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A simulation of the effects of early eradication of nematode infected trees on spread of pine wilt disease

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Abstract Pine wilt disease is currently among the most devastating pine tree plagues on earth. It is caused by the pinewood nematode *Bursaphelenchus xylophilus* in a perfect and well synchronized mutualistic relationship with beetles of the genus *Monochamus*. The disease has a fast and efficient mode of spread, which makes most of the efforts to control it practically insufficient. We investigate how early eradication of infected pine trees, i.e. eradication of trees which just ceased oleoresin exudation, may affect disease spread. In contrast to the sole eradication of killed trees, our results show that under an appropriate combination of eradication strategies: (1) there is a significant increase in the minimum pine density below which the disease fails to invade; (2) the region where reproductive Allee effects may take place are significantly enlarged. We implement optimal strategies for eradication through stochastic search optimization techniques, and conclude that disease extinction can be reached faster with an appropriate combination of eradication measures, minimizing the damage on healthy pine trees and operational costs.

Keywords Pine wilt disease · Allee effect · Pest control · Simulated annealing

Introduction

The pinewood nematode *Bursaphelenchus xylophilus* is the causative agent of pine wilt disease, one of the most serious threats to pine forests around the world. In Japan, for instance, it is believed that the nematode was introduced through wood trade with North America, Mamiya (1988), where some native species are resistant. Its first case was reported in 1905 in Nagasaki City, Kyushu Island, located in the southeast of the country. Since then, the disease spread throughout the country, destroying the majority of the vast pine forests dominated by the Japanese red pine, *Pinus densiflora*, (Futai 2008; Takasu 2009). The populations of Japanese black pine, *Pinus thunbergii* and the endangered species *Pinus armandii*, Nakamura and Akiba (2003), are also severely affected. The disease, currently present in the United States, Canada, Japan, China, Korea and Portugal (including Madeira island), generates

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concerns about the negative ecological and economical impact that its fast spread may produce once an invasion starts. Countries like Portugal, whose economy depends heavily on pine tree production (12% of its industrial GDP and 3.2% of the GDP, 10% of foreign trade, 5% of national employment, Webster and Mota (2008)) have to be prepared to confront the potentially devastating effects of a pine wilt disease outbreak. Because global dissemination of pinewood nematodes has occurred mainly through international trade of contaminated wood products made in countries where pinewood nematode presence has been detected, careful inspection and trade restrictions on potentially contaminated items are continuously being implemented around the world. For the control of local spread, an overwhelming number of studies focused on many aspects of the complex relationship between pine trees, beetles and nematodes has been published (Guang Zhao et al. 2008; Mota and Vieira 2008; Økland et al. 2010).

Early detection might be a determinant in the eradication of some invasive species (Gordillo 2011), and has proven to be decisive for the case of the pinewood nematode (Økland et al. 2010). Here we study how the early detection of infected trees and their immediate destruction might affect the spread of pine wilt disease. Our first goal is to address the impact of eradicating infected trees that just ceased oleoresin exudation (and consequently have a minimum or total absence of beetle eggs). This is done in Section "Materials and methods" using a model with difference equations, after a brief review of the standard equations used to study the spread of pine wilt disease. Second, in Section "Results", we use stochastic search techniques to numerically find approximate strategies that minimize the total losses caused by the disease. In the remaining part of this Introduction we briefly review the biology involved in the transmission of pine wilt disease and some of the current employed strategies for local control.

The lifecycle: nematodes and beetles

Pinewood nematodes rapidly spread among susceptible pine trees, causing their death just a few weeks after infection, thanks to their mutually beneficial relationship with sawyer beetles (genus *Monochamus*). These nematodes and the beetles have evolved to a cyclic bilateral mutualistic (at the population level) relationship that has been extensively studied (Guang Zhao et al. 2008; Togashi and Shigesada 2006), and which is briefly reviewed here. In Japan, the density of adult beetles per tree increases from early June, when many adults emerge from trees killed the previous year. Density peaks in July, and begins to decrease before the end of August. The adults completely disappear by October (Togashi 2008). Newly emerged beetles fly to healthy pine trees, carrying the pinewood nematode in their tracheal system, to feed on fresh bark. The nematodes infect the trees through the wounds made by the beetles. Once inside, the nematodes begin to feed on tree cells and reproduce at a high rate. In a few days, infected trees stop exuding oleoresin, the only defensive mechanism they have to repel bark beetles. It is only then, in weakened or recently killed trees, that beetles are able to oviposit. The beetle's eggs hatch in approximately one week and the larvae feed on the tree's inner bark. Meanwhile, trees are unable to resist the nematode invasion and die within a few weeks. The nematodes then begin to feed on fungi growing in the dead tree, which sustains their population for the winter and spring, when they surround the pupal chambers constructed by the beetle larvae and begin, in the late spring, to invade the tracheal system of the new enclosed adult beetles. The new beetles emerge from the dead trees in early June carrying pinewood nematodes, and the cycle starts once again.

Control of pine wilt disease spread

There are currently three basic strategies being used to control the local spread of pine wilt disease (Kamata 2011):

- **Destruction of nematode reservoirs** The most common method is the destruction of nematode infected pine trees containing pine sawyer larvae through physical, chemical or biological means. This method has to be implemented before new adult pine sawyers emerge.

- **Isolation of susceptible trees** The use of preventive aerial spraying with chemical insecticides has proven to be an effective mean of preventing infections (Kamata 2011). Its use has been reduced in recent years, however, because of the negative impact on surrounding ecosystems. The alternative use of ground spraying, which is much less damaging, turns out to be highly inefficient.
- **Increasing resistance in trees to the disease** The injection of nematicides into the trunk of pine trees is an effective method to prevent reproduction and to kill pinewood nematodes. The main drawbacks are the high costs of production and intense labour required for application. Usually these chemical preparations are employed on specific pine trees that need to be preserved because the use of insecticides is not possible (as in the case of trees in forests which sustain endangered species or in recreational areas (Kamata 2011)). Cross breeding with resistant species is another alternative to fight disease spread (Nose and Shiraishi 2008). However, it takes a long time to replace susceptible pines with resistant strains of pine.

The tactics mentioned above can be applied independently or in combination but may be subject to budget constraints, practical implementation or political convenience. The model proposed in Yoshimura et al. (1999) essentially addresses the efficiency of destruction of nematode reservoirs. Our study suggests that the destruction of *potential* nematode reservoirs offers a more efficient way to reduce the spread of the disease.

Early detection of infected trees

Pine trees rely on oleoresin exudation as a primary defence against bark beetles. After being infected with sufficient number of pinewood nematodes, trees suffer reduction or cessation of oleoresin exudation within a few weeks (Mamiya 1983). During the next stage of disease development the colour of the foliage changes to red or brown (Togashi 1989a, b).

There exist simple techniques to identify when a pine tree has changed its levels of oleoresin exudation flow. Such techniques allow managers to identify diseased trees before externally observable symptoms appear (Oda 1967). The destruction of infected trees as soon as any oleoresin exudation anomalies are detected would reduce or eliminate oviposition sites, suggesting the possibility inducing an *Allee effect*. An Allee effect is defined as the decrease of individual fitness at low conspecific densities (Courchamp et al. 2008; Gordillo 2011). Essentially, it can be understood as the failure of individuals in a population to replace themselves in the following generation. The Allee effect appears in this context if female beetles fail to find weakened or recently killed trees to oviposit: the density of such trees decreases as the density of adult beetles decreases.

Once early eradication is considered, it is relevant to ask the extent to which the combination of this procedure with eradication of pine sawyers, by insecticide or removal of killed trees, has to be done. The models described below predict that early eradication procedures may facilitate the control of pine wilt disease early on in an outbreak.

Materials and methods

The standard model for pine wilt disease

Using empirical data on the nematode's life cycle, in Yoshimura et al. (1999) constructed a difference equations model to describe the vector beetle and pine tree population dynamics. The model has been used to predict the impact of eradication efforts by insecticide or by the removal of infected trees at the end of each year, and has been further extended to include spatial dispersal (Takasu et al. 2000). Here, we make use of the non-spatial version, which is reviewed below.

Let H_t represent the population density of healthy pine trees at time t, and P_t the density of beetles. Here we assume that all beetles are vectors for the pinewood nematodes. Given the initial conditions H_0 and P_0, they satisfy the difference equations

$$H_{t+1} = e^{-\alpha P_t} H_t, \tag{1}$$

$$P_{t+1} = F(P_t, \tilde{H}_t)\tilde{H}_t, \tag{2}$$

where α represents the product of the average rate at which a pine tree is infected by a unit density of beetles per unit time and the period of maturation feeding (Royama 1971), $\tilde{H}_t = H_t - H_{t+1}$ is the number of infected pine trees at year t, and $F(P_t, \tilde{H}_t)$ is the number of adult beetles emerging from an infected dead pine tree in the following year. To find an expression for $F(P_t, \tilde{H}_t)$ Yoshimura et al. (1999) carefully designed experiments to observe the relationship between beetle egg density (number of eggs per m^2 of bark surface) and the density of emerging adults of the pine sawyer (number of adults per m^2 of bark surface). The data obtained was fitted with a hyperbolic curve using least squares. Combining the formula obtained with the total number of eggs laid in a unit area, which is given by a functional response curve of Holling type II, see Yoshimura et al. (1999) for details, the expression for $F(P_t, \tilde{H}_t)$ found is given by

$$F\left(P_t, \tilde{H}_t\right) = \frac{0.98\sigma SKP_t}{\left(a + \tilde{H}_t\right) S + 0.065\sigma KP_t}, \tag{3}$$

where the values 0.98 and 0.065 result from the fitting to the experimental data (Togashi 1989a, b, 1995), K is the maximum number of eggs deposited by a female beetle, σ is the beetle sex ratio, S is the area of bark surface per pine tree, and $1/a$ is the oviposition efficiency. All the parameters are positive constants also estimated from field data (Togashi 1989a, b).

The destruction of dead pine trees before mature beetles emerge is an environmentally safe, commonly practiced way to reduce the spread of pine wilt disease. This control is introduced in the equation for the beetle population through the parameter θ_t, which represents the eradication rate at year t (Yoshimura et al. 1999),

$$P_{t+1} = (1 - \theta_t) F\left(P_t, \tilde{H}_t\right) \tilde{H}_t, \tag{4}$$

We emphasize that θ_t represents the fraction of pine sawyers that are killed by the use of insecticide or the removal of infected trees at the end of year t, before they reach adulthood and emerge from dead trees.

Early eradication of infected trees

Let ϕ_t represent the fraction at year t, per unit area, of destroyed trees that recently ceased oleoresin exudation. In contrast to the destruction of trees that serve as eggs reservoirs, represented by the parameter θ_t, early eradication is focused on trees that are most likely to be free of beetle eggs, see Fig. 1. Thus, the only eggs that successfully hatch come from the remaining $(1 - \phi_t)\tilde{H}_t$ infected trees. If the eradication of beetles and

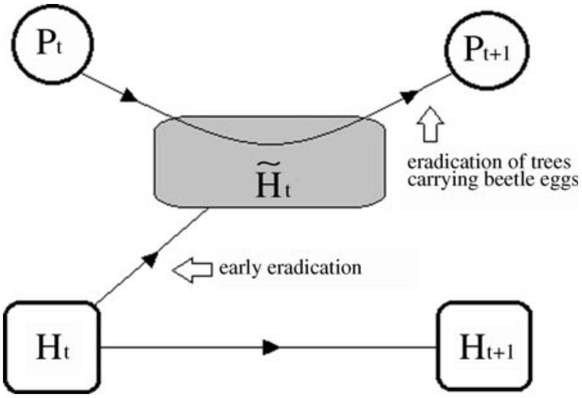

Fig. 1 Schematic representation of the disease dynamics (adapted from Yoshimura et al. (1999)). The oviposition on infected trees is represented in the figure by the *curved line* crossing the *box in gray* which corresponds to infected trees, $\tilde{H}_t$. Notice that early eradication is done *before* sawyer beetles oviposite on infected trees

dead trees is combined with the early eradication of infected trees, the equations describing the dynamics of the system are

$$H_{t+1} = e^{-\alpha P_t} H_t, \tag{5}$$

$$P_{t+1} = (1-\theta_t)(1-\phi_t) F_\phi\left(P_t, \tilde{H}_t\right)\tilde{H}_t, \tag{6}$$

where $F_\phi(P_t, \tilde{H}_t)$ represents the number of adult beetles emerging from an infected dead pine tree that *escaped* early eradication, obtained by replacing $(1-\phi_t)\tilde{H}_t$ in Eq. 3,

$$F_\phi\left(P_t, \tilde{H}_t\right) = \frac{0.98\sigma S K P_t}{\left(a + (1-\phi_t)\tilde{H}_t\right) S + 0.065\sigma K P_t}. \tag{7}$$

The basic reproductive ratio associated with the model, R, determines a condition for pine wilt spread: if $R > 1$ then the density of beetles will increase next year. Therefore, following Yoshimura et al. (1999),

$$R = R(\theta_0, \phi_0) = \frac{P_1}{P_0} = \frac{(1-\theta_0)(1-\phi_0) 0.98\sigma S K\left(1-e^{-\alpha P_0}\right) H_0}{\left(a + (1-\phi_0)\left(1-e^{-\alpha P_0}\right) H_0\right) S + 0.065\sigma K P_0}. \tag{8}$$

Results

The advantages of introducing early eradication

We use the expression for $R(\theta, \phi)$ obtained in Eq. 8 to determine the regions in the plane Beetle vs Pine where the beetle invasion is likely to be successful under different eradication strategies. Comparing Fig. 2a and b we observe that, keeping $\theta_t = \theta$ and $\phi_t = \phi$ constants for all t, the region for unsuccessful invasion increases rapidly as

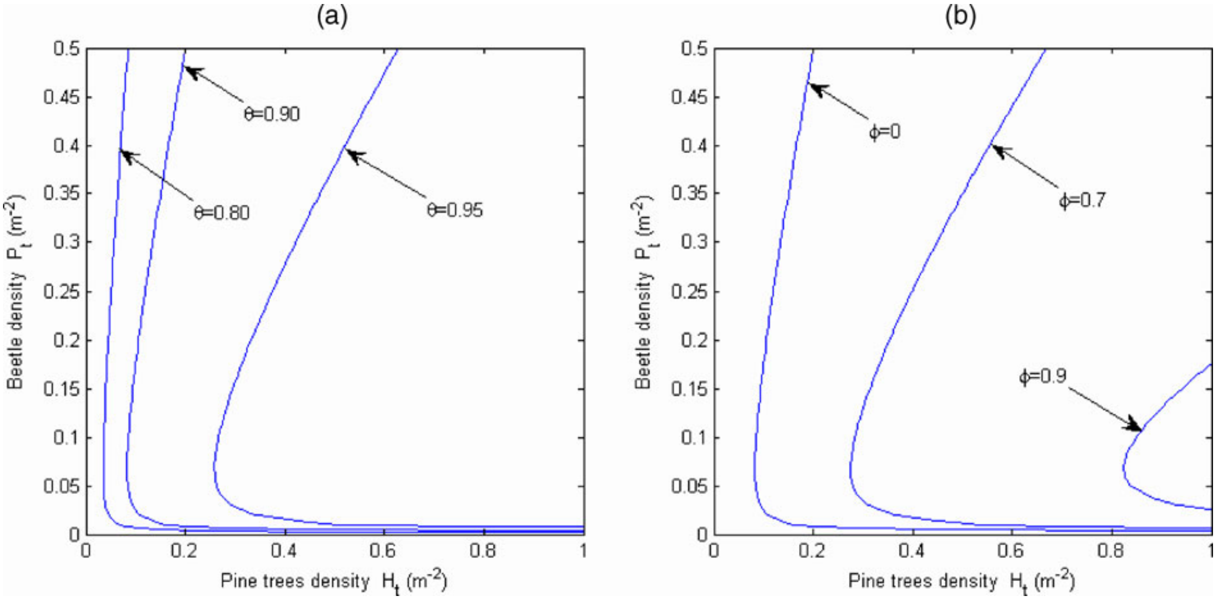

Fig. 2 **a** Boundary curves obtained in Yoshimura et al. (1999) using the condition $R(\theta, 0) = 1$ for three different values of θ. Each curve determines the regions where beetle invasion is successful or not. **b** Boundary curves obtained using $R(0.90, \phi) = 1$ for three different values of ϕ. A considerable enlargement of the region where the beetle invasion is unsuccessful is observed when an improvement in early eradication efficiency, from $\phi = 0.7$ to $\phi = 0.9$, is made. Notice that the *curves* defined by $R(0.95, 0)$ and $R(0.90, 0.7)$ are very close, giving an example of two different tactics that may offer similar results

the fraction of early eradicated infected trees increases. But even more important, the region corresponding to the appearance of an Allee effect (Yoshimura et al. 1999), substantially increases. Figure 2b shows that a mixed strategy, including early eradication, offers a stronger positive output for successful disease control. Even for $\theta = 0.96$, which is the estimated value for eradication from observations made at a pine stand in Ishikawa Prefecture in 1982 and 1983 (Yoshimura et al. 1999), a mixed strategy would prove to have a much better outcome. According to the model, a policy based solely on eradication with $\theta = 0.9$ and $\phi = 0$, for the corresponding densities recorded in that years, would have produced catastrophic results.

The progression of the disease under late eradication alone is compared with a combination that includes early eradication in Fig. 3a. Under the conditions of this example, although the levels of late eradication are high, it is impossible to avoid total invasion within the tree population. According to the model, the introduction of early eradication could efficiently help to avoid this tragedy. In Fig. 3b the level of late eradication is set high enough to avoid total invasion. Again, early eradication proves to be more efficient in the final output: there is less trees lost and the invasion is stopped faster.

Minimizing costs for combined eradication policies

For a given period of time, say N years, we represent the intensity levels of each method of eradication by the vector $(\hat{\theta}, \hat{\phi}) = (\theta_0, \ldots, \theta_{N-1}, \phi_0, \ldots, \phi_{N-1}) \in \mathbb{R}^{2N}$, where we have used the notation from Section "Materials and methods". Each year, this combination of procedures may be subject to cost constraints that considerably narrow the possibility of total eradication, turning desirable to optimize strategies in terms of both damage caused by the disease and the operational costs. Given the initial conditions (H_0, P_0) and possibly constant upper bounds on the strategy levels $0 \leq \Theta, \Phi \leq 1$ for a time period of N years, we look for the vector $(\hat{\theta}, \hat{\phi})$ that satisfies the

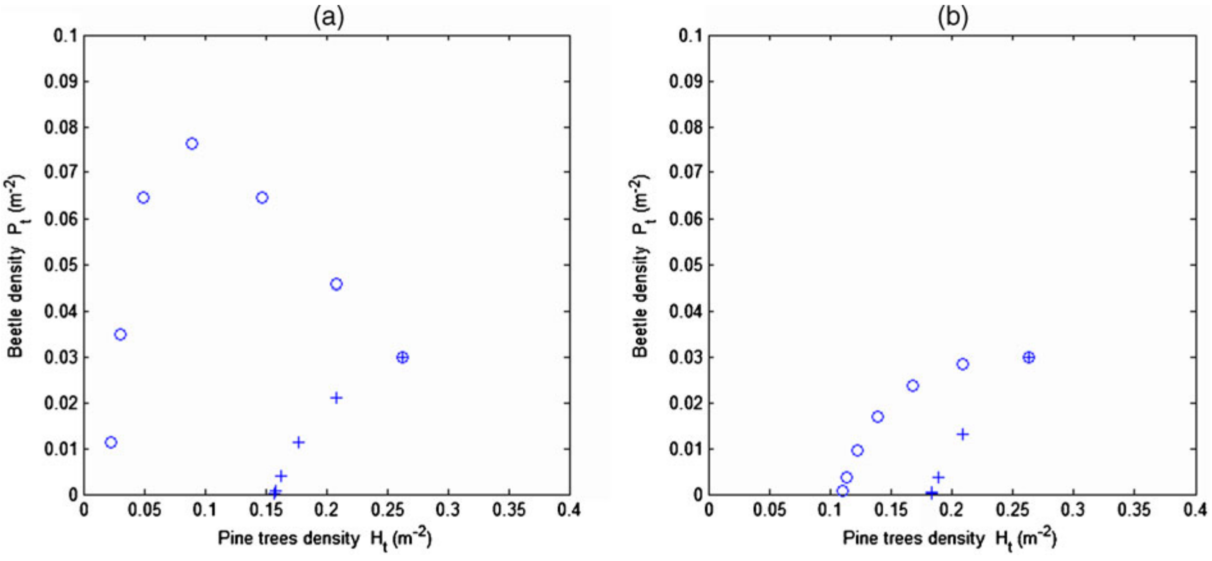

Fig. 3 **a** Prediction of the disease progression for $\theta = 0.92$ and $\phi = 0$ in *open circles* (○), and for $\theta = 0.92$ and $\phi = 0.7$ in *plus marks* (+), both having the same initial conditions. In the first case the effort to control the disease, although high, does not save the tree population from extinction. However, the model predicts that adding early eradication at the level 0.7, for instance, will stop the spread of the disease. **b** In this progression we have $\theta = 0.95$ and $\phi = 0$ in *open circles* (○), and $\theta = 0.95$ and $\phi = 0.7$ in *plus marks* (+). The higher value of θ guarantees that the disease stops spreading. However, the combination with early eradication attains the goal in less time and with less tree loss

feasibility conditions $0 \leq \theta_t \leq \Theta \leq 1$, $0 \leq \phi_t \leq \Phi \leq 1$ and $R(\theta_t, \phi_t) \leq 1$, $t = 0, ..., N-1$, which minimizes the cost function defined below. For the simulations, we take into consideration the costs of early eradication with respect to late eradication procedures, and also introduce the cost due to the economic losses produced by each tree that has been destroyed, C_t:

A_t = average cost of late eradication procedures per infected tree at year t,

B_t = average cost of early eradication per infected tree at year t,

C_t = average economic losses per tree at year t.

We assume that early eradication is more expensive than late eradication, but the economic loss generated by damaged trees is much bigger than both of them, $C_t >> B_t > A_t$. Thus, we propose to minimize the function

$$J(\theta, \phi) = \sum_{t=0}^{N-1} (A_t\theta_t(1-\phi_t) + B_t\phi_t + C_t)(H_t - H_{t+1}), \tag{9}$$

where the term $B_t\phi_t$ is the cost associated with the fraction of trees to which early eradication is applied, and $A_t\theta_t(1-\phi_t)$ is the cost of those that escaped early eradication, $1-\phi_t$, but are subject to late eradication.

We use a simulated annealing algorithm (Kirkpatrick et al. 1983; Häggström 2002; Spall 2003), to search for a sequence of parameter values that minimize the objective function (10) in a given number of years. First we identify the points in the partition $P = \{x_i = ih : i = 0, ...100; h = 0.01\}$ with the values of the control

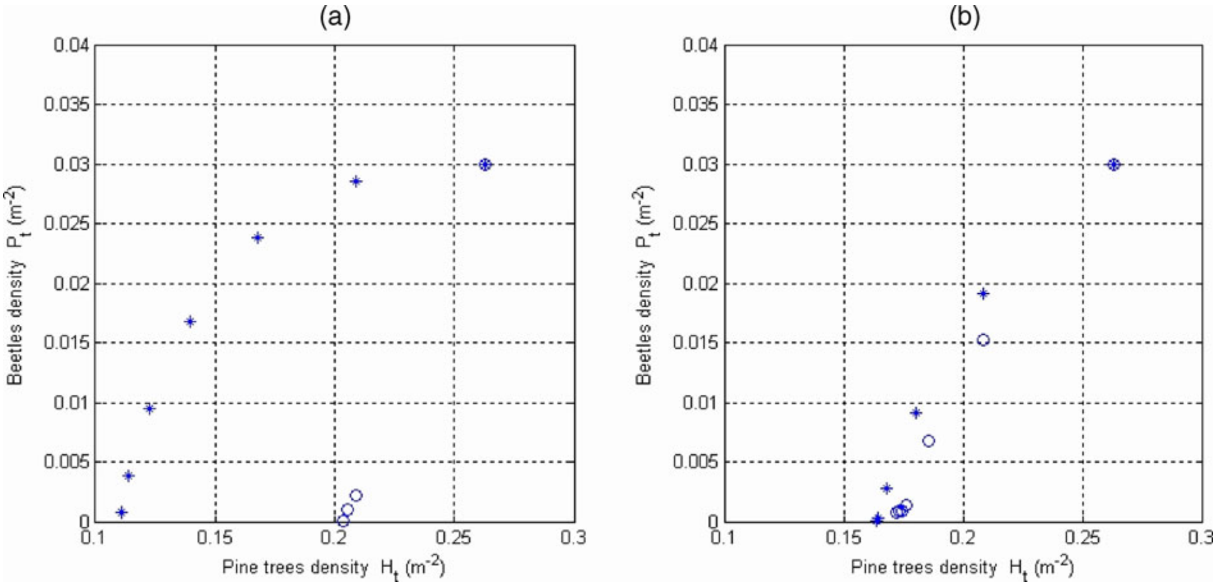

Fig. 4 Results of combined application strategies for $N = 6$ years. We assume that the rates of eradication are below 0.96, due to practical constrains. The initial conditions are the same as in Fig. 3, and eradication costs are equal for all years, with $A_t = A = 1$, $B_t = B = 10A$ and $C_t = C = 10{,}000$. **a** The application of a strategy with $\theta_t = 0.95$ and $\phi_t = 0$ is represented in *stars* (*), and an approximate optimal strategy using simulated annealing in *open circles* (∘), with $\hat{\theta} = (0.96, 0.91, 0, 0, 0, 0)$ and for $\hat{\phi} = (0.96, 0, 0.96, 0.96, 0, 0)$. It was found that the value of J for the first strategy was ≈2.5 times the value obtained through the approximate optimal strategy. **b** Here we assume a fixed strategy of early eradication equal to $\phi_t = 0.5$, $t = 1, ..., 6$. The disease progression associated to $\theta_t = 0.95$, $t = 1, ..., 6$ is shown in *stars* (*). An approximation to the optimal strategy found is given by $\hat{\theta} = (0.96, 0.95, 0.96, 0.56, 0, 0)$, shown *open circles* (∘). Notice that the optimal approximation does not require dead tree eradication every year, even with a very low early eradication effort

parameters, and consider the set $[P \times P]^N$, with N the number of years, as the space of feasible points where the algorithm searches for a minimizing point. Figure 4a shows the progression of the disease predicted by the model with $\theta_t = 0.95$ and $\phi_t = 0$ for all t in a period of six years, and the resulting progression using an approximated optimal strategy, which we found with the algorithm. For Fig. 4b, it is assumed that a strategy of $\phi_t = 0.5$ is implemented every year. The values for the optimal strategy θ_t are not necessarily high or even positive every year, as in this example, which may be surprising. This counterintuitive pattern occurs because the optimal strategy pushes the progression into the Allee effect regions quickly, making the annual eradication of killed trees unnecessary.

Discussion

We have analyzed how the immediate eradication of pine trees that recently ceased oleoresin exudation may help to contain the spread of pine wilt disease. Equations 5 and 6 predict the progression of the disease as function of the efficiency of eradication of recently infected trees, in addition to the variables and parameters employed in the standard model (Yoshimura et al. 1999). The numerical results suggest that implementing eradication of infected pine trees during the first stages after contagion, in combination with the usual control measures, will considerably increase the size of the region for which the disease's chances of successful invasion are low, see Fig. 2 Notice in particular how the region where the Allee effect takes places expands significantly. By considering the removal of infected trees at different times, see Fig. 1, the disease could be eradicated faster, even if the efficiency rate for eradication of recently killed trees is as low as 80–90%. At these levels, eradication procedures alone would be highly inefficient, see Fig. 2a.

Our study suggests that: (1) early eradication might alleviate an outbreak of pine wilt disease because it induces the necessary conditions for an Allee effect appearance, increasing the possibility of faster disease eradication; and (2) a computational way to find eradication strategies that minimize the damage produced by the disease and the cost generated by the control efforts. We point out, however, that in some countries logging practices provide abundant resources of fresh dead wood, making the breeding of beetles and the transfer of nematodes independent of pine killing (Økland et al. 2010). Also, the Allee effect is unlikely to appear if the nematodes are assumed to efficiently spread in already existing and widely distributed populations of beetles (Økland et al. 2010).

Here we use a stochastic optimization algorithm (simulated annealing) to obtain parameter values that approximately minimize the total costs caused by the disease. These approximations can be found in such a way that they adapt to different control constrains. For instance, in the numerical examples presented, we found the approximate minimizer $(\hat{\theta}, \hat{\phi})$ along six years, Fig. 4a, and also found the approximate minimizing solution given that early eradication is fixed with constant efficiency of 0.5, Fig. 4b. The strategies found using the algorithm not only reduce the time for disease extinction with a high final density of survival trees, but they do that with minimal operational costs.

We remark that the computations made here involved parameter values estimated in Yoshimura et al. (1999) for a particular field study. These values may vary considerably in geographic regions with different characteristics: the risk of an epidemic of pine wilt disease is strongly related to high temperatures. The presence of nematodes within the local ecosystems of Nordic pine forests will not generally lead to the development of pine wilt disease due to low temperatures during the summer (Økland et al. 2010). Latitude, regional topography, tree-species, etc. have to be carefully taken into account before any conclusions from the models here are drawn.

We believe that the ideas exposed here should be useful to policy makers or agricultural and environmental authorities, as a tool to gain insight into the possible outcome of control programs. The destruction of pine trees nearby an infected tree is usual in today's eradication practice, which can be seen as an extreme form of early eradication. Having surrounding trees eliminated before they present any symptom is a practice far from being optimal because it implies the likely destruction of healthy trees (as well as all associated costs). In contrast, optimal eradication may not require 100% efficiency, because it makes use of the Allee effect to fight the disease. It would be of interest to have this evaluation of optimal measures search integrated into the non-spatial and spatial individual based models proposed in Takasu (2009).

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