strategy is thus an efficient survey strategy that can be easily simulated in our theoretical study. Therefore, we employed two simple contrasting search strategies: random sampling and adaptive cluster sampling.

72 The objectives of this theoretical work are: 1) to create simulation models of pest management using a spatially-explicit individual-based model and spatially-implicit Monte-Carlo simulations, 2) to derive simple functions describing the  
75 number of pest that managers control as a function of pest density and corroborate the simulation models, 3) to characterize the impact of the different components on the functional response shape and compare with predator functional  
78 response components and shapes, and 4) to validate this new framework by applying it to data using the example of mountain pine beetle in Cypress Hills, Saskatchewan. Using monetary cost for the manager as an equivalent of  
81 temporal cost for a predator, we are able to make the analogy between functional responses in predator-prey interactions and human-pest management systems. This opens the door to applying functional response to manager-pest relationships.  
84

## 2. Methods

We simulated management strategies of pest removal using two approaches:  
87 a spatially-explicit individual-based model and spatially-implicit Monte-Carlo  
simulations, and confirmed the results in the simplest cases by deriving ana-  
lytical solutions to mathematical models representing the simulation scenarios.  
90 First, we presented the computational (§2.1 and §2.2) and mathematical (§2.3)  
models corresponding to the first two objectives. Second, we explained how the  
different parameters defined in the models help in connecting our ideas to the  
93 functional response framework (§2.4). Finally, we applied our models to the  
mountain pine beetle example (§2.5).

In this study, we explored various scenarios so as to capture different functional  
96 response behaviours. Each scenario has two elements: 1) a pest spatial pattern  
in a 2-dimensional domain, and 2) a management strategy.

We divided the domain into cells of varying size on a  $16 \times 16$  grid. Depending on  
99 the scenario, the cell size was  $1 \times 1$ ,  $2 \times 2$  or  $8 \times 8$ . Each cell was characterized by  
its spatial position in the domain and by the number of pest items it contained.  
Fig. 1 represents the process for each simulation run and sections 2.1 and 2.2  
102 provide details on each component. The symbols used in this study are described  
in Table 1.

### 2.1. Simulating Pest Distributions

105 We examined four types of spatial patterns: random, clustered within-cells,  
clustered between-cells and regular point patterns.

#### 2.1.1. Random point process

108 The random point process employed a homogeneous Poisson process us-  
ing the `rpoispp` function of the R package `spatstat` (Baddeley et al. 2015;  
R Core Team 2016). A grid with rectangular cells of constant area ( $A$ ) was  
111 then superimposed over the whole spatial domain. Each cell had the same  
probability of having a pest, thus, they were independent of each other.

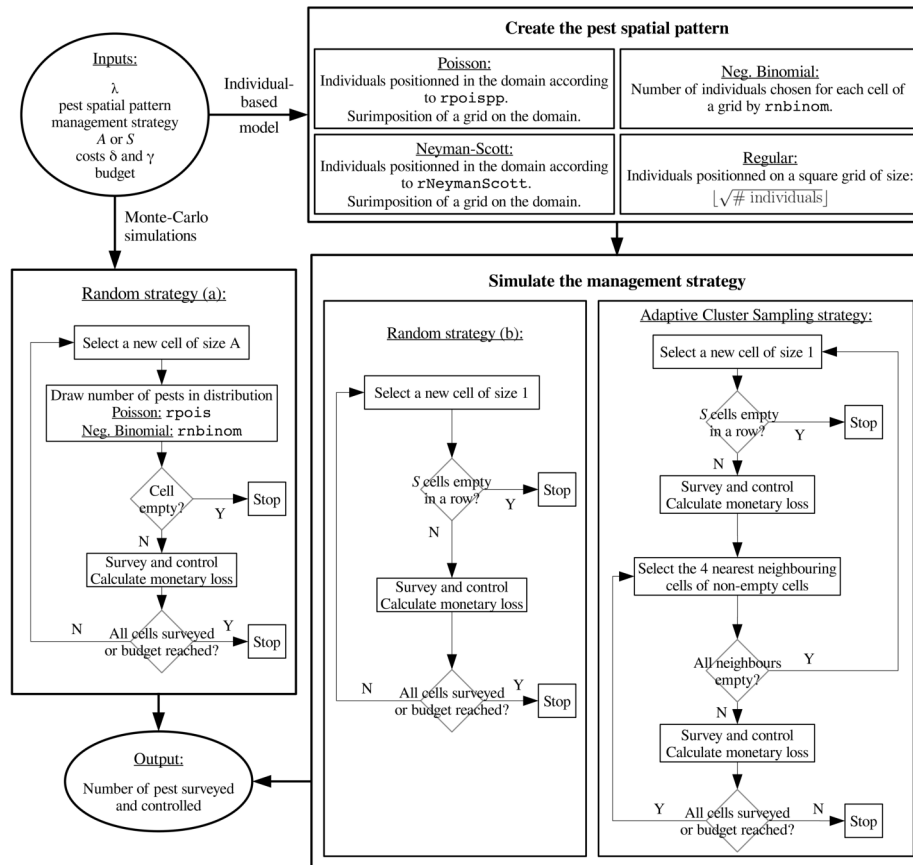


Figure 1: Conceptual diagram representing the process determining each simulation run. Start at the top left of the diagram.

### 2.1.2. Within-cell cluster point process

114 The within-cell cluster point process sampled a Negative binomial distribu-  
 tion for the number of pests in each grid cell using the `rnbinom` function of the  
 R package `stats` (R Core Team 2016). We used the overdispersion parameter  
 117  $k$  fixed to 1 to describe the amount of clustering in the distribution. With this  
 method, clusters happened within a cell and thus, grid cells were independent of  
 each other. This spatial distribution led to no spatial correlation in the density  
 120 of pests between cells but greater variability in the density of pests from one  
 cell to another than for between-cell clustering. The spatial resolution of the

Table 1: Description of the symbols used in the text.

Symbol	Description
$\lambda$	Pest intensity or Average number of individuals in a size-1 grid cell
$\delta$	Cost of surveying a size-1 cell
$\gamma$	Cost of removing a pest individual
$A$	Cell size/area or Number of contiguous size-1 cells
$S$	Nb. of empty cells to survey in a row before stopping the search process
search area	Search area refers indistinctively to $A$ or $S$
$M$	Domain area where management takes place
$\phi$	Probability of finding at least one individual in a grid cell of area $A$
$D$	Expected area explored by managers
$E$	Expected number of individuals that are surveyed and controlled
$B$	Management budget
$k$	Amount of clustering in the negative binomial distribution
$\psi_A$	Probability of finding zero individuals in a cell of area $A$

simulated pest data depended on the size of the square cells in the grid that we  
123 overlaid on top of the spatial domain.

### 2.1.3. Between-cell cluster point process

The between-cell cluster point process employed a Neyman-Scott process  
126 using the `rNeymanScott` function of the R package `spatstat`. This method  
distributed “parent” points in the domain according to a Poisson point process.  
Then, it drew the actual points from a Gaussian distribution around each parent.  
129 The final step consisted of removing the parents. A grid with rectangular cells of  
constant area ( $A$ ) was then superimposed over the whole spatial domain. Thus,  
there was a spatial correlation of the density of pests between cells.

### 132 2.1.4. Regular point process

The regular point process distributed individuals regularly on a square grid  
of size equal to the square root of the total number of individuals in the domain  
135 rounded down to the nearest integer. We positioned remaining individuals using  
the same process. We added some noise proportional to the distance between  
individuals so as to reproduce a more biologically relevant spatial pattern. In

138 order to be distributed uniformly in the domain, each point depended on the  
location of its neighbours. Thus, the number of individuals in each cell was  
dependent on each other.

141 Fig. 2 shows an example of each spatial distribution of points for an average  
intensity of 0.2 individuals per grid cell.

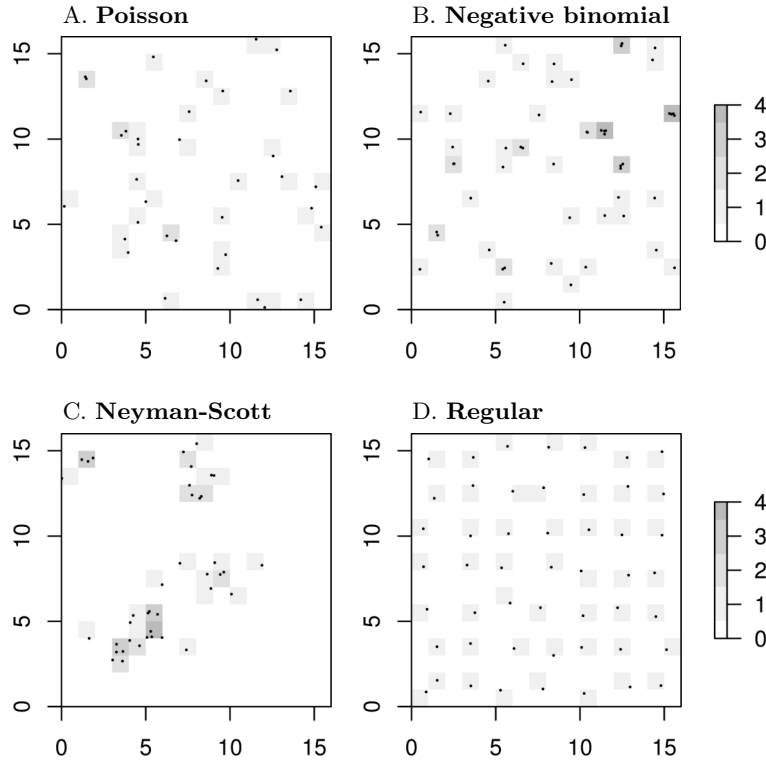


Figure 2: Spatial distributions of pests on a  $16 \times 16$  lattice with an intensity of 0.2 individual per grid cell: A. Poisson spatial distribution, B. Negative binomial (within-cell cluster) spatial distribution with an overdispersion parameter  $k = 1$ , C. Neyman-Scott (between-cell cluster) spatial distribution and D. Regular spatial distribution. The black dots represent the actual point patterns from which the lattice spatial distributions are derived. The shades of grey represent the number of pests per grid cell: white (zero individuals) to the darkest grey (four individuals).



## 2.2. Simulating Manager Search Strategies

144 We simulated three different management strategies. The first two were  
both random searches that differed in the implementation of the search area  
parameter: a random search strategy (a) in which management stops after the  
147 manager discovers one empty cell of variable size and a random search strategy  
(b) in which the manager stops searching after a specified number of consecutive  
empty cells of size 1. The third strategy was the adaptive cluster sampling  
150 strategy.

### 2.2.1. Random Strategy (a): stop after single empty cell of area $A$

Using a spatially-implicit Monte-Carlo approach, we simulated the random  
153 strategy (a) (stop after single empty cell of area  $A$ ) for the spatially uncorrelated  
pest spatial distribution (Poisson and negative binomial) with intensity  $\lambda$  on a  
bounded rectangular spatial domain of area  $M$ . This approach could only work  
156 with spatially uncorrelated distribution given the spatially-implicit nature of  
the process. The management then proceeded as follows. 1) One cell in the  
grid was randomly selected. The number of pest in the cell was drawn from a  
159 Poisson or a negative binomial distribution using, respectively, the R functions  
`rpois` and `rnbinom`. If the initial cell contained no individuals, the survey  
stopped. If it contained at least one individual, all individuals inside it were  
162 surveyed/controlled/eradicated and another cell was chosen at random. 2) This  
same process was repeated for the next cell and the procedure was repeated until  
either no individuals were found in a quadrat, all the cells in the management  
165 area were surveyed, or the budget was reached. Note that the random selection  
of a new cell was from the cells that had not already been surveyed. Since the  
survey area  $A$  could be considerably large, when a step would put managers over  
168 the budget, only the fraction of the area allowed by the budget was managed.

### 2.2.2. Random Strategy (b): stop after $S$ empty cells

For the random search strategy (b), we used a spatially-explicit individual-  
171 based model that we simulated on all four pest spatial distributions. This

model was computationally intensive compared to the Monte-Carlo approach so we did not use it for strategy (a). The random search strategy (b) consisted of randomly choosing cells without replacement and removing any pest contained in it. The process stopped when it reached the budget or the maximum number of empty cells surveyed in a row ( $S$ ), whose value depended on the scenario. We depleted the budget in two ways depending on the scenario: by deducting the cost of surveying a cell ( $\delta$ ) \* the number of cells surveyed at this step, and by deducting the cost of removing a pest item ( $\gamma$ ) \* the number of pest items removed at this step. We did not take any action/step that would put managers over the budget.

### *2.2.3. Adaptive cluster sampling strategy*

In the adaptive cluster sampling strategy, we chose an initial cell to survey. If at least one pest was present in the cell, we added the 4 adjacent neighbouring cells to the survey (Von Neumann neighbourhood). We repeated this around the new cells that contained pests. At each step, we removed pests found in the surveyed cells. If we found no pest in the initial cell or in all of the neighbouring cell at some step, we chose a new initial cell randomly and the process resumed. The process stopped when it reached the budget or the maximum number of empty cells surveyed in a row ( $S$ ). See Fig. 3 for an illustration of this process. Again, we depleted the budget allowance by an amount defined by the cost of surveying a cell ( $\delta$ ) \* the number of cells surveyed at this step, and the cost of removing a pest item ( $\gamma$ ) \* the number of pest items removed at this step. Since the added neighbourhood could be of considerable size, when a step would put managers over the budget, only the fraction of the area allowed by the budget was managed.

The random strategy (b) (stop after  $S$  empty cells) and the adaptive cluster sampling strategy were deployed on all four pest distributions and the grid applied on the domain had cells of constant size  $1 \times 1$ .

For the strategies simulated with a spatially-explicit model (random strategy (b) and adaptive cluster sampling), we defined, for simplicity, the domain as a

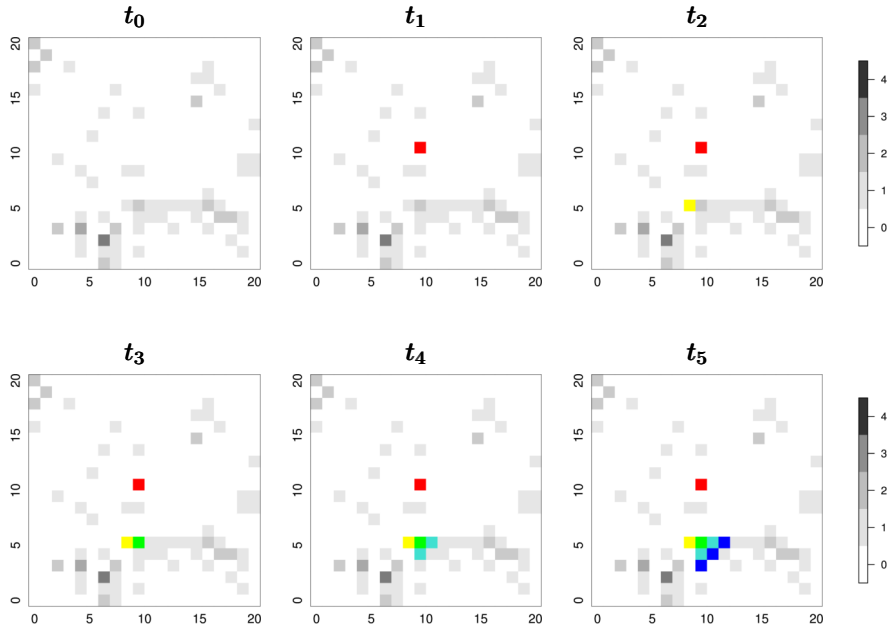


Figure 3: Step by step images of the adaptive cluster sampling strategy inspecting a clustered (Neyman-Scott process) spatial distributions of pests (in shades of grey: from white, zero individual, to the darkest grey, four individuals) on a  $20 \times 20$  lattice with an intensity of 0.2 individual per grid cell. The colors represent the steps taken by the algorithm. The first step (in red) hit an empty cell so another cell is chosen at random (in yellow). The yellow cell contains one individual so it is removed and the 4 cells of the Von Neumann neighbourhood are surveyed. One of them contains individuals (in green). Individuals are removed and the neighbourhood of the green cell is surveyed. In this neighbourhood, two cells contain individuals (in turquoise) so they are removed and the Von Neumann neighbourhood of both cells is surveyed. In this new neighbourhood, three cells contains individuals (in blue). The process goes on.

torus, which means that when a manager traversed the border of the domain, the manager reappeared on the other side of the domain.

### 204 2.3. Mathematical Models

We derived mathematical models of the random sampling in which man-  
 207 agement stops after the manager discovers one empty cell of area  $A$  (random  
 strategy (a) described in §2.2.1) and the manager random sampling in which the

manager stops searching after  $S$  consecutive empty size-1 cells (random strategy (b) described in §2.2.2) for pest distributions that are spatially uncorrelated  
 210 from one cell to another (Poisson and Negative binomial spatial distributions).

2.3.1. *Random Strategy (a): stop after single empty cell of area  $A$*

The probability of finding at least one individual in a grid cell of area  $A$   
 213 ( $A < M$ ) with a Poisson spatial distribution of individuals is

$$Pr(X > 0; \lambda, A) = 1 - \exp(-\lambda A) = \phi. \quad (1)$$

Note that  $\phi < 1$ . We can then write an expression for the expected area explored by managers ( $D$ ) using a strategy like the one described in the previous section.  
 216 We can call this the '*area of discovery*' to connect it to the functional response ideas.

$$\begin{aligned} D(\lambda, A, M) &= A(1 + \phi + \phi^2 + \dots + \phi^{M/A-1}), \\ &= A \left( \sum_{i=0}^{M/A-1} \phi^i \right), \\ &= A \left( \frac{1 - \phi^{M/A}}{1 - \phi} \right). \end{aligned} \quad (2)$$

Note that in equation (2) managers are unable to explore more area than there  
 219 is in the management area  $M$  and so the maximum number of quadrats is  $M/A$ . The number of pests that are eradicated/controlled/surveyed ( $E$ ) is proportional to the area explored

$$E(\lambda, A, M) = D(\lambda, A, M)\lambda, \quad (3)$$

222 Therefore, the number of pests that are eradicated/controlled/surveyed is

$$E(\lambda, A, M) = A\lambda \left( \frac{1 - \phi^{M/A}}{1 - \phi} \right). \quad (4)$$

If there is a limited management budget  $B$ , each quadrat costs  $\delta$ , and the cost  $\gamma$  is associated with eradicating each pest in addition to treating an infested

225 cell, then the maximum number of quadrats of area  $A$  that can be explored is  
 $\frac{B}{A(\lambda\gamma+\delta)} \leq \frac{M}{A}$ . We assume that the budget restricts exploration such that an  
area less than the full area of the management zone can be explored. The idea of  
228 adding a budget, a cost per quadrat, and a cost per individual is similar to divid-  
ing the total foraging time into searching time and handling time in the Holling's  
disc equation. The number of pests that are eradicated/controlled/surveyed be-  
231 comes

$$E(\lambda, A, B, \delta, \gamma) = A\lambda \left( \frac{1 - \phi^{\frac{B}{A(\lambda\gamma+\delta)}}}{1 - \phi} \right). \quad (5)$$

If instead we assume that individuals are distributed according to the Negative  
binomial distribution and that the number of pests in any cell is independent  
234 of the number in any other cell, we write for a cell of area 1

$$Pr(X > 0; \lambda, k) = 1 - \left( 1 + \frac{\lambda}{k} \right)^{-k} = \phi. \quad (6)$$

In equation (6),  $k$  represents the amount of clustering from one cell to another  
with small  $k$  corresponding a high degree of clustering.

237 For cells of area  $A > 1$ , the Negative binomial distributed pest data would have  
a different spatial resolution as we sample on cells of area  $A$ . Equation (6)  
becomes then:

$$Pr(X > 0; \lambda, A, k) = 1 - \left( 1 + \frac{\lambda A}{k} \right)^{-k} = \phi. \quad (7)$$

240 As  $k \rightarrow \infty$ , equation (7) converges to the Poisson case given by equation (1).  
The derivations for the numbers of individuals eradicated (Eqs. (4)–(5)) are  
still valid for this case.

Table 2: Expected number of pests controlled ( $E$ ) for random strategy (a).

Spatial distribution	$E$	$\phi$
Poisson	Eq.(5): $A\lambda \left( \frac{1 - \phi^{\frac{B}{A(\lambda\gamma+\delta)}}}{1 - \phi} \right)$	Eq.(1): $1 - \exp(-\lambda A)$
Negative binomial	Eq.(5): $A\lambda \left( \frac{1 - \phi^{\frac{B}{A(\lambda\gamma+\delta)}}}{1 - \phi} \right)$	Eq.(7): $1 - \left( 1 + \frac{\lambda A}{k} \right)^{-k}$

243 Table 2 summarizes the equations used for the expected number of pests controlled depending on the pest spatial distribution for random strategy (a).

244 *2.3.2. Random Strategy (b): stop after S empty cells*

246 In strategy (a),  $A$  represents the cell area or the survey of  $A$  contiguous size-1 cells and the process stops after one empty step. In strategy (b), however, the manager surveys an integer number  $S$  of empty cells before stopping. The  
 249 main difference between random strategy (a) and random strategy (b) is that the expected number of individuals removed by exploring  $A$  contiguous size-1 cells would, in theory, be affected by the spatial distribution of individuals while  
 252 exploring  $S$  randomly picked size-1 cells would not. Below we compare mathematical models of the management functional response for random manager searches when pests are distributed according to a Poisson point process and  
 255 when pests are distributed according to a negative binomial point process. Our derivations illustrate that the expected number of individuals removed can depend on the pest distribution when multiple empty cells are required before the  
 258 manager stops looking for additional pests.

In the case of a Poisson distributed resource, from equation (1), we get the probability that a cell  $i$  of area  $A$  has zero individuals:

$$Pr(X_i = 0; \lambda, A) = \exp(-\lambda A) = \psi_A. \quad (8)$$

261 The probability that  $S$  different cells of area  $A$  have zero individuals in each cell is:

$$\begin{aligned} Pr(X_{1,\dots,S} = 0; \lambda, A, S) &= (\psi_A)^S & (9) \\ &= (\exp(-\lambda A))^S \\ &= \exp(-\lambda AS). \end{aligned}$$

$A$  and  $S$  being multiplied, the probability that a cell ( $S = 1$ ) of area  $A = x$  has  
 264 zero individuals ( $\psi_A^1$ ) is the same as the probability that  $x$  different size-1 cells ( $S = x, A = 1$ ) have zero individuals in each cell ( $\psi_1^x$ ). So in this context,  $\psi_A^1 = \psi_1^S$ . For this reason, the mean number of individuals managed obtained from

267 the simulation process described above should match the analytical solution  
provided in equation (5) using equation (1).

In the case of a resource distributed with a negative binomial distribution, from  
270 equation (7), we get the probability that a cell  $i$  of area  $A$  has zero individuals:

$$Pr(X_i = 0; \lambda, A, k) = \left(1 + \frac{\lambda A}{k}\right)^{-k} = \psi_A. \quad (10)$$

The probability that  $S$  different cells of area  $A$  have zero individuals in each cell  
is:

$$\begin{aligned} Pr(X_{1,\dots,S} = 0; \lambda, A, S, k) &= (\psi_A)^S & (11) \\ &= \left(\left(1 + \frac{\lambda A}{k}\right)^{-k}\right)^S \\ &= \left(1 + \frac{\lambda A}{k}\right)^{-kS}. \end{aligned}$$

273 In this case,  $A$  and  $S$  are not multiplied, so the probability that a cell ( $S = 1$ )  
of area  $A = x$  has zero individuals ( $\psi_A^1$ ) is generally not equal to the probability  
that  $x$  different size-1 cells ( $S = x, A = 1$ ) have zero individuals in each cell ( $\psi_1^S$ ).

276 So in this context,  $\psi_A^1 \neq \psi_1^S$ . The mean number of individuals managed obtained  
from the simulation process described above should generally not match the  
analytical solution provided in equation (5) using equation (7). In this case,  
279 instead of equation (7), we can use

$$Pr(X_S > 0; \lambda, A, S, k) = 1 - \left(1 + \frac{\lambda A}{k}\right)^{-kS} = \phi. \quad (12)$$

Table 3 summarizes the equations used for the expected number of pests controlled  
using the random strategy (b) depending on the pest spatial distribution.

Table 3: Expected number of pests controlled (E) for random strategy (b).

Spatial distribution	E	$\phi$
Poisson	Eq.(5): $A\lambda \left(\frac{1-\phi \frac{B}{A(\lambda\gamma+\delta)}}{1-\phi}\right)$	1- Eq.(9): $1 - \exp(-\lambda AS)$
Negative binomial	Eq.(5): $A\lambda \left(\frac{1-\phi \frac{B}{A(\lambda\gamma+\delta)}}{1-\phi}\right)$	Eq.(12): $1 - \left(1 + \frac{\lambda A}{k}\right)^{-kS}$

282 *2.4. Correspondence with functional responses types*

To compare human-pest management to functional response in predator-prey interactions, we considered that pests to managers were like prey to predators in the functional response framework. We then assumed that the budget allocated to a manager corresponded to the foraging time for a predator. Keeping the comparison between monetary and temporal costs in mind and with the assumption that the behaviour “processing food/pest” is independent from the behaviour “searching for food/pest”, we could make the correspondence between the time needed to search for a prey and the monetary cost requested to search for a pest (survey), and between the time needed to consume a prey and the monetary cost requested to remove a pest. In a Type I functional response scenario, the predator is not affected by its capacity to consume a prey so the number of prey consumed increases linearly with the intensity of prey in the domain. Thus, by setting the cost of removing a pest item ( $\gamma$ ) to 0, we expected to obtain a linear relationship (Holling Type I) between the number of pest removed and the intensity of pests in the domain. In a Type II functional response scenario, the predator is limited by its capacity to consume a prey so as the intensity of prey in the domain increases, the predator cannot consume more than a certain number of prey and the curve saturates. Thus, by setting the cost of removing a pest item ( $\gamma$ ) to be larger than 0 while maintaining a large search area ( $A$  and  $S$  both impact the search area), we expected to obtain a hyperbolic relationship (Holling Type II) between the number of pest removed for a fixed cost and the intensity of pests in the domain. In a Type III functional response scenario, at low intensities of prey, some mechanisms make it more difficult for the predator to find and consume a prey than at higher intensities. Some researchers explain this concept using predators’ behaviour (Turchin 2013). A generalist predator might switch to another prey when the focus prey density is too low leading to a Type III whereas a specialist would have no choice but to continue searching for the focus prey leading to a Type II. In a pest management context, a manager might act like a specialist by wanting to remove all pest or like a generalist by being satisfied with a low pest number



and switching to another management activity. Thus, by setting the maximum number of empty cells surveyed in a row before stopping ( $S$ ) (or its equivalent  
315  $A$ : number of contiguous size-1 cells, see previous section) to a low number and by setting  $\gamma > 0$ , we would expect that equation (5) takes the sigmoid shape of a Type III functional response. We thereby simulate a manager estimating that  
318 the probability of encountering a pest is too low to be worth the search effort at a low pest density.

## 2.5. Application

321 We applied our modelling framework to the mountain pine beetle (*Dendroctonus ponderosae*, Hopkins 1902) management in Cypress Hills, Saskatchewan, Canada. The mountain pine beetle is a bark beetle that infests and kills pine  
324 trees in western North-America. Mountain pine beetles have two main population stages: an endemic stage in which there are not enough individuals to overcome healthy trees, so populations persist by attacking damaged trees in  
327 association with other bark beetles, and an epidemic stage in which mountain pine beetles are a threat to vast stands of healthy pines. There are currently several epidemic populations, including one in the Cypress Hills park. Mountain  
330 pine beetle populations exhibit a type of Allee effect (Allee 1931; Stephens et al. 1999): below a certain number of individuals, a local epidemic population cannot persist and will either go extinct or turn to an endemic population stage.

### 333 2.5.1. Pest spatial distribution

During an epidemic, the attacked trees are usually spatially aggregated due to beetle offspring emerging from one previously attacked tree and attacking  
336 susceptible trees within several hundred meters (Safranyik and Carroll 2006; Robertson et al. 2007). This pattern resembles the Neyman-Scott process described in section 2.1.3. Therefore, we fitted a Neyman-Scott process to attacked  
339 trees locations in 2011 and 2012 from several portions of the park with different pest densities using the `vargamma.estpcf` function of the R package `spatstat`. This function uses the pair correlation function to fit the point process to a

342 point pattern by the method of minimum contrast.

In addition to the parameter values, we modified the Neyman-Scott process in our simulations to draw points around parents from a fat-tail distribution (here  
345 an exponential distribution) which corresponds better to the mountain pine beetle behaviour than a Gaussian distribution due to the occurrence of long-distance dispersal events (Safranyik and Carroll 2006; Robertson et al. 2007; Goodsman et al. 2016).

### 2.5.2. Management strategy

The management strategy implemented in Cypress Hills consists of locating  
351 previously attacked trees (red-top trees easily detectable during aerial surveys) and surveying the surrounding neighbourhood for new attacks. We simulated this process by adapting the adaptive cluster sampling strategy. The strategy is  
354 deployed at the location of previously attacked trees instead of random locations. The process continues until all cells containing previously attacked trees are surveyed. We set the managers ability to detect newly attacked trees within  
357 the survey area to 89% (value obtained for Cypress Hills from M. Kunegel-Lion, unpublished data).

### 2.5.3. Simulations

360 Using the fitted pest spatial distribution and the modified adaptive cluster sampling strategy, we simulated the management process 10 000 times for each pest density on a 6.5×9.9km rectangular domain with grid cells of size  
363 100×100m. Thus, the grain and extent of the domain is the same order of magnitude as the grain and extent of the management area in Cypress Hills. The management costs ( $\delta$  and  $\gamma$ ), and the total budget ( $B$ ) values were chosen as  
366 proportional to the actual costs and budget in the park for 2011 and 2012. We then compared the curve obtained to actual numbers of attacked trees controlled in several areas of the park presenting different densities of attacked trees during  
369 2011 and 2012.

#### 2.5.4. Management goal feasibility

Knowing about management functional responses shape can help us assess  
372 the feasibility of a management goal. We chose two ways of expressing a man-  
agement goal: 1) managers would like to remove at least  $x\%$  of all the pests,  
and 2) managers would like to leave no more than  $x$  individuals per unit of  
375 area. This second management goal makes sense for populations exhibiting an  
Allee effect, as the mountain pine beetle does. Indeed, it is not necessary to  
put more effort into control when the pest population will not persist below a  
378 certain number. We simulated the management process described above 1000  
times for increasing budget values and compared the management functional  
response curves obtained to the two management goals. To place the functional  
381 response curves and the management goals on the same scale, we divided the  
number of individuals removed by the domain area, thereby graphing the den-  
sity of pest controlled by the total pest density. Note that this only changed  
384 the  $y$ -axis scale and therefore the interpretation of the curve did not change.

### 3. Results

For each combination of pest distribution, management strategy, and pa-  
387 rameter values, we compared the means of 2000 simulations to the analytical  
solutions, when calculated. The budget value used in the simulations and an-  
alytical solutions was 300, limiting the number of cells managers can explore.  
390 The values of  $\delta$  and  $\gamma$  were either 10 or 0 and the values of  $A$  and  $S$  either  
64 (one  $8\times 8$ -cell or 64  $1\times 1$ -cells), 4 (one  $2\times 2$ -cell or four  $1\times 1$ -cells) or 1 (one  
 $1\times 1$ -cell) depending on the scenario. We generated all negative binomial point  
393 processes using the parameter  $k = 1$  in both the simulations and the analytical  
solution.

#### 3.1. Varying the management costs

396 When the cost of surveying a cell  $\delta$  increases, the functional response slope  
decreases and when the cost of removing a pest item  $\gamma$  increases, the functional

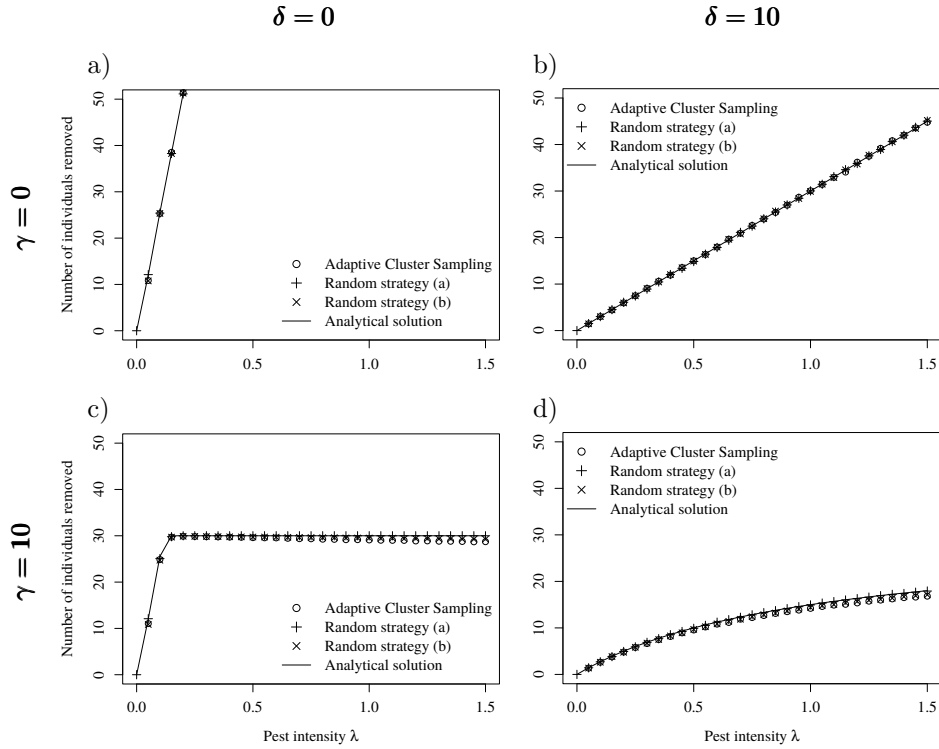


Figure 4: Functional response curves when varying the management costs ( $\delta$  the cost of surveying a cell and  $\gamma$  the cost of removing a pest) for fixed values of  $A = 64$  and  $S = 1$  for the random strategy (a) and  $A = 1$  and  $S = 64$  for the random strategy (b) and the adaptive cluster sampling strategy, and for a Poisson pest spatial distribution. Circles represent the means of 2000 simulations of the adaptive cluster sampling strategy, pluses of the random strategy (a), and crosses of the random strategy (b). Solid lines represent the values for the analytical solution of random strategy (a) and (b).

response curve saturates as seen on Fig. 4 for the Poisson distribution. This  
 399 is true for all the management strategies and their analytical solutions on all  
 pest distributions. Note that the curve on Fig. 4a) continues to increase linearly  
 above 50 individuals removed. See appendix A for the non-truncated graph.

402 *3.2. Varying the management strategy and the pest spatial distribution*

For a Poisson pest spatial distribution, the functional response curves for  
 the simulations of the random strategies (a) and (b) are the same as predicted

405 by the derivations of analytical solutions. For a negative binomial pest spatial  
distribution, the functional response curves for the simulations of the random  
strategies (a) and (b) are extremely similar even though the expected means  
408 differ due to a different pest spatial resolution. This can be seen on Fig. 5.

Unexpectedly, the pest spatial distribution does little to change the functional  
response curves. The adaptive cluster sampling and the random strategies  
411 present the same pattern with little variation from one strategy to another  
except for Neyman-Scott and regular pest spatial distribution. Indeed for a  
Neyman-Scott distribution, the adaptive cluster sampling strategy does often  
414 better than the random strategy (b) especially for the parameters values  $\delta = 10$ ,  
 $\gamma = 0$  (Fig. 5). For a regular distribution, the adaptive cluster sampling strat-  
egy results in oscillations around the random strategy mean especially for the  
417 parameters values  $\delta = 10$ ,  $\gamma = 0$  (Fig. 5).

### 3.3. Varying the search area

As expected, decreasing the search area, as represented by  $A$  or  $S$  (see Meth-  
420 ods section), decreases the number of pests found and controlled at low pest in-  
tensity levels for both random strategies and leads to a curve resembling a Type  
III when  $\gamma = 10$  (Fig. 6). In the Negative binomial case, there are differences  
423 between random strategies which might be due to the difference between  $A$  and  
 $S$  as shown in equation (12) or to the difference in the pest spatial resolution  
when  $A = 1$  and when  $A > 1$ . Those two cases cannot be distinguished given  
426 our parameter values.

### 3.4. Theoretical results summary

Additional simulations (see Appendix B) show that when  $A$  or  $S$  are large,  
429 the cost per cell to survey  $\delta > 0$  and the cost per pest to remove  $\gamma \rightarrow 0$ , the  
functional response tended to a Type I. When  $A$  or  $S$  are large,  $\gamma > 0$  and  $\delta \rightarrow 0$ ,  
the functional response tends to a Type I/II which is linear like a Type I at first  
with a progressive saturation like a Type II (Jeschke et al., 2004). When  $\gamma$  and  
432  $\delta > 0$ , the functional response tends to a Type II. To summarize, to obtain a

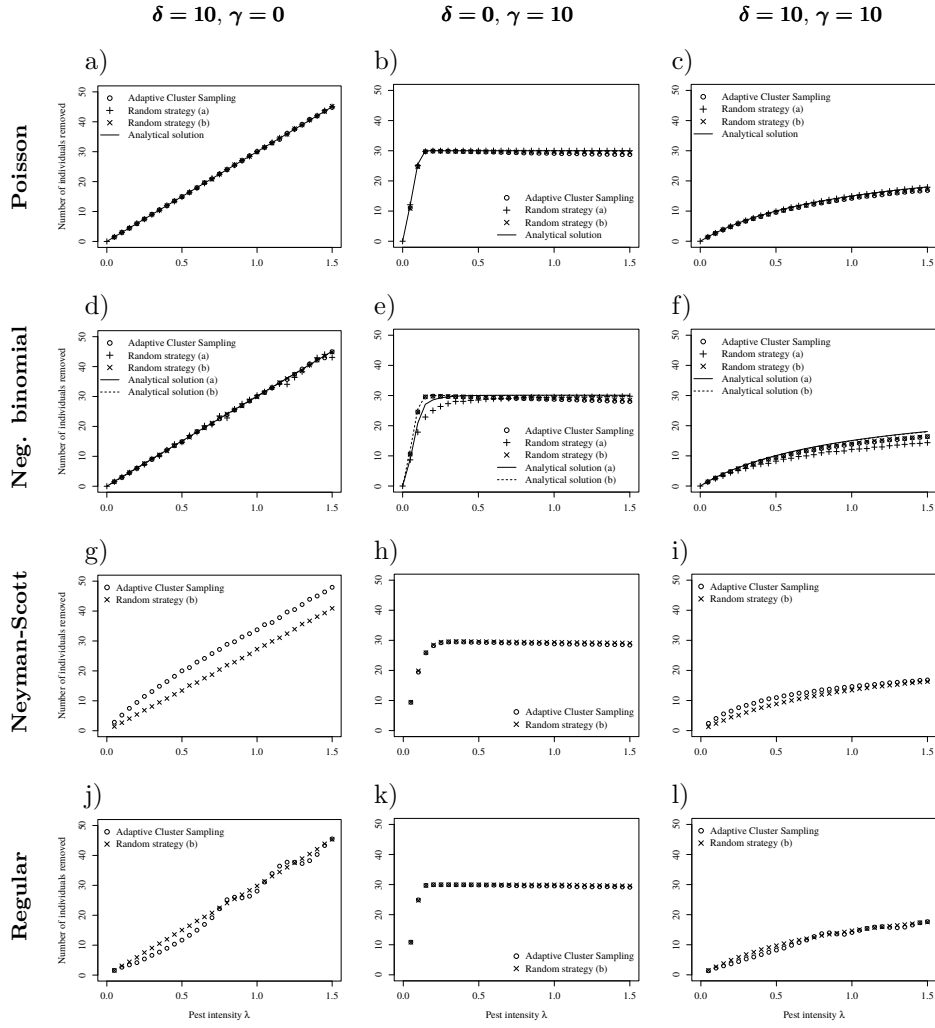


Figure 5: Functional response curves when varying the management strategy and the pest spatial distribution for fixed values of  $A = 64$  and  $S = 1$  for the random strategy (a) and  $A = 1$  and  $S = 64$  for the random strategy (b) and the Adaptive Cluster Sampling strategy. Circles represent the means of 2000 simulations of the Adaptive Cluster Sampling strategy, pluses of the random strategy (a), and crosses of the random strategy (b). Solid lines represent the values for the analytical solution of random strategy (a) and (b) in the Poisson case and for the analytical solution of random strategy (a) in the negative binomial case. Dotted lines represent the values for the analytical solution of random strategy (b) in the negative binomial case.

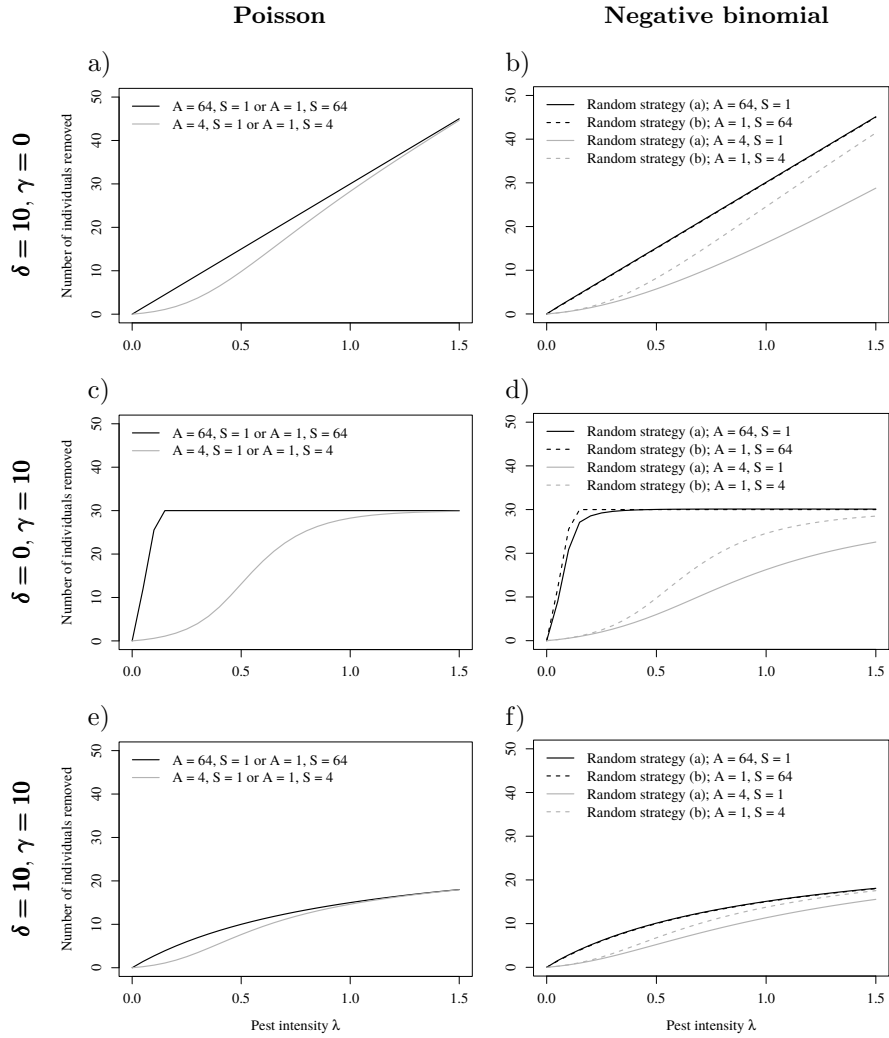


Figure 6: Functional response analytical solutions when varying the cell area  $A$  or the number of empty steps to survey in a row  $S$  for the random strategy (a) and (b). Black lines represent  $A = 64, S = 1$  or  $A = 1, S = 64$  while grey lines represent  $A = 4, S = 1$  or  $A = 1, S = 4$ . Solid lines represent the values for the analytical solution of random strategy (a) and (b) in the Poisson case and for the analytical solution of random strategy (a) in the negative binomial case. Dotted lines represent the values for the analytical solution of random strategy (b) in the negative binomial case.

Type I, we set  $\delta > 0$  and  $\gamma = 0$ . To obtain a Type I/II, we set  $\delta = 0$  and  $\gamma > 0$ .  
 435 To obtain a Type II, we set  $\delta > 0$  and  $\gamma > 0$ . To obtain a Type III, we set  $A$  or  
 $S$  small,  $\delta$  small and  $\gamma > 0$  (Fig. 6).

In addition, variations in budget did not change the qualitative shapes of func-  
 438 tional responses.

In conclusion, the pest spatial distribution did not have a large impact on the  
 functional response shape and neither did the search strategy. However, the  
 441 costs associated with the management strategy as well as the search area had  
 a great impact on the functional response type, as expected. The analytical  
 solutions generally corroborated the simulations although a slight mismatch is  
 444 apparent, especially for the negative binomial case: the mean values from the  
 simulations of random strategies (a) and (b) are below their respective expected  
 means.

447 *3.5. Correspondence with predator functional response*

Using Holling’s disk equation (Holling 1959b; Table 4):

$$N_a = \frac{a'TN}{1 + a'T_h N}, \quad (13)$$

we can compare the parameters from predator and manager functional re-  
 450 sponses. Table 4 summarize the parameter equivalences.

Table 4: Correspondence between predator and manager functional response components.

Predator-prey		Manager-pest	
Nb. of prey items attacked	$N_a$	Nb. of pest items removed	$E$
Prey density	$N$	Pest density	$\lambda$
Total foraging time	$T$	Budget	$B$
Encounter rate	$a'$	Detection rate	$1/\delta$
Handling time	$T_h$	Cost of pest removal	$\gamma$
Slope	$a'T$	Slope	$B/\delta$
Asymptote	$T/T_h$	Asymptote	$B/\gamma$



As stated before, the cost of pest removal ( $\gamma$ ) is the manager equivalent of the handling time ( $T_h$ ). This is corroborated by the similar effect of  $\gamma$  and  $T_h$  on functional responses. Indeed, as seen on Fig 4, introducing this cost causes the apparition of an asymptote in the curve. Likewise, the survey cost ( $\delta$ ) is the manager equivalent of the searching time. At low densities of prey/pest, the predator/manager spends more of its time/budget on searching rather than handling/removing. This is presented in equation 13 by the encounter rate  $a'$ , which represents the searching efficiency or the number of prey items attacked per unit of time at low prey densities. The manager equivalent to  $a'$  would then be  $1/\delta$ . Additionally, the total foraging time ( $T$ ) in predator functional response would be the manager's budget ( $B$ ). Therefore, the slope of the response, corresponding to  $a'T$ , will be  $B/\delta$  and the asymptote, corresponding to  $T/T_h$ ,  $B/\gamma$  (Table 4). For  $\delta = 10$  and  $B = 300$  (Fig. 4b) and d)), the slope at low densities is 30 which corresponds to  $B/\delta = 300/10$ . For  $\gamma = 10$  and  $B = 300$  (Fig. 4c) and d)), the asymptote is 30 which corresponds to  $B/\gamma = 300/10$ . These comparisons hold for different values of  $\delta > 0$  and  $\gamma > 0$  (Appendix B). These equivalences allow us to use equation 13 as an approximation for equation 5 as long as  $A$  is large,  $\delta > 0$ , the management strategy random, and the pest spatial distribution Poisson. See Appendix C for the comparison between the results of equations 5 and 13.

### 3.6. Application

The fitted pest spatial distribution of the mountain pine beetle infested trees has the mean number of points per cluster  $67 \pm 55$  (standard deviation) and the mean cluster size  $266 \pm 131$ . The management strategy has costs of surveying a cell  $\delta = 231$  units and cost of removing a pest  $\gamma = 181$  units for a budget set to 144 000 units.

All actual numbers of attacked trees controlled but one are within 95% of the simulations' distribution as seen on Fig. 7. The remaining number is within 99% of the simulations' distribution. The simulations' mean shows a Type II functional response.

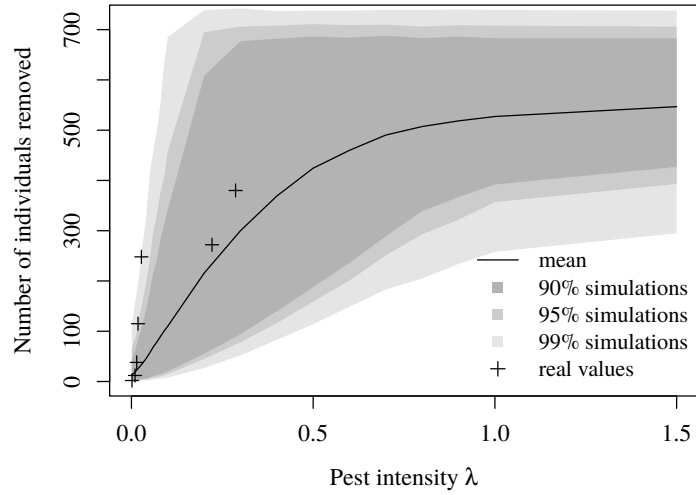


Figure 7: Functional response of the mountain pine beetle management in Cypress Hills, Saskatchewan. The black line represents the mean of 10 000 simulations of the management process. The grey areas represent 90%, 95% and 99% of the simulations' distribution. The points represent the actual values obtained by managers in Cypress Hills in 2011 and 2012.

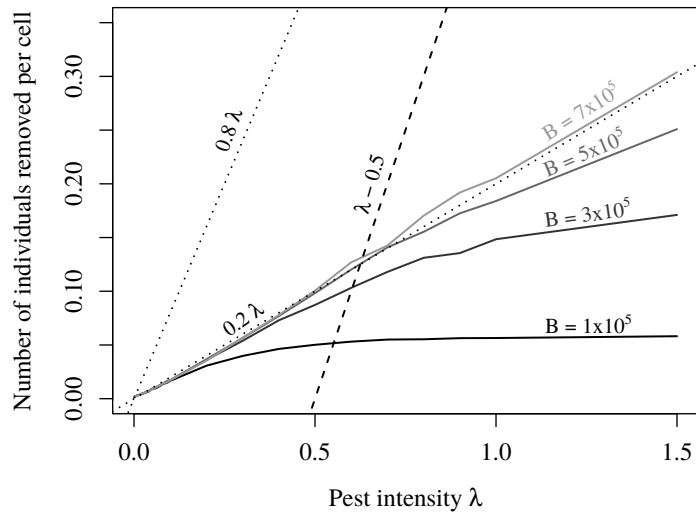


Figure 8: Functional response of the mountain pine beetle management in Cypress Hills, Saskatchewan. Solid lines represent the mean of 1000 simulations of the management process for different budget values:  $1 \times 10^5$ ,  $3 \times 10^5$ ,  $5 \times 10^5$ , and  $7 \times 10^5$ . Dotted lines represent the management goal 1): removing 80% and 20% of all the individuals. The dashed line represents the management goal 2): removing all individuals above the threshold 0.5 individual per cell.

According to Table 4, we expected that an increase in budget would lead to an increase in slope and asymptote. However, our simulations show that the asymptote increases with an increasing budget but the slope does not (Fig. 8). Applying the adaptive cluster sampling search to Cypress Hills instead of the search described in section 2.5 shows that it is the type of search strategy and not the parameter values that is responsible for the constant slope at low pest intensity (see Appendix D). Indeed, the adaptive cluster sampling process searches cells until the budget is reached whereas the process described in section 2.5 only searches cells around a fixed number of previously infested trees which limits the number of individuals managers could control with a certain budget. Fig. 8 also shows the management goals. If the functional response curve is on or above the management line, the goal is reached, otherwise not enough individuals are controlled to meet the management goal. If the desired management efficiency is above 20% removal, the goal is unattainable regardless of the budget (Fig. 8). If, however, the goal is the removal of all individuals above a certain threshold, it is possible to have an effective management at low pest intensity depending on the budget and the threshold value.

#### 4. Discussion

Considering that pests to managers were like prey to predators, we were able to draw an analogy between functional responses in predator-prey interactions and human-pest management. The searching and handling time were replaced by the surveying and removal costs. The costs associated with the management strategy as well as the search area were the main factors influencing the functional response type as expected. The point process and the search strategy impacted the manager efficacy to a lesser extent. Our framework was applied to the mountain pine beetle epidemic in Cypress Hills, Saskatchewan, Canada.

There is a slight mismatch between the analytical solutions of the two random strategies and their simulations. Indeed, the mean values from the simulations are below their respective expected means. In the simulations, if a step

510 would put managers over the budget, only a fraction of the area would be ac-  
tually surveyed and controlled (random strategy (a)) or the step would not be  
taken (random strategy (b)). Therefore, the whole budget might not be used  
513 due to rounding in the calculations and the number of pest controlled would  
then be slightly lower than what it could have been without this process. This  
could explain the differences between simulation means and analytical solutions  
516 of the random strategies (a) and (b). However, the functional response shape  
does not change between the simulations and the analytical solutions. Accord-  
ingly, we can assume that the functional response shapes in the case of the  
519 adaptive cluster sampling and in the case of the Neyman-Scott and regular pest  
distributions are not biased by the budget handling process of the simulations  
although the values might be slightly underestimated.

522 The pest spatial resolution was chosen at the scale of an area- $A$  grid cell. This  
resolution does not impact the Poisson results when the area changes as the  
sum of Poisson-distributed variables is also Poisson-distributed. However, this  
525 is not the case for negative binomially distributed pests. Changing the cell area  
changes the distribution grain. Therefore, random strategies (a) and (b) con-  
sider a different distribution grain for the negative binomial distribution and  
528 the results cannot be compared. For management simulations involving the  
Neyman-Scott and regular distributions, we only consider random strategy (b)  
and the adaptive cluster sampling strategy which have the same cell size  $A = 1$   
531 and, therefore, can be readily compared.

In the functional response theory, the predator distribution is assumed homo-  
geneous. The impact of a clumped predator population on the kill rate lead  
534 to the establishment of the aggregative response theory (Cosner et al. 1999).  
However, the functional response theory originally assumes also a homogeneous  
distribution of prey in the domain. This could weaken the application of this  
537 framework to real systems where the prey distribution is often heterogeneous  
as well as dynamic in time (Arditi and Ginzburg 1989; Ives et al. 1999). Sev-  
eral studies mention this issue. Nachman (2006) found that switching the prey  
540 spatial distribution from random to aggregated changed the functional response

type from a Type II to a Type III as predators adopt a non-random searching behaviour and aggregate in prey clusters. Hossie and Murray (2016) found that  
543 for ratio-dependent functional responses, *i.e.* functional responses depending on the density of predators, the pest spatial distribution changed the functional response shape. Rincon et al. (2017) found that the functional response shape  
546 differs with the difference between the predator and the prey distributions and with the predator foraging strategy. Those studies differ from ours by the fact that several predators interact and the interaction between predator and prey  
549 aggregation patterns lead to a change in the functional response shape. However, in our case of a single predator/manager, we highlight the minimal impact of the point process on the functional response shape. Thus, for prey-dependent  
552 functional responses, in opposition to ratio-dependent functional responses, the prey spatial distribution seems to have little significance.

Similarly, our results show the minimal impact of the management strategy on  
555 the functional response shape. This agrees with Berec et al. (2015) who found that survey spatial arrangements (random or regularly spaced) have little impact on the pest detection probability. This is an important information for  
558 pest managers who can then minimize costs by choosing a cheaper strategy. However, we should keep in mind that when the pest is spatially clustered, a method resembling the adaptive cluster sampling provide slightly better results.  
561 Unlike other studies focused on predator functional responses when the predator uses a random search strategy (*e.g.* Avgar et al. 2011), our results show that the mean number of individuals controlled varies, to some degree, with the  
564 spatial distribution of pests. Avgar et al. (2011) found that when employing a random search strategy, the expected number of individuals managed should be the same regardless of the individual spatial distribution because the prob-  
567 ability to have at least one individual in a random cell becomes independent of the adjacent cells. If we take into account the specifics of our study, we can explain the difference. Considering random search strategy (a): multiple con-  
570 tiguous size-1 cells are randomly selected so the number of individuals controlled is spatially correlated for the Neyman-Scott and regular processes. Therefore,

the expected number of individuals managed in those cases will be different  
573 than the expected number of individuals managed from a Poisson process or a  
negative binomial distribution. The Poisson and negative binomial cases should  
have the same means since the cells are not spatially correlated. Considering  
576 random search strategy (b): with a Neyman-Scott spatial pattern it is more  
likely to get multiple consecutive empty cells before stopping than for a Poisson  
spatial pattern. For a regular pattern, it is less likely. The expected number of  
579 individuals managed for a Neyman-Scott and regular processes would be differ-  
ent than for a Poisson process or a negative binomial distribution. Again, the  
Poisson and negative binomial cases should have the same means since the cells  
582 are not spatially correlated.

We show that non-random search (adaptive cluster sampling) on an aggregated  
pest spatial distribution such as the one produced by a Neyman-Scott process  
585 leads to higher numbers of pest controlled than on a random pest distribution.  
However, this is not the case on a Negative binomial distribution. This differ-  
ence is due to the details of the adaptive cluster sampling process. Indeed, in  
588 this strategy, the managers make decisions on which cells to survey. Considering  
that the Neyman-Scott process produces aggregation among cells whereas the  
Negative binomial process produces aggregation within cells with the among-  
591 cell pattern resembling a random pattern, it makes sense for the random and  
adaptive cluster sampling strategies to be similar on a Negative binomial pest  
spatial distribution but different on a Neyman-Scott distribution. Managers  
594 following a non-random search strategy on a Neyman-Scott pest spatial distri-  
bution are more efficient than managers following a random search since they  
explore the neighbouring cells when they find pests in a cell. This result agrees  
597 with Nachman (2006) who found in the analysis of their predator-prey model  
that predators searching non-randomly on an aggregated prey distribution have  
higher predation rates than random search.

600 Functional response theory is widely used to assess the impact of a predator on  
a prey population (*e.g.* Messier 1994; Finke and Denno 2002). This framework  
provides a well-studied and reliable method to assess the impact of management

603 on a pest population. Furthermore, knowing aspects of the functional response  
can inform pest management in several different ways. Human management  
could be efficiently and quantitatively compared to other control methods such  
606 as biological control. This idea would be extended to give comparisons across  
different methods and different locations. For instance, different methods could  
be compared at the same location or the same method could be compared at  
609 different locations by contrasting functional response curves obtained analyti-  
cally or by simulation.

To give further insight, manager functional responses could be included in dy-  
612 namical systems to represent human impact on a pest population. For example,  
in the Cypress Hills case, future steps could include using this functional re-  
sponse in a population dynamics model to study the evolution of the beetle  
615 population over the years with a realistic incorporation of the management ef-  
fect on the population. In the same way functional response curves inform  
about stability of predator-prey interactions (Dick et al. 2013), in our study,  
618 they could tell managers whether control would leave a refuge for the pest or  
lead to the pest extinction. Indeed, in a Type III functional response scenario,  
management is less efficient at low pest densities and, thus, small pest popula-  
621 tions could persist (Murdoch and Oaten 1975). However in a Type II functional  
response scenario most pest would be eradicated, even if they occur at low den-  
sity (Hassell 1978). With respect to control of mountain pine beetle in Cypress  
624 Hills, the Type II functional response suggests a high efficiency of managers  
at low pest densities. This is consistent with the strict management policy in  
Cypress Hills to try to control all infested trees. The fact that true values for  
627 the number of individuals controlled lie above those simulated in Fig. 7 suggests  
that managers in Cypress Hills are likely finding the means to make the process  
even more efficient than our model would predict.

630 From a practical perspective, managers are typically interested in controlling  
a certain proportion of pests, given an environmental context and a particu-  
lar strategy. For example, in some areas of the province of Alberta, Canada,  
633 infested by the mountain pine beetle, the management goal is to reduce pop-

ulations by 80% (Alberta Sustainable Resource Development 2007) using individual tree removal. Our model results, as shown in Fig. 7 and 8, allow for such a calculation to be made. By comparing this goal to the detection and control rate (= slope of the functional response curve; equivalent to the attack rate), the management functional response can give direct insights on the goal feasibility. We illustrated this point using the Cypress Hills case study. The results showed that an 80% control efficiency, such as the target used in some areas in Alberta, would not be feasible in Cypress Hills given the current management strategy and parameters values. If the functional response resembled a type III instead of a type II, there could be cases where management would be efficient only at intermediate pest intensity. However, decreasing the pest population below a certain threshold would be more appropriate than a removal percentage in the Cypress Hills case. Goodsman and Lewis (2016) found Allee threshold values of  $3.789 \times 10^{-4}$  and  $5.311 \times 10^{-5}$  infested stems per  $\text{m}^2$  for two times series of mountain pine beetle infestation in central Idaho. Therefore, a management threshold of 0.5 individuals per  $100 \times 100\text{m}$  cell such as the one used in the Cypress Hills example would be below such Allee threshold. Moreover, we showed that the pest intensity in Cypress Hills is always below 0.5 individual per cell which means that managers are probably efficiently reducing local mountain pine beetle populations below the Allee threshold. However, a non-spatial Allee threshold could be an issue as the within-tree productivity of the beetle varies in time and space (Goodsman and Lewis 2016). As an alternative, varying the management strategy, such as adding search locations beyond the neighbourhood of previously infested trees until the budget is reached, would allow managers to meet a certain removal percentage depending on the budget amount.

In summary, functional response is a tool to help pest management, for example by providing a means to assess current strategies, to compare with alternative strategies, to test various strategies *in silico* before implementation, to provide a realistic control component in a population dynamics model, and to assess the feasibility of a management goal.



One constraint to the application of this method, as in regular functional  
666 response studies, is the need for several levels of pest density to be able to draw  
a functional response curve. In our application to mountain pine beetle, we  
got around this issue by dividing the infested area in portions of different pest  
669 densities. This might not be sufficient to draw an entire functional response  
curve but simple simulations could help complete the curve in this case.

Researchers often complement the functional response with a numerical response  
672 in predator numbers and sometimes an aggregative response describing the dis-  
tribution of predators (Turchin 2013). We could argue that in a human-pest  
management scenario, the numerical and aggregative responses are negligible or  
675 even non-existent. Indeed, the number or aggregation level of managers might  
not be relevant for two reasons: 1) managers usually group as a team/unit, in  
our study, this unit represent “the manager” and 2) there is no competition  
678 between managers or teams, when enough persons are present to make sev-  
eral teams they often do not survey the same area but rather divide the entire  
management domain between themselves in order to be efficient. However, one  
681 could study the social impact of pest management and thus be interested in  
new hires in response to an increasing pest abundance. This could be modelled  
by a growing manager population and be analogous to predator numerical re-  
684 sponses. Finally, the cost of moving from one location to another was not taken  
into account in our study for simplicity but it could be added easily.

To conclude, the functional response framework can be adapted to model  
687 human-pest interactions and provide insights on management. Furthermore,  
this framework could be generalized to any interaction involving humans “pre-  
dating” on their environment. Indeed, instead of managing pest species, the  
690 goal could simply be the study of human impact on a resource or species at  
risk. The shape of the functional response curve would then inform us about  
the quantitative influence humans have on certain populations and could be  
693 included in harvest models.

## Appendices

### Appendix A

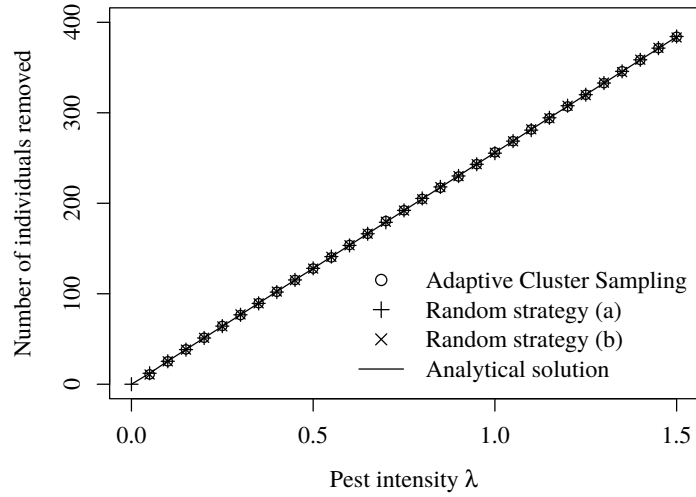


Figure A.1: Functional response curves for fixed values of  $\delta = 0$ ,  $\gamma = 0$ ,  $A = 64$  and  $S = 1$  for the random strategy (a) and  $A = 1$  and  $S = 64$  for the random strategy (b) and the Adaptive Cluster Sampling strategy, and for a Poisson pest spatial distribution. Circles represent the means of 2000 simulations of the Adaptive Cluster Sampling strategy, pluses of the random strategy (a), and crosses of the random strategy (b). Solid lines represent the values for the analytical solution of random strategy (a) and (b).

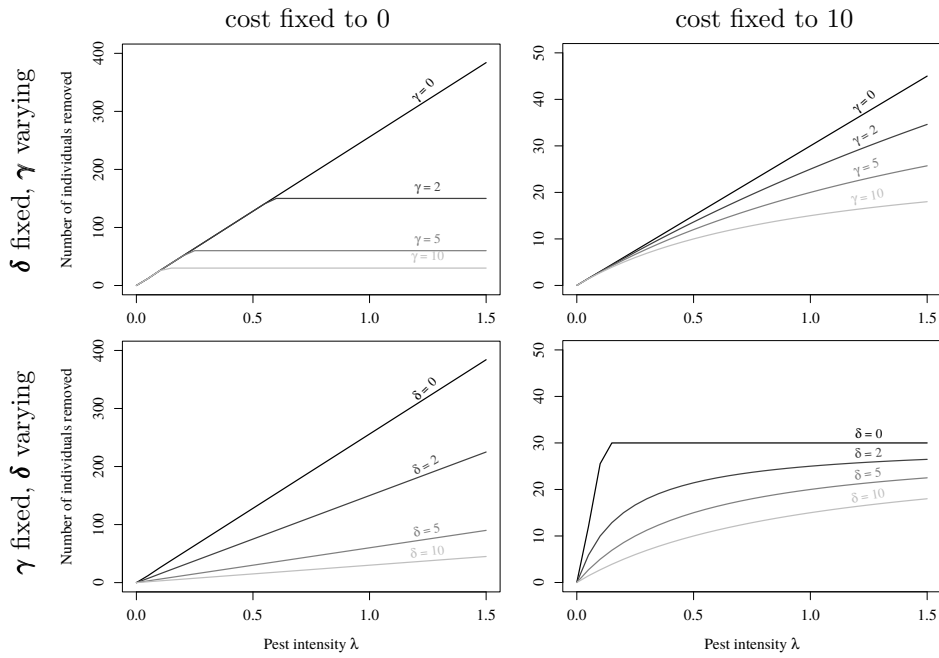


Figure B.1: Functional response curves showing the impact of one of the cost parameters (the survey cost  $\delta$  or the removal cost  $\gamma$ ) when the other is fixed for the random strategies (a) and (b) on a Poisson pest spatial distribution. The shades of grey represent the values for the varying cost parameter from black (cost = 0) to light grey (cost = 10). The search area is set to 64 and the budget to 300.

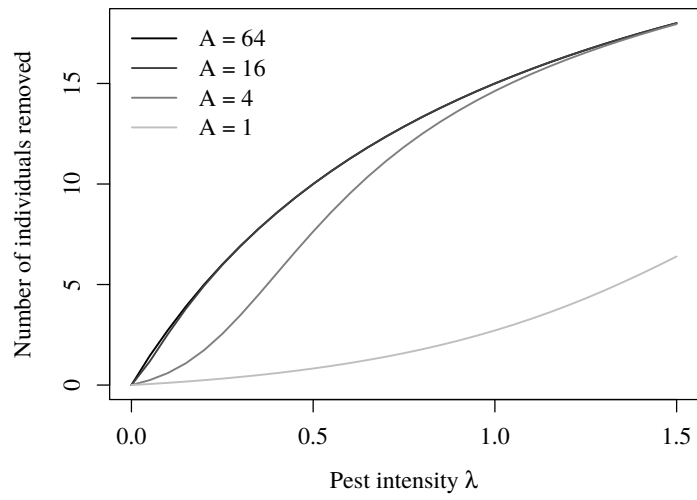


Figure B.2: Functional response curves for fixed values of survey cost  $\delta = 10$ , removal cost  $\gamma = 10$  and for the random strategies (a) and (b) on a Poisson pest spatial distribution. The shades of grey represent the values of the search area  $A$ : light grey  $A = 1$  to black  $A = 64$ .

Appendix C

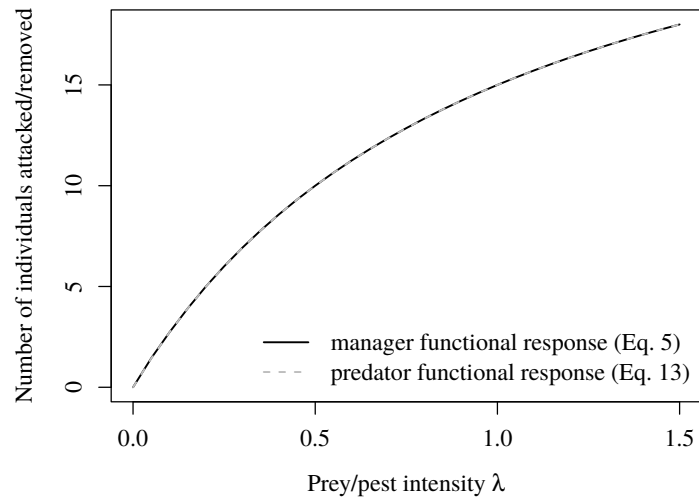


Figure C.1: Functional response curves for fixed values of survey cost  $\delta = 10$ , removal cost  $\gamma = 10$  and for a random strategy on a Poisson pest spatial distribution. The search area is set to 64 and the budget to 300. The black solid line represents the result of equation 5 and the grey dotted line represents the result of equation 13.

Appendix D

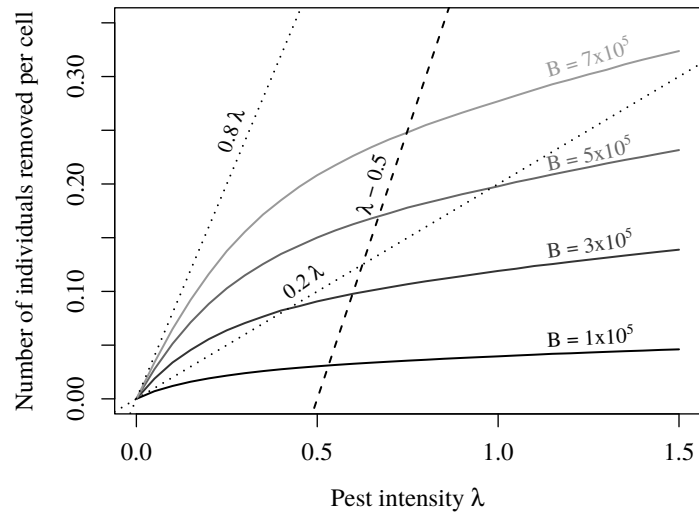


Figure D.1: Functional response of the mountain pine beetle management in Cypress Hills, Saskatchewan using the adaptive cluster sampling process. Solid lines represent the mean of 1000 simulations of the management process for different budget values:  $1 \times 10^5$ ,  $3 \times 10^5$ ,  $5 \times 10^5$ , and  $7 \times 10^5$ . Dotted lines represent the management goal 1): removing 80% and 20% of all the individuals. The dashed line represent the management goal 2): removing all individuals above the threshold 0.5 individual per cell

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**References**

Alberta Sustainable Resource Development, 2007. Mountain Pine Beetle Management Strategy.  
714

Allee, W.C., 1931. Animal aggregations, in: A study in general sociology. The University of Chicago Press, Chicago.

717 Arditi, R., Ginzburg, L.R., 1989. Coupling in predator-prey dynamics: ratio-dependence. *Journal of theoretical biology* 139, 311–326.

Avgar, T., Kuefler, D., Fryxell, J.M., 2011. Linking Rates of Diffusion and  
720 Consumption in Relation to Resources. *The American Naturalist* 178, 182–190. doi:10.1086/660825.

Baddeley, A., Rubak, E., Turner, R., 2015. Spatial Point Patterns: Methodology  
723 and Applications with R. Chapman and Hall/CRC Press, London.

Berec, L., Kean, J.M., Epanchin-Niell, R., Liebhold, A.M., Haight, R.G., 2015. Designing efficient surveys: spatial arrangement of sample points

- 726 for detection of invasive species. *Biological Invasions* 17, 445–459.  
doi:10.1007/s10530-014-0742-x.
- Cosner, C., DeAngelis, D.L., Ault, J.S., Olson, D.B., 1999. Effects of Spatial  
729 Grouping on the Functional Response of Predators. *Theoretical Population  
Biology* 56, 65–75. doi:10.1006/tpbi.1999.1414.
- Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J.,  
732 Robinson, T.B., Kumschick, S., Weyl, O.L.F., Dunn, A.M., Hatcher, M.J.,  
Paterson, R.A., Farnsworth, K.D., Richardson, D.M., 2013. Advancing im-  
pact prediction and hypothesis testing in invasion ecology using a com-  
parative functional response approach. *Biological Invasions* 16, 735–753.  
735 doi:10.1007/s10530-013-0550-8.
- Finke, D.L., Denno, R.F., 2002. Intraguild Predation Diminished in Complex-  
738 Structured Vegetation: Implications for Prey Suppression. *Ecology* 83, 643–  
652. doi:10.1890/0012-9658(2002)083[0643:IPDICS]2.0.CO;2.
- Goodsman, D.W., Koch, D., Whitehouse, C., Evenden, M.L., Cooke, B.J.,  
741 Lewis, M.A., 2016. Aggregation and a strong Allee effect in a cooperative out-  
break insect. *Ecological Applications* 26, 2623–2636. doi:10.1002/eap.1404.
- Goodsman, D.W., Lewis, M.A., 2016. The minimum founding population in  
744 dispersing organisms subject to strong Allee effects. *Methods in Ecology and  
Evolution* 7, 1100–1109. doi:10.1111/2041-210X.12573.
- Gustafson, E.J., 1998. Quantifying landscape spatial pattern: what is the state  
747 of the art? *Ecosystems* 1, 143–156.
- Hassell, M.P., 1978. *The Dynamics of Arthropod Predator-prey Systems*.  
Princeton University Press.
- 750 He, Y., Zhao, J., Zheng, Y., Desneux, N., Wu, K., 2012. Lethal effect of imi-  
dactoprid on the coccinellid predator *Serangium japonicum* and sublethal ef-  
fects on predator voracity and on functional response to the whitefly *Bemisia*  
753 *tabaci*. *Ecotoxicology* 21, 1291–1300. doi:10.1007/s10646-012-0883-6.



- Hochberg, M.E., Holt, R.D., 1999. The uniformity and density of pest exploitation as guides to success in biological control, in: Theoretical approaches to biology control. eds b.a. hawkins & h.v. cornell ed.. Cambridge University Press, Cambridge, pp. 71–88.
- Holling, C.S., 1959a. The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly. *The Canadian Entomologist* 91, 293–320. doi:10.4039/Ent91293-5.
- Holling, C.S., 1959b. Some Characteristics of Simple Types of Predation and Parasitism. *The Canadian Entomologist* 91, 385–398. doi:10.4039/Ent91385-7.
- Hopkins, B., Skellam, J.G., 1954. A New Method for determining the Type of Distribution of Plant Individuals. *Annals of Botany* 18, 213–227.
- Hossie, T.J., Murray, D.L., 2016. Spatial arrangement of prey affects the shape of ratio-dependent functional response in strongly antagonistic predators. *Ecology* 97, 834–841. doi:10.1890/15-1535.1.
- Ives, A.R., Schooler, S.S., Jagar, V.J., Knuteson, S.E., Grbic, M., Settle, W.H., 1999. Variability and Parasitoid Foraging Efficiency: A Case Study of Pea Aphids and *Aphidius ervi*. *The American Naturalist* 154, 652–673. doi:10.1086/303269.
- Jeschke, J.M., Kopp, M., Tollrian, R., 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biological Reviews* 79, 337–349. doi:10.1017/S1464793103006286.
- Levin, S.A., 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology* 73, 1943–1967. doi:10.2307/1941447.
- Liu, B., Teng, Z., Chen, L., 2006. Analysis of a predator-prey model with Holling II functional response concerning impulsive control strategy. *Journal of Computational and Applied Mathematics* 193, 347–362. doi:10.1016/j.cam.2005.06.023.

- Maxwell, B.D., Backus, V., Hohmann, M.G., Irvine, K.M., Lawrence, P., Lehn-  
783 hoff, E.A., Rew, L.J., 2012. Comparison of Transect-Based Standard and  
Adaptive Sampling Methods for Invasive Plant Species. *Invasive Plant Sci-  
ence and Management* 5, 178–193. doi:10.1614/IPSM-D-11-00022.1.
- 786 Messier, F., 1994. Ungulate Population Models with Predation: A Case Study  
with the North American Moose. *Ecology* 75, 478–488. doi:10.2307/1939551.
- Mills, N.J., Getz, W.M., 1996. Ecological Resource ModellingModelling the bi-  
789 ological control of insect pests: a review of host-parasitoid models. *Ecological  
Modelling* 92, 121–143. doi:10.1016/0304-3800(95)00177-8.
- Murdoch, W.W., Oaten, A., 1975. Predation and Population Stability. *Ad-  
792 vances in Ecological Research* 9, 1–131.
- Nachman, G., 2006. A functional response model of a predator population  
foraging in a patchy habitat. *Journal of Animal Ecology* 75, 948–958.  
795 doi:10.1111/j.1365-2656.2006.01114.x.
- R Core Team, 2016. R: A Language and Environment for Statistical Com-  
puting. R Foundation for Statistical Computing, Vienna, Austria. URL:  
798 <https://www.R-project.org/>.
- Rincon, D.F., Caas, L.A., Hoy, C.W., 2017. Modeling changes in predator  
functional response to prey across spatial scales. *Theoretical Ecology* , 1–  
801 13doi:10.1007/s12080-017-0338-z.
- Robertson, C., Nelson, T.A., Boots, B., 2007. Mountain Pine Beetle Dispersal:  
The SpatialTemporal Interaction of Infestations. *Forest Science* 53, 395–405.
- 804 Safranyik, L., Carroll, A.L., 2006. The biology and epidemiology of the mountain  
pine beetle in lodgepole pine forests., in: Safranyik, L., Wilson, B. (Eds.), *The  
mountain pine beetle: a synthesis of biology, management and impacts on  
807 lodgepole pine*. Natural Resources Canada, Canadian Forest Service, Pacific  
Forestry Centre, Victoria, Canada, pp. 3–66.

- Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What Is the Allee  
810 Effect? *Oikos* 87, 185–190. doi:10.2307/3547011.
- Sutherland, W.J., 2001. Sustainable exploitation: a review of principles and  
methods. *Wildlife Biology* 7, 131–140.
- 813 Thompson, S.K., 1990. Adaptive Cluster Sampling. *Journal of the American  
Statistical Association* 85, 1050. doi:10.2307/2289601.
- Turchin, P., 2013. *Complex Population Dynamics: A Theoretical/Empirical  
816 Synthesis (MPB-35) : A Theoretical/Empirical Synthesis (MPB-35)*. Monographs in Population Biology, Princeton University Press, Princeton.
- Van Den Berg, H., Ankasah, D., Muhammad, A., Rusli, R., Widayanto, H.A.,  
819 Wirasto, H.B., Yully, I., 1997. Evaluating the Role of Predation in Population  
Fluctuations of the Soybean Aphid *Aphis glycines* in Farmer's Fields in  
Indonesia. *Journal of Applied Ecology* 34, 971–984. doi:10.2307/2405287.