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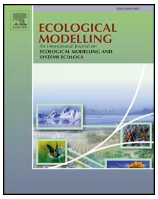

When managers forage for pests: Implementing the functional response in pest management

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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.

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

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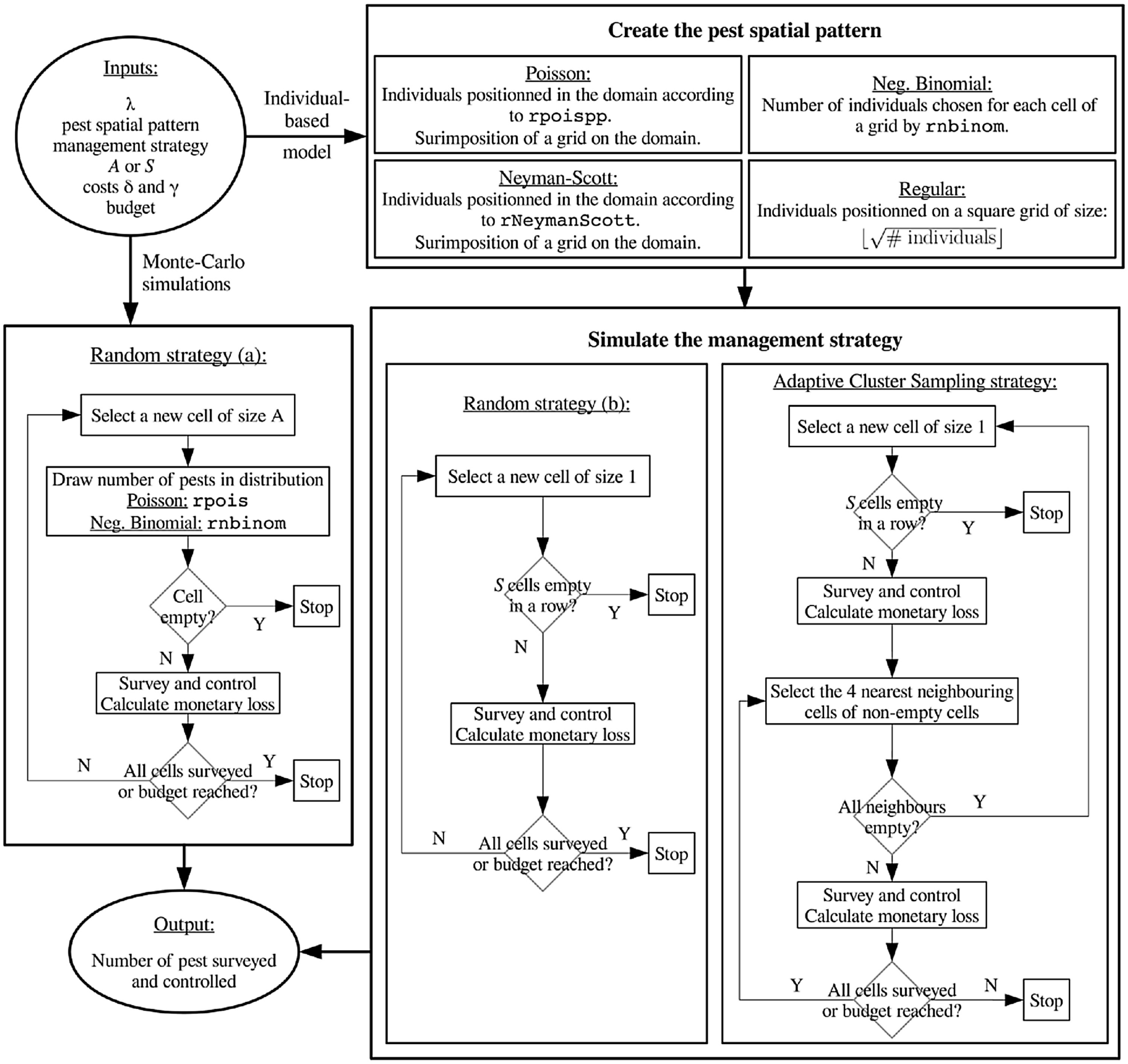

Fig. 1. Conceptual diagram representing the process determining each simulation run. Start at the top left of the diagram.

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 alloted 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). 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 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 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 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.

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 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 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 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.

2. Methods

We simulated management strategies of pest removal using two approaches: a spatially-explicit individual-based model and spatially-implicit Monte-Carlo simulations, and confirmed the results in the simplest cases by deriving analytical solutions to mathematical models representing the simulation scenarios. First, we presented the computational (Section 2.1 and Section 2.2) and mathematical (Section 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 functional response framework (Section 2.4). Finally, we applied our models to the mountain pine beetle example (Section 2.5).

In this study, we explored various scenarios so as to capture different functional 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 × 16 grid. Depending on the scenario, the cell size was 1 × 1, 2 × 2 or 8 × 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 provide details on each component. The symbols used in this study are described in Table 1.

2.1. Simulating pest distributions

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

2.1.1. Random point process

The random point process employed a homogeneous Poisson process using 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 then superimposed over the whole spatial domain. Each cell had the same probability of having a pest, thus, they were independent of each other.

Table 1
Description of the symbols used in the text.

Symbol	Description
λ	Pest intensity or Average number of individuals in a size-1 grid cell
δ	Cost of surveying a size-1 cell
γ	Cost of removing a pest individual
A	Cell size/area or Number of contiguous size-1 cells
S	Number 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
ϕ	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
ψ_A	Probability of finding zero individuals in a cell of area A

2.1.2. Within-cell cluster point process

The within-cell cluster point process sampled a Negative binomial distribution 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 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 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 simulated pest data depended on the size of the square cells in the grid that we 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 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. 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.

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 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 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.

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

2.2. Simulating manager search strategies

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 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 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 strategy (a) (stop after single empty cell of area A) for the spatially uncorrelated pest spatial distribution (Poisson and negative binomial) with intensity λ on a bounded rectangular spatial domain of area M. This approach could only work 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 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 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 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 the budget, only the fraction of the area allowed by the

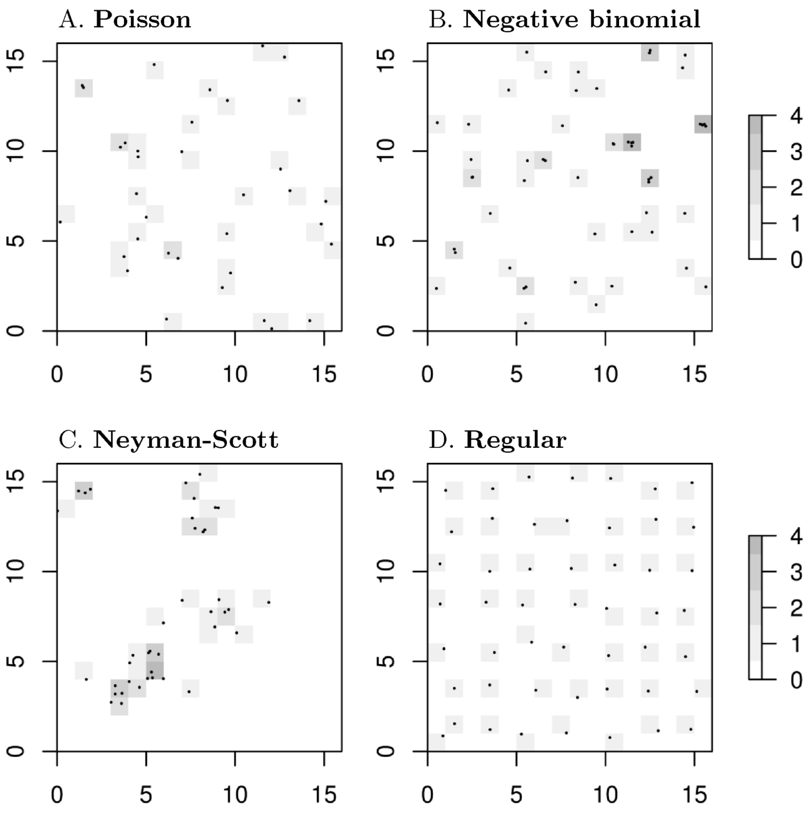

Fig. 2. Spatial distributions of pests on a 16 × 16 lattice with an intensity of 0.2 individual per grid cell: (A) Poisson spatial distribution, (B) Negative binomial (within-cell cluster) spatial distribution with an overdispersion parameter $k = 1$, (C) Neyman-Scott (between-cell cluster) spatial distribution 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).

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-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 (δ) * the number of cells surveyed at this step, and by deducting the cost of removing a pest item (γ) * 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 (δ) * the number of cells surveyed at this step, and the cost of removing a pest item (γ) * 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 × 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 torus, which means that when a manager traversed the border of the domain, the manager reappeared on the other side of the domain.

2.3. Mathematical models

We derived mathematical models of the random sampling in which management stops after the manager discovers one empty cell of area A (random strategy (a) described in Section 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 Section 2.2.2) for pest distributions that are spatially uncorrelated 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 ($A < M$) with a Poisson spatial distribution of individuals is

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

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. We can call this the '*area of discovery*' to connect it to the functional response ideas.

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

Note that in Eq. (2) managers are unable to explore more area than there 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

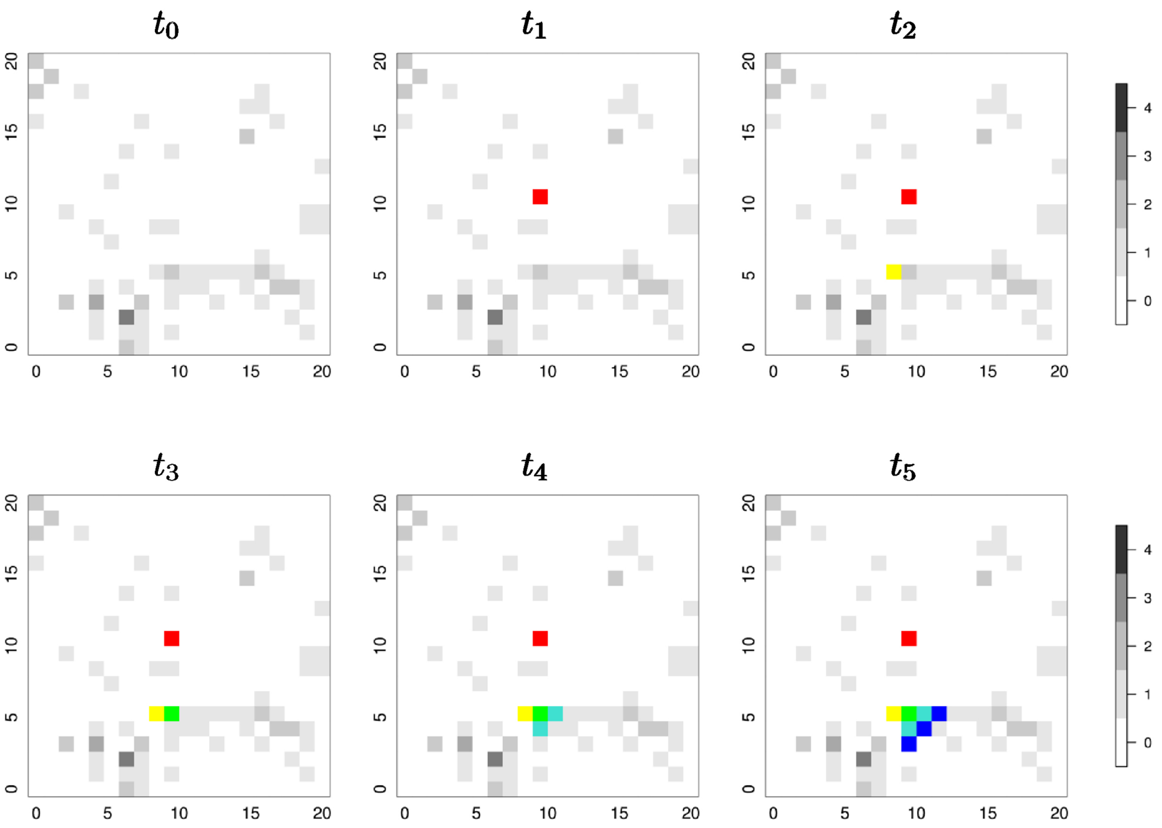

Fig. 3. Step by step images of the adaptive cluster sampling strategy inspecting a clustered (Neyman-Scott process) spatial distributions of pests (in shades of grey: from white, zero individual, to the darkest grey, four individuals) on a 20 × 20 lattice with an intensity of 0.2 individual per grid 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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$$E(\lambda, A, M) = D(\lambda, A, M)\lambda, \tag{3}$$

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

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

If there is a limited management budget B, each quadrat costs δ, and the cost γ is associated with eradicating each pest in addition to treating an infested 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 adding a budget, a cost per quadrat, and a cost per individual is similar to dividing 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 becomes

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

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 of the number in any other cell, we write for a cell of area 1

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

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

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. Eq. (6) becomes then:

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

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

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

2.3.2. Random strategy (b): stop after S empty cells

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

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

Spatial distribution	E	ϕ
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): $1-\left(1+\frac{\lambda A}{k}\right)^{-k}$

strategy (b), however, the manager surveys an integer number S of empty cells before stopping. The 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 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 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 manager stops looking for additional pests.

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

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

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

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

A and S being multiplied, the probability that a cell ($S = 1$) of area $A = x$ has zero individuals (ψ_A^1) is the same as the probability that x different size-1 cells ($S = x$, $A = 1$) have zero individuals in each cell (ψ_1^S). So in this context, $\psi_A^1 = \psi_1^S$. For this reason, the mean number of individuals managed obtained from the simulation process described above should match the analytical solution provided in Eq. (5) using Eq. (1).

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

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

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

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

In this case, A and S are not multiplied, so the probability that a cell ($S = 1$) of area $A = x$ has zero individuals (ψ_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 (ψ_1^S). 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 Eq. (5) using Eq. (7). In this case, instead of Eq. (7), we can use

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

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	ϕ
Poisson	Eq. (5): $A\lambda\left(\dfrac{1-\phi^{\frac{B}{A(\lambda\gamma+\delta)}}}{1-\phi}\right)$	$1 -$ Eq. (9): $1 - \exp(-\lambda A\ S)$
Negative binomial	Eq. (5): $A\lambda\left(\dfrac{1-\phi^{\frac{B}{A(\lambda\gamma+\delta)}}}{1-\phi}\right)$	Eq. (12): $1 - \left(1 + \frac{\lambda A}{k}\right)^{-\mathrm{k\ S}}$

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 (γ) 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 (γ) 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 A: number of contiguous size-1 cells, see previous section) to a low number and by setting $\gamma > 0$, we would expect that Eq. (5) takes the sigmoid shape of a Type III functional response. We thereby simulate a manager estimating that the probability of encountering a pest is too low to be worth the search effort at a low pest density.

2.5. *Application*

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 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 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 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.

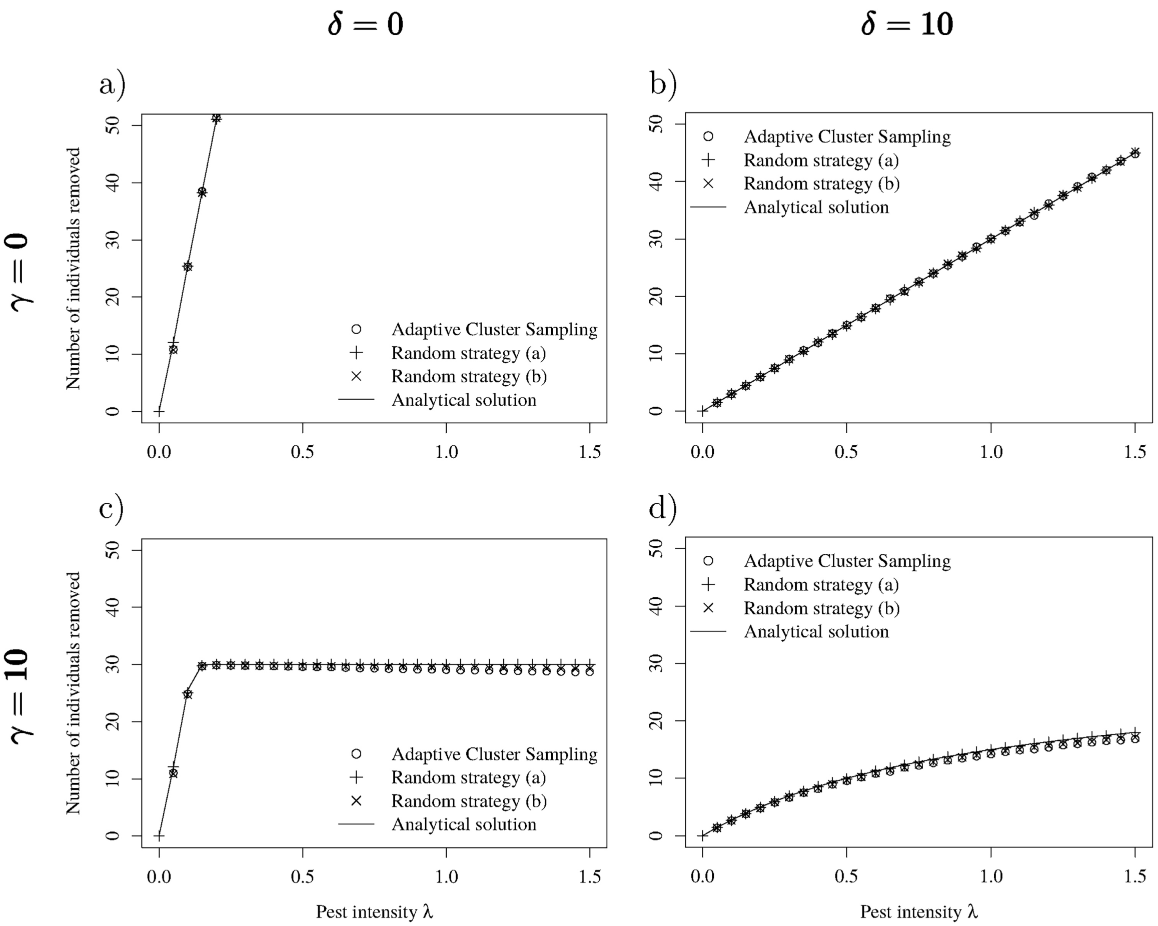

Fig. 4. Functional response curves when varying the management costs (δ the cost of surveying a cell and γ the cost of removing a pest) for fixed values of $A = 64$ and $S = 1$ for the random strategy (a) and $A = 1$ and $S = 64$ for the random strategy (b) and the adaptive cluster campling strategy, 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).

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 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 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 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 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 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 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 the survey area to 89% (value obtained for Cypress Hills from M. Kunegel-Lion, unpublished data).

2.5.3. *Simulations*

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 km × 9.9 km rectangular domain with grid cells of size 100 m × 100 m. 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 (δ and γ), and the total budget (B) values were chosen as 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 2011 and 2012.

2.5.4. *Management goal feasibility*

Knowing about management functional responses shape can help us assess the feasibility of a management goal. We chose two ways of expressing a management 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 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 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 response curves and the management goals on the same scale, we divided the number of individuals removed by the domain area, thereby graphing the density of pest controlled by the total pest density. Note that this only changed 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 parameter values, we compared the means of 2000 simulations to the analytical solutions, when calculated. The budget value used in the simulations and analytical solutions was 300, limiting the number of cells managers can explore. The values of δ and γ were either 10 or 0 and the values of A and S either 64 (one 8 × 8-cell or 64 1 × 1-cells), 4 (one 2 × 2-cell or four 1 × 1-cells) or 1 (one 1 × 1-cell) depending on the scenario. We generated all negative binomial point processes using the parameter $k = 1$ in both the simulations and the analytical solution.

3.1. Varying the management costs

When the cost of surveying a cell δ increases, the functional response slope decreases and when the cost of removing a pest item γ increases, the functional response curve saturates as seen on Fig. 4 for the Poisson distribution. This 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, Fig. A.1 for the non-truncated graph.

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 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 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 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 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 strategy results in oscillations around the random strategy mean especially for the 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 Section 2), decreases the number of pests found and controlled at low pest intensity 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 between random strategies which might be due to the difference between A and S as shown in Eq. (12) or to the difference in the pest spatial resolution when $A = 1$ and when $A > 1$. Those two cases cannot be distinguished given our parameter values.

3.4. Theoretical results summary

Additional simulations (see Appendix B, Fig. B.1 and B.2) show that when A or S are large, the cost per cell to survey $\delta > 0$ and the cost per pest to remove $\gamma \to 0$, the functional response tended to a Type I. When A or S are large, $\gamma > 0$ and $\delta \to 0$, 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 γ and $\delta > 0$, the functional response tends to a Type II. To summarize, to obtain a Type I, we set $\delta > 0$ and $\gamma = 0$. To obtain a Type I/II, we set $\delta = 0$ and $\gamma > 0$. To obtain a Type II, we set $\delta > 0$ and $\gamma > 0$. To obtain a Type III, we set A or S small, δ small and $\gamma > 0$ (Fig. 6).

In addition, variations in budget did not change the qualitative shapes of functional 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 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 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.

3.5. Correspondence with predator functional response

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

$$N_a = \frac{a'\mathrm{T}N}{1 + a'T_h N}, \tag{13}$$

we can compare the parameters from predator and manager functional responses. Table 4 summarize the parameter equivalences.

As stated before, the cost of pest removal (γ) is the manager equivalent of the handling time (T_h). This is corroborated by the similar effect of γ 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 (δ) 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 Eq. (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/δ and the asymptote, corresponding to T/T_h, B/γ (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, Fig. B.1 and B.2). These equivalences allow us to use Eq. (13) as an approximation for Eq. (5) as long as A is large, $\delta > 0$, the management strategy random, and the pest spatial distribution Poisson. See Appendix C, Fig. C.1 for the comparison between the results of Eqs. (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 ± 55 (standard deviation) and the mean cluster size 266 ± 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.

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

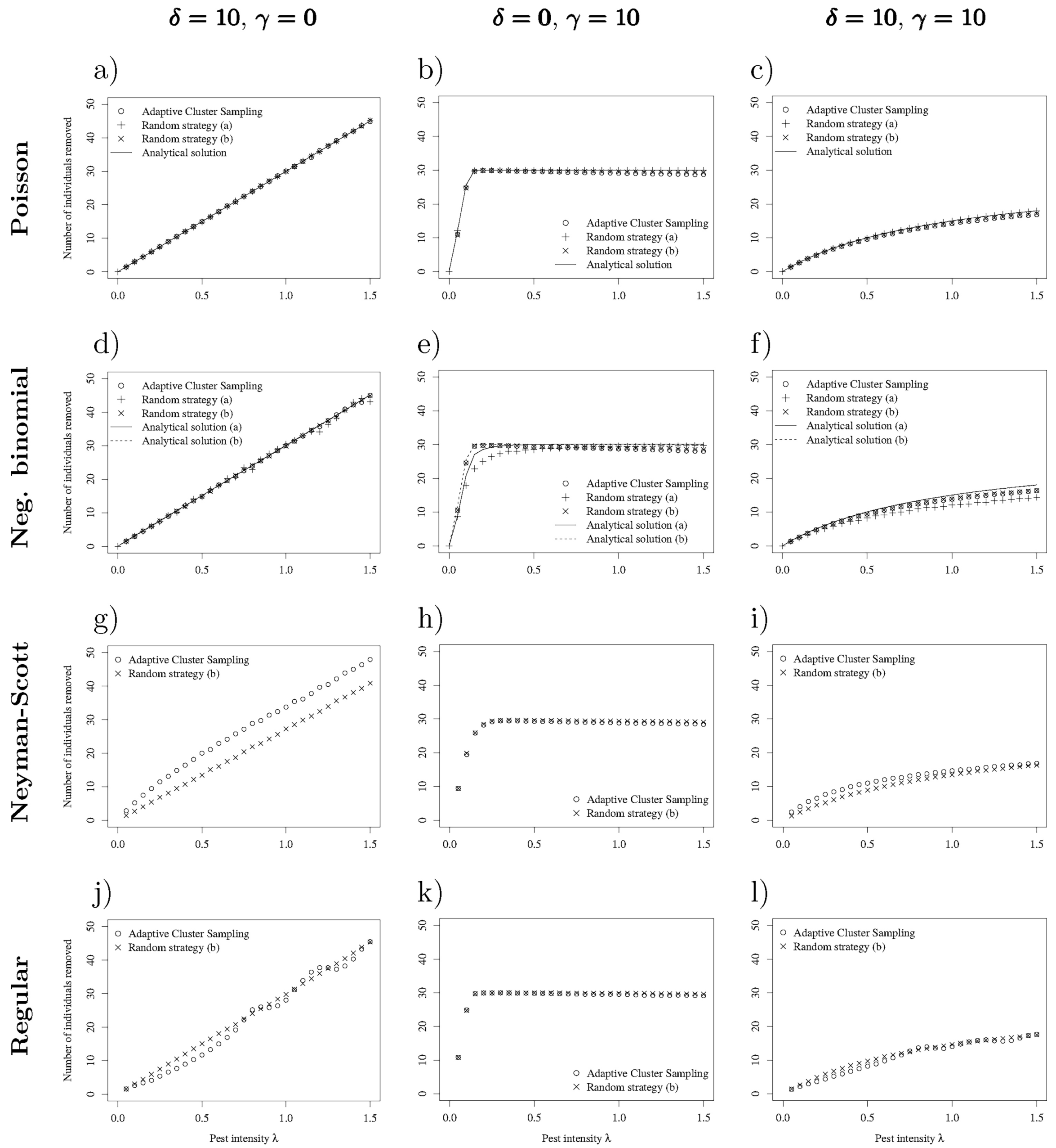

Fig. 5. Functional response curves when varying the management strategy and the pest spatial distribution for fixed values of $A = 64$ and $S = 1$ for the random strategy (a) and $A = 1$ and $S = 64$ for the random strategy (b) and the Adaptive Cluster Sampling strategy. Circles represent the means of 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.

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, Fig. D.1). 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

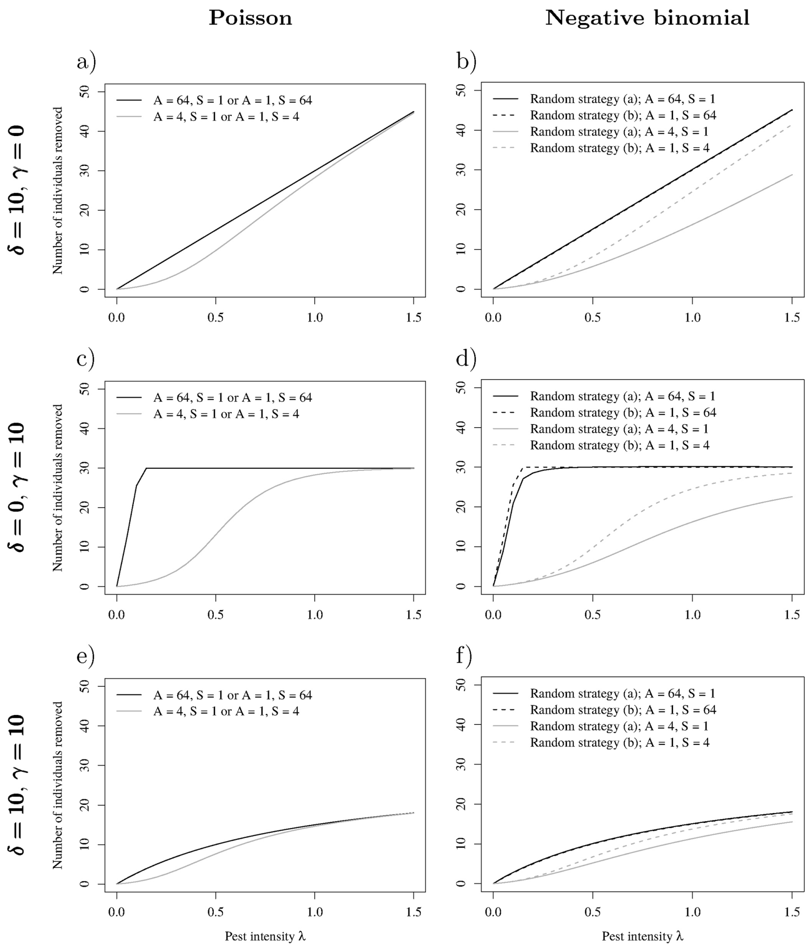

Fig. 6. Functional response analytical solutions when varying the cell area A or the number of empty steps to survey in a row S for the random strategy (a) and (b). Black lines represent $A = 64$, $S = 1$ or $A = 1$, $S = 64$ while grey lines represent $A = 4$, $S = 1$ or $A = 1$, $S = 4$. Solid lines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

Table 4
Correspondence between predator and manager functional response components.

Predator–prey		Manager–pest	
Number of prey items attacked	N_a	Number of pest items removed	E
Prey density	N	Pest density	λ
Total foraging time	T	Budget	B
Encounter rate	a'	Detection rate	$1/\delta$
Handling time	T_h	Cost of pest removal	γ
Slope	$a'T$	Slope	B/δ
Asymptote	T/T_h	Asymptote	B/γ

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 would put managers over the budget, only a fraction of the area would be actually surveyed and controlled (random strategy (a)) or the step would not be taken (random strategy (b)). Therefore, the whole budget might not be used 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 of the random strategies (a) and (b). However, the functional response shape does not change between the simulations and the analytical solutions. Accordingly, we can assume that the functional response shapes in the case of the 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.

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 is not the case for negative binomially distributed pests. Changing the cell area changes the distribution grain. Therefore, random strategies (a) and (b) consider a different distribution grain for the negative binomial distribution and 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 $A = 1$ and, therefore, can be readily compared.

In the functional response theory, the predator distribution is assumed homogeneous. The impact of a clumped predator population on the kill rate lead 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 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). Several studies mention this issue. Nachman (2006) found that switching the prey 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 for ratio-dependent functional

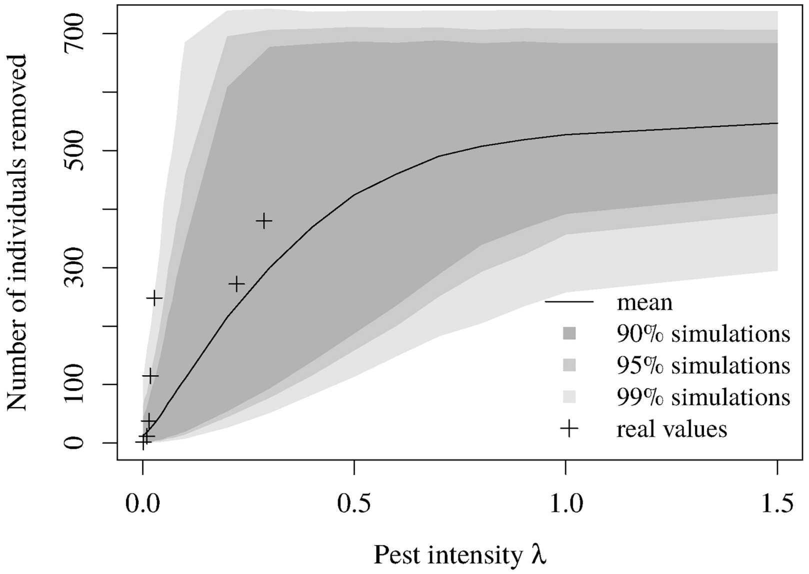

Fig. 7. Functional response of the mountain pine beetle management in Cypress Hills, Saskatchewan. The black line represents the mean of 10 000 simulations of the management process. The grey areas represent 90%, 95% and 99% of the simulations' distribution. The points represent the actual values obtained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

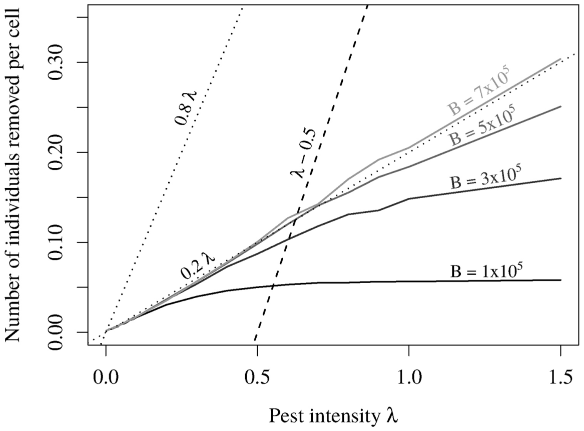

Fig. 8. Functional response of the mountain pine beetle management in Cypress Hills, Saskatchewan. Solid lines represent the mean of 1000 simulations of the management process for different budget values: 1×10^5, 3×10^5, 5×10^5, and 7×10^5. Dotted lines represent the management goal 1: removing 80% and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

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 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 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 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 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 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. 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 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 probability 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 contiguous 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 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 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 individuals managed for a Neyman-Scott and regular processes would be different 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 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 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 difference is due to the details of the adaptive cluster sampling process. Indeed, in 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-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 following a non-random search strategy on a Neyman-Scott pest spatial distribution 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 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.

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 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 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 different locations by contrasting functional response curves obtained analytically or by simulation.

To give further insight, manager functional responses could be included in dynamical systems to represent human impact on a pest population. For example, in the Cypress Hills case, future steps could include using this functional response in a population dynamics model to study the evolution of the beetle population over the years with a realistic incorporation of the management effect on the population. In the same way functional response curves inform about stability of predator–prey interactions (Dick et al., 2013), in our study, 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 populations 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 density (Hassell, 1978). With respect to control of mountain pine beetle in Cypress 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 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.

From a practical perspective, managers are typically interested in controlling a certain proportion of pests, given an environmental context and a particular strategy. For example, in some areas of the province of Alberta, Canada, infested by the mountain pine beetle, the management goal is to reduce populations by 80% (Alberta Sustainable Resource Development, 2007) using individual tree removal. Our model results, as shown in Figs. 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 3.789×10^{-4} and 5.311×10^{-5} infested stems per m^2 for two times series of mountain pine beetle infestation in central Idaho. Therefore, a management threshold of 0.5 individuals per $100\,m \times 100\,m$ 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 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 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 in predator numbers and sometimes an aggregative response describing the distribution of predators (Turchin, 2013). We could argue that in a human-pest management scenario, the numerical and aggregative responses are negligible or 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 between managers or teams, when enough persons are present to make several 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 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 responses. 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 human–pest interactions and provide insights on management. Furthermore, this framework could be generalized to any interaction involving humans “predating” on their environment. Indeed, instead of managing pest species, the 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 included in harvest models.

Acknowledgments

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Appendices

Appendix A

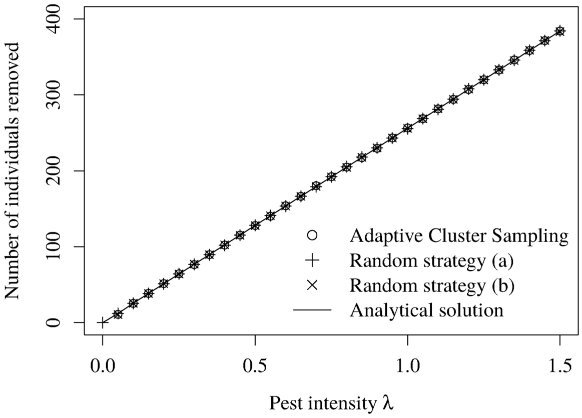

Fig. A.1. Functional response curves for fixed values of $\delta = 0$, $\gamma = 0$, $A = 64$ and $S = 1$ for the random strategy (a) and $A = 1$ and $S = 64$ for the random strategy (b) and the Adaptive Cluster Sampling strategy, and for a Poisson pest spatial distribution. Circles represent the means 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).

Appendix B

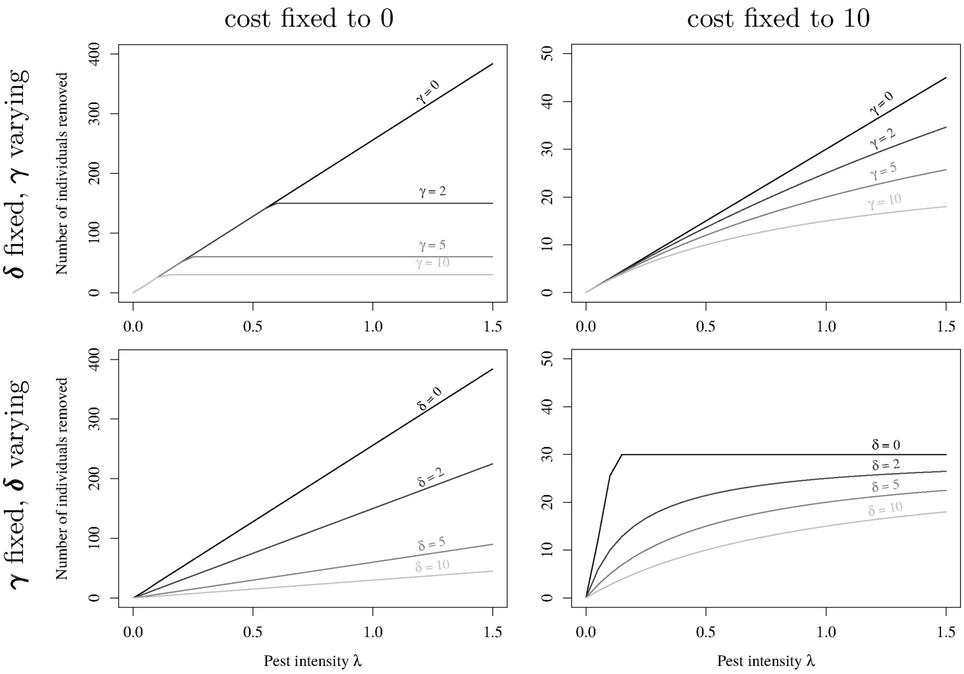

Fig. B.1. Functional response curves showing the impact of one of the cost parameters (the survey cost δ or the removal cost γ) when the other is fixed for the random strategies (a) and (b) on a Poisson pest spatial distribution. The shades of grey represent the values for the varying cost parameter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

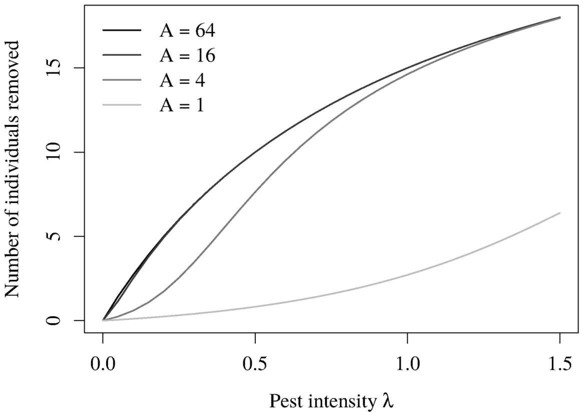

Fig. B.2. Functional response curves for fixed values of survey cost $\delta = 10$, removal cost $\gamma = 10$ and for the random strategies (a) and (b) on a Poisson pest spatial distribution. The shades of grey represent the values of the search area A: light grey $A = 1$ to black $A = 64$.

Appendix C

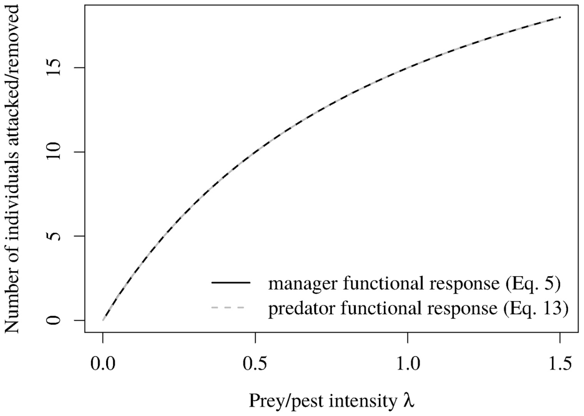

Fig. C.1. Functional response curves for fixed values of survey cost $\delta = 10$, removal cost $\gamma = 10$ and for a random strategy on a Poisson pest spatial distribution. The search area is set to 64 and the budget to 300. The black solid line represents the result of Eq. (5) and the grey dotted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

Appendix D

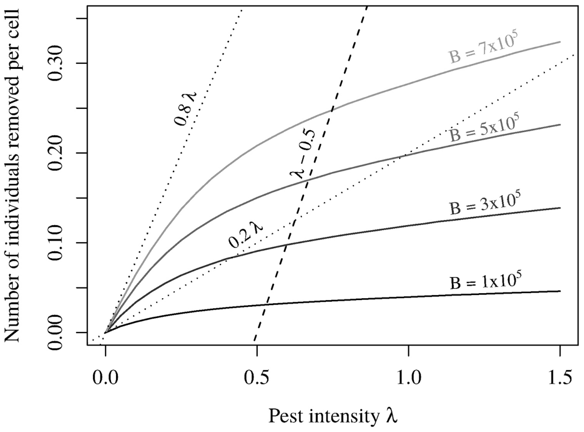

Fig. D.1. Functional response of the mountain pine beetle management in Cypress Hills, Saskatchewan using the adaptive cluster sampling process. Solid lines represent the mean of 1000 simulations of the management process for different budget values: 1×10^5, 3×10^5, 5×10^5, and 7×10^5. Dotted lines represent 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.

References

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

Allee, W.C., 1931. Animal aggregations. A Study in General Sociology. The University of Chicago Press, Chicago.

Arditi, R., Ginzburg, L.R., 1989. Coupling in predator-prey dynamics: ratio-dependence. J. Theor. Biol. 139, 311–326.

Avgar, T., Kuefler, D., Fryxell, J.M., 2011. Linking rates of diffusion and consumption in relation to resources. Am. Nat. 178, 182–190. https://doi.org/10.1086/660825.

Baddeley, A., Rubak, E., Turner, R., 2015. Spatial Point Patterns: Methodology 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 for detection of invasive species. Biol. Invas. 17, 445–459. https://doi.org/10.1007/s10530-014-0742-x.

Cosner, C., DeAngelis, D.L., Ault, J.S., Olson, D.B., 1999. Effects of spatial grouping on the functional response of predators. Theor. Popul. Biol. 56, 65–75. https://doi.org/10.1006/tpbi.1999.1414.

Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., 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 impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biol. Invas. 16, 735–753. https://doi.org/10.1007/s10530-013-0550-8.

Finke, D.L., Denno, R.F., 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology 83, 643–652. https://doi.org/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., Lewis, M.A., 2016. Aggregation and a strong Allee effect in a cooperative outbreak insect. Ecol. Appl. 26, 2623–2636. https://doi.org/10.1002/eap.1404.

Goodsman, D.W., Lewis, M.A., 2016. The minimum founding population in dispersing organisms subject to strong Allee effects. Methods Ecol. Evol. 7, 1100–1109. https://doi.org/10.1111/2041-210X.12573.

Gustafson, E.J., 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1, 143–156.

Hassell, M.P., 1978. The Dynamics of Arthropod Predator-prey Systems. Princeton University Press.

He, Y., Zhao, J., Zheng, Y., Desneux, N., Wu, K., 2012. Lethal effect of imidacloprid on the coccinellid predator *Serangium japonicum* and sublethal effects on predator voracity and on functional response to the whitefly *Bemisia tabaci*. Ecotoxicology 21, 1291–1300. https://doi.org/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: Hawkins, B.A., Cornell, H.V. (Eds.), Theoretical Approaches to Biology Control. 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. Can. Entomol. 91, 293–320. https://doi.org/10.4039/Ent91293-5.

Holling, C.S., 1959b. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91, 385–398. https://doi.org/10.4039/Ent91385-7.

Hopkins, B., Skellam, J.G., 1954. A new method for determining the type of distribution of plant individuals. Ann. Bot. 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. https://doi.org/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*. Am. Nat. 154, 652–673. https://doi.org/10.1086/303269.

Jeschke, J.M., Kopp, M., Tollrian, R., 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biol. Rev. 79, 337–349. https://doi.org/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. https://doi.org/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. J. Comput. Appl. Math. 193, 347–362. https://doi.org/10.1016/j.cam.2005.06.023.

Maxwell, B.D., Backus, V., Hohmann, M.G., Irvine, K.M., Lawrence, P., Lehnhoff, E.A., Rew, L.J., 2012. Comparison of transect-based standard and adaptive sampling methods for invasive plant species. Invas. Plant Sci. Manag. 5, 178–193. https://doi.org/10.1614/IPSM-D-11-00022.1.

Messier, F., 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75, 478–488. https://doi.org/10.2307/1939551.

Mills, N.J., Getz, W.M., 1996. Modelling the biological control of insect pests: a review of host-parasitoid models. Ecol. Model. 92, 121–143. https://doi.org/10.1016/0304-3800(95)00177-8.

Murdoch, W.W., Oaten, A., 1975. Predation and population stability. Adv. Ecol. Res. 9, 1–131.

Nachman, G., 2006. A functional response model of a predator population foraging in a patchy habitat. J. Anim. Ecol. 75, 948–958. https://doi.org/10.1111/j. 1365-2656.2006.01114.x.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rincon, D.F., Cañas, L.A., Hoy, C.W., 2017. Modeling changes in predator functional response to prey across spatial scales. Theor. Ecol. 1–13. https://doi.org/10.1007/s12080-017-0338-z.

Robertson, C., Nelson, T.A., Boots, B., 2007. Mountain pine beetle dispersal: the spatial-temporal interaction of infestations. Forest Sci. 53, 395–405.

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 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 effect? Oikos 87, 185–190. https://doi.org/10.2307/3547011.

Sutherland, W.J., 2001. Sustainable exploitation: a review of principles and methods. Wildl. Biol. 7, 131–140.

Thompson, S.K., 1990. Adaptive cluster sampling. J. Am. Stat. Assoc. 85, 1050. https://doi.org/10.2307/2289601.

Turchin, P., 2013. Complex Population Dynamics: 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., 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. J. Appl. Ecol. 34, 971–984. https://doi.org/10.2307/2405287.