Modelling the impact of an invasive insect via reaction-diffusion

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ABSTRACT

An exotic, specialist seed chalcid, *Megastigmus schimitscheki*, has been introduced along with its cedar host seeds from Turkey to southeastern France during the early 1990s. It is now expanding in plantations of Atlas Cedar (*Cedrus atlantica*). We propose a model to predict the expansion and impact of this insect. This model couples a time-discrete equation for the ovo-larval stage with a two-dimensional reaction-diffusion equation for the adult stage, through a formula linking the solution of the reaction-diffusion equation to a seed attack rate. Two main diffusion operators, of Fokker–Planck and Fickian types, are tested. We show that taking account of the dependence of the insect mobility with respect to spatial heterogeneity, and choosing the appropriate diffusion operator, are critical factors for obtaining good predictions.

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1. Introduction

As a result of technological advances and of trade globalisation, forest products are moved around the globe with an ever-increasing speed and frequency. This movement has precipitated a substantial increase in biological invasions by allowing organisms to pass the natural barriers that limit their dispersal [1]. In the West Palearctic, 8 of the 21 species recorded in the seed chalcid genus *Megastigmus* Dalman (Hymenoptera: Torymidae) are exotic invasive species introduced through seed trade [2]. Modelling the expansion processes of such invasive species, and the related damages to forests and tree plantations, becomes a priority.

Fabre et al. [3] just recorded a newly invasive seed chalcid, *Megastigmus schimitscheki* Novitzky (Hymenoptera: Torymidae) in southeastern France. The insect has probably been introduced from Asia Minor (Turkey) along with seeds of Cedar-of-Lebanon (*Cedrus libani* A. Rich.), during the period 1990–1993, in the region of Mont-Ventoux. The study [3] provides many useful data in order to build a model. In particular it is shown that the biological characteristics of *M. schimitscheki* in both native and invaded areas are rather similar to those of other *Megastigmus* seed chalcids which have been extensively studied in Europe, North America and Japan (e.g. [2,4–6]). Because of this recent introduction, *M. schimitscheki* did not recruit any predators in France yet. In addition, the insect is facing little competition for the exploitation of seed resources because the new host, *Cedrus atlantica*, is also introduced (but from North Africa) and its cones and seeds are still not colonised by the indigenous entomofauna. There is only one competitor, *Megastigmus pinsapinis* Hoffmeyer, another *Megastigmus* seed chalcid which has been introduced half a century ago from North Africa [2]. However, *M. pinsapinis* seems dominated by *M. schimitscheki* [3]. These patterns make the modelling of expansion and related damages easier than in the case of species introduced since a longer time and facing a large cortege of natural enemies and competitors. It allows in particular the use of single-species models.

Reaction-diffusion models have proved themselves to be well adapted for describing some invasive species expansion in homogeneous and heterogeneous environments [7,8], especially when one cannot follow the movement of each organism independently (for review, see also [9–11]). The life-cycle of *M. schimitscheki* is composed of two distinct stages: the ovo-larval stage (at least 2 years) and the adult stage (average duration of 10 days per individual). The dispersal occurs during the adult stage, which begins by progressive emergence of the adults from eggs, and ends by the death of the adults. During this dispersal stage, laying – or, equivalently, attack – can occur, if the insects find free cedar seeds. To our knowledge, there is no standard methodology for coupling the ovo-larval stage time-discrete model with a reaction-diffusion model for the adult stage. It requires to model adult progressive emergence and to relate the adult population density, obtained as the solution of the reaction-diffusion model, with cedar seed attack rates.

The spatial heterogeneity considered in this paper is the presence or absence of cedar plantations. To deal with insect dispersion in such a patchy landscape, two main types of diffusion operators are found in the reaction-diffusion literature: the Fokker–Planck diffusion operator, and the Fickian diffusion operator. Fokker–

Planck diffusion, which can be obtained as the macroscopic limit of uncorrelated random walks with spatially-dependent move lengths, has been observed to be more adapted than the Fickian one for modelling ecological processes in varying environments [9,11,12]. Fickian diffusion is usually derived from physical relationships between particle flux, concentration and concentration gradient; the flux is assumed to be linearly linked to the particle concentration gradient (Fick's law), with a coefficient that accounts for the spatial variations of the environment. Contrary to Fokker–Planck diffusion, the flux is spatially isotropic, which tends to homogenise particle concentration. Fickian diffusion is generally more adapted for solving theoretical problems (although some theoretical results are also available for Fokker–Planck diffusion operators, see e.g. the discussion section of [13]). Both are widely used in the ecological modelling literature (see e.g. [8] for examples of models with Fickian diffusion, and [14] for an example of Fokker–Planck diffusion).

In Section 2, we propose a reaction-diffusion model for the adult stage, and a discrete model for the ovo-larval stage. These two models are coupled through a formula linking the solution of the reaction-diffusion model (adult population density) and the cedar seed attack rates. In Section 3, Fokker–Planck and Fickian diffusion are discussed and further compared through numerical computations.

2. The model

2.1. Insect behaviour and simplifying hypotheses

Several biological traits facilitate the establishment of *Megastigmus* seed chalcids in exotic countries: (i) an ability to extend larval diapause in seeds for up to 5 years in most species, allowing them to bridge periods where seeds are unavailable because of masting phenomenon [15]; (ii) parthenogenesis (the females can reproduce without males [2,6]). The data obtained by Fabre et al. [3] and Boivin [16] revealed about the same proportion of females and males at emergence (mean male/female ratio: 0.99, standard deviation: 0.28). This allows us to neglect the fecundation processes, and to focus on female dispersion only.

Female emergence occurs over a 6- to 11-day period, with a quite constant rate ([3, Fig. 2]). Similarly as in the related species, *Megastigmus spermotrophus*, the mean individual life expectancy is assumed to last 10 days [17]. A simplified life cycle of *M. schimitscheki* is given in Fig. 1.

The chalcid *M. schimitscheki* is considered as specifically related to seeds of cedars (*Cedrus* spp.). Furthermore, behavioural observations using video-recording showed that adults having landed on isolated host trees, bearing no cones or only a few ones, usually fly up in a slow vertical movement to the tree top, and then are blown away from the tree (A. Roques, unpublished observations). Visual and olfactory attractiveness of cedar cones have also been observed [18,19]. Thus, we make the assumption that, inside the cedar plantations, the adults remain at low altitude, while outside the plantations, they fly at a higher altitude, and are therefore subject to stronger winds and air turbulence [20].

Neglecting environment topography, and the forest and plantations other than cedar, we consider that the environment is made of two components: cedar plantations and other regions.

2.2. Model for the adult stage

Note. In this section, insect emergence is assumed to occur during year n.

Reaction-diffusion models are known to work properly in some situations of redistribution of small organisms. In the models proposed below, the reaction part of the equations is not totally standard. Indeed, it does not have to take the reproduction into account, and thus differs from classical nonlinearities. However, it has to take account of the insect progressive emergence and of the individual mortality. As we mentioned Section 1 of this paper, two types of diffusion operators are considered, leading to two models. The model with a Fokker–Planck diffusion:

$$\frac{\partial u}{\partial t}(t, \mathbf{x}) = \nabla^2 (D(\mathbf{x})u) - \frac{u}{v} + f(t, \mathbf{x}), \tag{2.1}$$
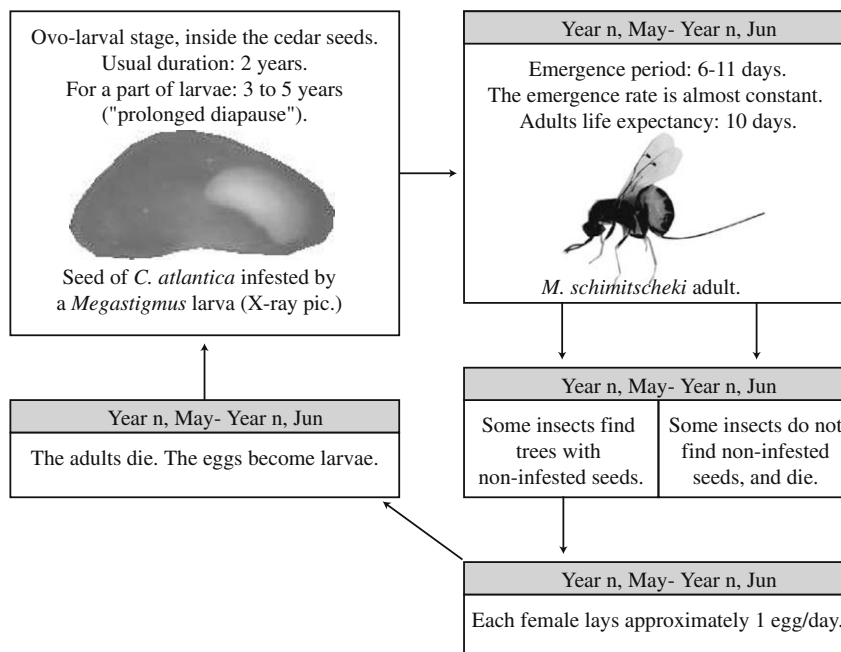
and the model with Fickian diffusion:

Fig. 1. Simplified life-cycle of *M. schimitscheki*.

$$\frac{\partial u}{\partial t}(t, \mathbf{x}) = \nabla(D(\mathbf{x})\nabla u) - \frac{u}{v} + f(t, \mathbf{x}). \tag{2.2}$$

In order to assess the usefulness of considering such models with a space-dependent coefficient $D(\mathbf{x})$, we also introduce the model with constant diffusion coefficient D_0:

$$\frac{\partial u}{\partial t}(t, \mathbf{x}) = D_0 \nabla^2 u - \frac{u}{v} + f(t, \mathbf{x}). \tag{2.3}$$

In each model, $t \in [0, N_d]$. The initial time $t = 0$ corresponds to the beginning of emergence, and N_d is an arbitrary time, sufficiently large such that living adults cannot be found at $t = N_d$. The unknown $u(t, \mathbf{x})$ is the female adults population density at time t and spatial coordinate $\mathbf{x} = (x, y)$. These equations are considered in a bounded domain $\Omega \subset \mathbb{R}^2$, with lethal boundary conditions $u = 0$ on $\partial\Omega$. The domain Ω is chosen large enough so that taking lethal boundaries is realistic, since in fact, almost no individual reaches the boundary.

The coefficient $D(\mathbf{x})$ in model (2.1) is called *motility*. In model (2.2), $D(\mathbf{x})$ is called *diffusivity* [9]. The idea of considering such spatially-dependent motility and diffusivity coefficients was motivated by the biological observations (Section 2.1) regarding the behaviour of *M. schimitscheki*. Indeed, if the insects increase their flight altitude as they leave a cedar plantation, they become subject to stronger winds and turbulences [20], and their mobility is thus increased. Though the wind effects are usually modelled by adding an advective term of the form $\mathbf{v}(t, \mathbf{x}) \cdot \nabla u$ to the equation, it appears here to be more judicious to incorporate these effects into the "random" dispersion term, since the local wind cannot be measured in practice, and may take very different directions, in function of the local topography.

The mortality rate is assumed to be constant in time. This is modelled by the term $-\frac{u}{v}$, which means that, at each time unit, a proportion $1/v$ of the individuals dies. A straightforward computation leads to $v =$ life expectancy.

Note. The dispersion operators considered in these models are conservative. However, because of the mortality term, $-u/v$, and of the lethal boundary conditions, the population density converges to 0 as t increases, and is almost 0 at $t = N_d$, which is consistent with the definition of N_d.

The progressive emergence of the individuals occurs during a time period $[0, N_{em}]$. It is modelled by the term $f(t, \mathbf{x})$. Defining the scalar field $m(\mathbf{x})$ as the density, before emergence, of female adults that will emerge during year n, at the position $\mathbf{x} \in \mathbb{R}^2$, we have:

$$f(\mathbf{x}, t) = \frac{m(\mathbf{x})}{N_{em}} \quad \text{for } t \in [0, N_{em}], \quad \text{and } f(\mathbf{x}, t) = 0 \quad \text{for } t > N_{em}. \tag{2.4}$$

The underlying assumption in (2.4) is that the emergence rate is constant (see Section 2.1). The function $m(\mathbf{x})$ is computed as follows. Let n_p be the number of cedar plantations in Ω. We denote these plantations by P_i, for $i = 1, \ldots, n_p$, and by $\mathscr{A}(P_i)$ their respective areas. The function $m(\mathbf{x})$ is given by the formula:

$$m(\mathbf{x}) = \frac{U_n(P_i)}{\mathscr{A}(P_i)}. \tag{2.5}$$

Here, $U_n(P_i)$ corresponds to the number of female adults that will emerge during year n in plantation P_i, and is given by the ovo-larval stage model (see Section 2.4).

2.3. Computation of the attack rates

To our knowledge, no standard method exists for computing attack rates (or other type of impacts), from the population density solution of a reaction-diffusion model. We derived a formula linking the attack rates in each plantation with the solution u of the model and some biological parameters.

Let P_i be a given plantation, $F_n(P_i)$ the fructification of year n (number of seeds) in plantation P_i, and E_i the expectancy of the number of new eggs laid in this plantation. Let $\overline{U}_n = \sum_{j=1}^{n_p} U_n(P_j)$, be the total number of female adults which emerge during year n. For large values of $\overline{U}_n$ (for *M. schimitscheki*, we generally deal with values of $\overline{U}_n$ above 10^4), and assuming that the individuals are independent, E_i can be computed in the following way:

$$E_i = \min\left\{\varepsilon T_i \overline{U}_n, F_n(P_i)\right\}, \tag{2.6}$$

where ε is the mean laying frequency (number of eggs per unit of time) and T_i is the mean time spent in plantation P_i. The number of individuals in plantation P_i, at time t, is equal to $\int_{P_i} u(t, \mathbf{x}) d\mathbf{x}$. Thus, the mean time spent by each individual in P_i is:

$$T_i = \frac{\int_0^{N_d} \int_{P_i} u(t, \mathbf{x}) d\mathbf{x} dt}{\overline{U}_n}. \tag{2.7}$$

Combining (2.6) and (2.7), we get:

$$E_i = \min\left\{\varepsilon \int_0^{N_d} \int_{P_i} u(t, \mathbf{x}) d\mathbf{x} dt, F_n(P_i)\right\}. \tag{2.8}$$

Thus, the estimated attack rate $A_n(P_i)$ of year n in the plantation P_i, at the end of the adult stage, is:

$$A_n(P_i) = \min\left\{\frac{\varepsilon}{F_n(P_i)} \int_0^{N_d} \int_{P_i} u(t, \mathbf{x}) dt d\mathbf{x}, 1\right\}. \tag{2.9}$$

2.4. Model for the ovo-larval stage

For each year k, the fructifications and attack rates in each plantation P_i are denoted by $F_k(P_i)$ and $A_k(P_i)$, respectively. The number $U_k(P_i)$ of female adults that will emerge, during year n, in the plantation P_i is defined recursively by:

$$U_n(P_i) = \sum_{k=2}^{5} \sigma_k \frac{A_{n-k}(P_i)F_{n-k}(P_i)}{2}, \tag{2.10}$$

where σ_k is a factor corresponding to the ratio of individuals laid during year $n - k$, which emerge during year n. This factor takes account of the prolonged diapause rates (see Section 2.1), and the mortality during the ovo-larval stage. In accordance with empirical observations, we assumed here that the ratio female/male was 1, hence the divisor 2.

3. Comparison of models (2.1)–(2.3): numerical computations

As recalled in Section 1 of this paper, the Fokker–Planck diffusion term $\nabla^2(D(\mathbf{x})u)$ of model (2.1), seems to be better-adapted to the modelling of insect dispersal than the Fickian diffusion term $\nabla(D(\mathbf{x})\nabla u)$ of model (2.2) which is, on the other hand, well adapted for physical problems such as the description of the heat propagation in an inhomogeneous medium. Assume that the coefficient $D(\mathbf{x})$ is 2 times differentiable and, in accordance with the observations of Section 2.1, is lower inside the plantations than outside the plantations. We have:

$$\nabla^2(D(\mathbf{x})u) = \nabla(D(\mathbf{x})\nabla u + u\nabla D(\mathbf{x})). \tag{3.1}$$

Thus, in the model with Fokker–Planck diffusion, an additional convection term $\nabla(u\nabla D(\mathbf{x}))$ appears compared to the model with Fickian diffusion. In regions where $D(\mathbf{x})$ is constant, this term vanishes, and the dispersion operators are therefore equivalent. However, at the interface between plantations and outside the plantations, with this additional term, the individuals in the first model with Fokker–

Planck diffusion, are more likely to go from the regions where the motility $D(\mathbf{x})$ is high to the regions where $D(\mathbf{x})$ is low. Thus, the first model should predict higher attack rates than the second one, at least in the regions of emergence. Note that, when D is constant in Ω, models (2.1) and (2.2) are both equivalent to model (2.3).

In order to get a better idea of the differences between the models (2.1)–(2.3), we carried out numerical simulations of the adult expansion and related attack rates, on a hypothetical landscape distribution. Most of the parameter values were deduced from previous empirical studies.

The landscape distribution that we considered is presented in Fig. 2. We considered a square domain Ω, of sides 100 km, and including four cedar plantations of same circular shape, with a radius $R = 0.5$ km. This leads to areas of 78 ha, which is realistic in the context of southeastern France cedar plantations. We labelled these plantation P_0, P_1, P_2 and P_3, and we assumed that the number of emerging females $U_0(P_i)$, $i = 0,\ldots,3$ was known (we assumed the first year of invasion to be $n = 0$). Namely, we took $U_0(P_0) = 10^5$, and $U_0(P_i) = 0$ for $i = 1,\ldots,3$. Thus P_0 was assumed to be the "source" point of the insect expansion. Plantation P_1 and P_2 were placed at 5 and 15 km, respectively, to the East of P_0. Plantation P_3 was placed at 15 km to the South of P_0. The fructifications $F_n(P_i)$, for $i = 0,\ldots,3$ and $n \geqslant 0$, were assumed to be independent of the year n, and equal to 10^6 seeds in each plantation, which is reasonable for plantations of this size (data obtained from the French National Forestry Office). The initial ratio (emerging males + females)/ (available seeds) is therefore of 0.2 in P_0.

The mortality rate, $1/v$, was directly computed using a life expectancy $v = 10$ days [17]. The mean laying rate $\varepsilon = 1$ was obtained from previously conducted experiments on $M.$ $schimitscheki$ [16]. The length of the emergence period was set to $N_{em} = 9$ days (cf. Section 2.1), and N_d was set to 40 days. In models (2.1) and
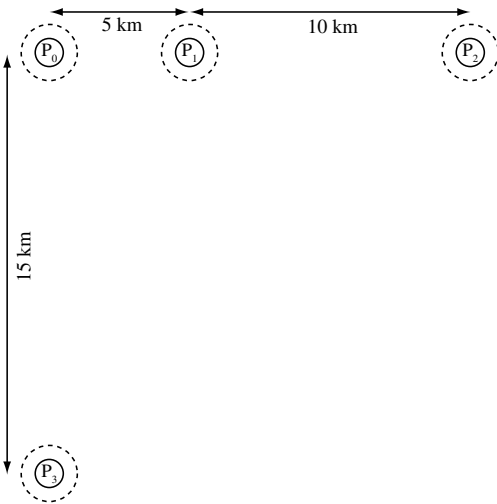

Fig. 2. Hypothetical plantation distribution used for the numerical computations. The plantations are represented by plain circles. The dashed circles delimit the regions where $D(\mathbf{x})$ is not constant in models (2.1) and (2.2), when $\rho = 0.5$ km. The boundary of the domain Ω, whose centre is assumed to be located in P_0, is not represented here.
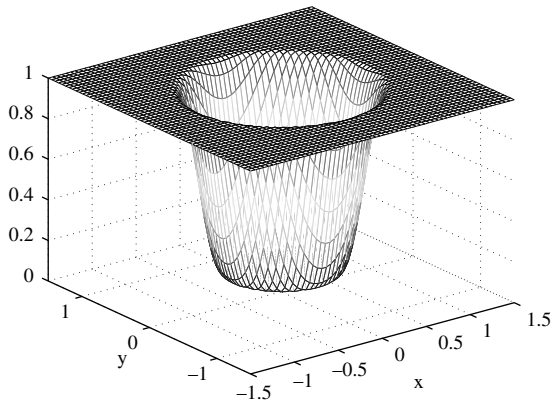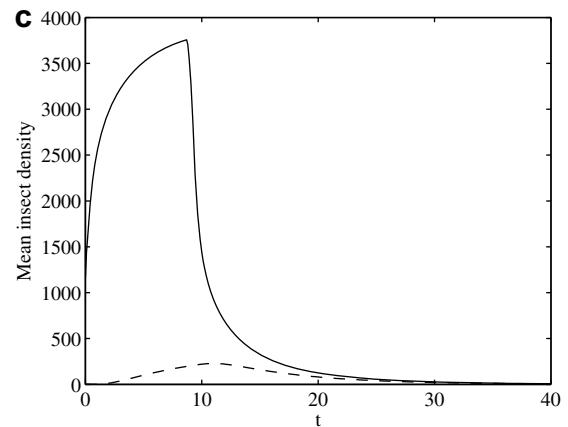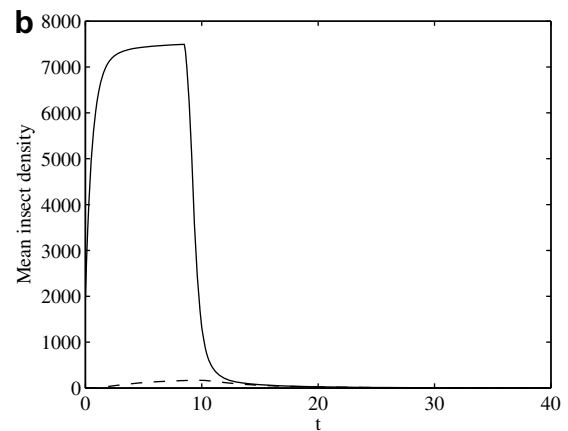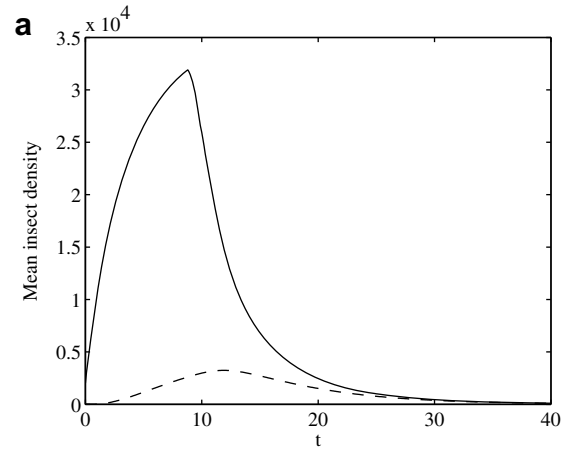

Fig. 3. The function $D(\mathbf{x})$, defined by (3.2), near a circular plantation of radius $R = 0.5$, and centered in the point $(0,0)$. In this plot, it is assumed that $a = 0.1$, $b = 1$ and $\rho = 0.5$.

Fig. 4. Mean population densities in plantations P_0 (solid lines) and P_1 (dashed lines), during the time-span $[0, N_d]$ (first year of invasion). (a) Model (2.1) with $a = 0.1$ and $b = 5$. (b) Model (2.2) with $a = 0.1$ and $b = 5$. (c) Model (2.3) with $D_0 = 1$.

(2.2), the only parameter which was not known precisely was the function $D(\mathbf{x})$ (or the constant D_0 for model (2.3)). We assumed that $D(\mathbf{x})$ was constant equal to a value $a > 0$ inside the plantations, and was also constant but equal to a certain value $b > a$, at a distance $R + \rho$ of the plantation centres. In the rings comprised between a distance R and $R + \rho$ from the plantation centres, we assumed that $D(\mathbf{x})$ was radially increasing, from the centre of the closest plantation. More precisely, setting: $r(\mathbf{x}) =$ (distance between $\mathbf{x}$ and the centre of the closest plantation), we have:

$$\begin{cases} D(\mathbf{x}) = a & \text{if } r(\mathbf{x}) \leqslant R, \\ D(\mathbf{x}) = a + \frac{(b-a)(r(\mathbf{x})-R)^3}{\rho^5}\left[6\left(R - r(\mathbf{x}) + \frac{5}{4}\rho\right)^2 + \frac{5}{8}\rho^2\right] & \text{if } R < r(\mathbf{x}) < R + \rho, \\ D(\mathbf{x}) = b & \text{if } r(\mathbf{x}) \geqslant R + \rho. \end{cases}$$
$$(3.2)$$

This function is depicted in Fig. 3, for particular values of the parameters a, b, R and ρ.

In our computations, the parameter a varied between 0.01 and 0.1 km²/day, corresponding to low rates of movement inside the plantations (see [8] for some observed values of D, for different species), and the value of b was assumed to be between 1 and 10 km²/day, corresponding, respectively, to intermediate, and high rates of movement. Model (2.3) was solved for $D_0 \in [0.01, 5]$. Unless otherwise mentioned, we set $\rho = R = 0.5$ km.

We solved the reaction-diffusion models thanks to a finite elements method, using the Comsol© software.

3.1. Results

3.1.1. Impact of the invasion after one year

Solving each model of adult dispersal, we numerically obtained population densities $u(t,\mathbf{x})$, for $t \in [0, N_d]$ and $x \in \Omega$. The corresponding attack rates, in percent of available seeds, $100 \times A_0(P_i)$, in plantations P_i, $i = 0, \ldots, 3$ were computed thanks to formula (2.9). We focused our analysis on attack rates rather than on population densities, since, in practice, only the attack rates are measured (see, however, Fig. 4 for an overview of the population densities solutions of our models, in P_0 and P_1, for particular values of the parameters).

For model (2.1), the attack rates in plantations P_0, P_1, P_2 and P_3 at the end of the invasion are depicted in Fig. 5. Depending on the values of a and b, they range from 21.0% to 76.7% in P_0, from 1.0% to 5.9% in P_1, from 0.0% to 1.0% in P_2, and from 0.0% to 1.2% in P_3. The attack rates tend to increase with b. This phenomenon is probably the consequence of an higher convection coefficient, oriented inside the plantations, for large values of b. Note that the attack rates in plantations P_2 are slightly smaller than in P_3, for *every* value of the parameters a and b.

The attack rates obtained with model (2.2), in plantations P_0 and P_1, are presented in Fig. 6. These attack rates range from 4.7% to 31.2% in P_0, and from 0.1% to 0.2% in P_1, and tend to decrease with b in these plantations. They remain at 0.0% in the other plantations.

(a) $100 \times A_0(P_0)$

(b) $100 \times A_0(P_1)$

(c) $100 \times A_0(P_2)$

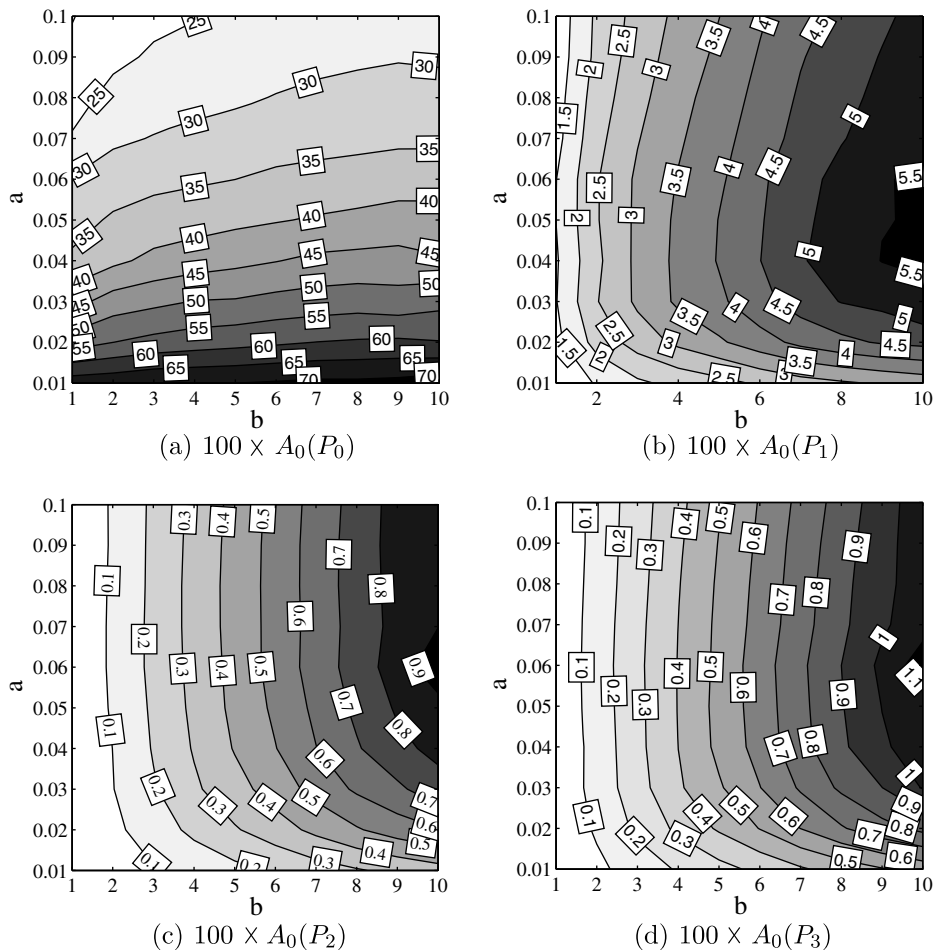

(d) $100 \times A_0(P_3)$

Fig. 5. Model (2.1): contour lines of the predicted attack rates after one year, $100 \times A_0(P_i)$, in each plantation P_i, $i = 0, \ldots, 3$, in function of the parameters a, b.
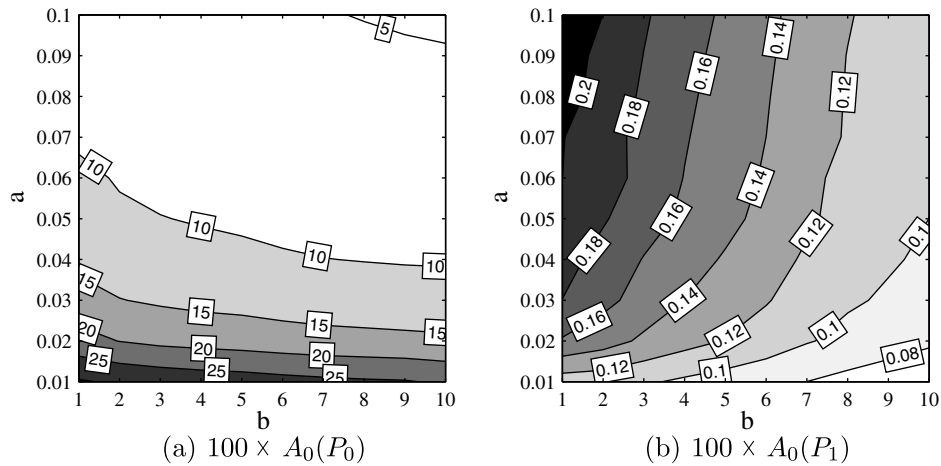
Fig. 6. Model (2.2). (a) and (b) Contour lines of the attack rates $100 \times A_0(P_i)$, $i = 1,2$, in function of the parameters a, b.

Lastly, for model (2.3), when $D_0 \in [0.01, 5]$, the attack rates in P_0 decrease with D_0, ranging from 0.8% when $D_0 = 5$ to 46.2% when $D_0 = 0.01$. They never exceed 0.2% in P_1, and remain at 0.0% for any value of D_0 in the two other plantations.

In all cases, the attack rates given by models (2.2) and (2.3) are small compared to those given by model (2.1), especially in plantations other than the source one.

Note. We also tested the effects of the parameters N_{em} and ρ. When $N_{em} = 1$, corresponding to a massive emergence of all the individuals in one day, the attack rates are hardly increased compared to the case of an emergence over a nine-day period. For values of $\rho \neq 0.5$, the above results are slightly modified. In the interval $[0.1, 1]$, as ρ

increases, the attack rates in the source plantation P_0 tend to increase, while they decrease in the other plantations. However, qualitatively, the results remain similar to the case $\rho = 0.5$.

3.1.2. Impact of the invasion after 7 years

With the same parameters described at the beginning of Section 3.1, we tested the full invasion model, over a period of 7 years. This model combines the model for adult dispersal (either (2.1), (2.2) or (2.3)), with the model (2.10) for the ovo-larval stage, through equation (2.9), which describes the attack rates.

Following the observations of [3], the factors σ_k were set to $\sigma_2 = 0.8$, $\sigma_3 = 0.2$, and $\sigma_i = 0$ for $i > 3$, corresponding to 80% of
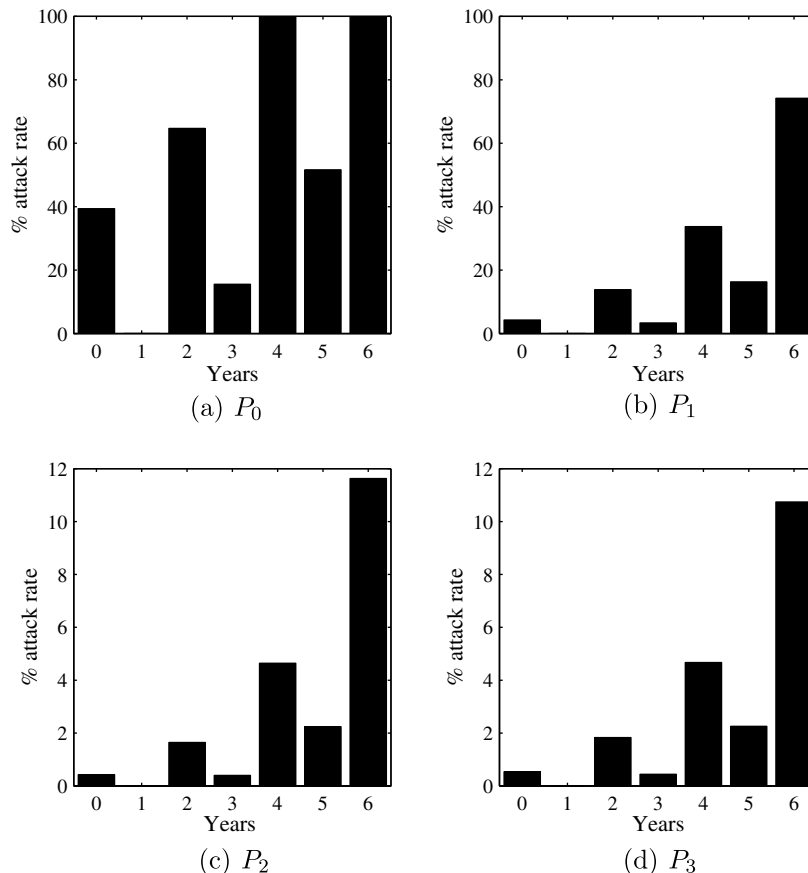

Fig. 7. Predicted attack rates, in each plantation P_i, $i = 0, \ldots, 3$, over 7 years, when adult dispersal is modelled by (2.1), with $a = 0.05$ and $b = 5$. In each plantation, both series of attack rates during the odd and even years increase, meaning a successful settlement of the insects, and spatial expansion of the invasion.
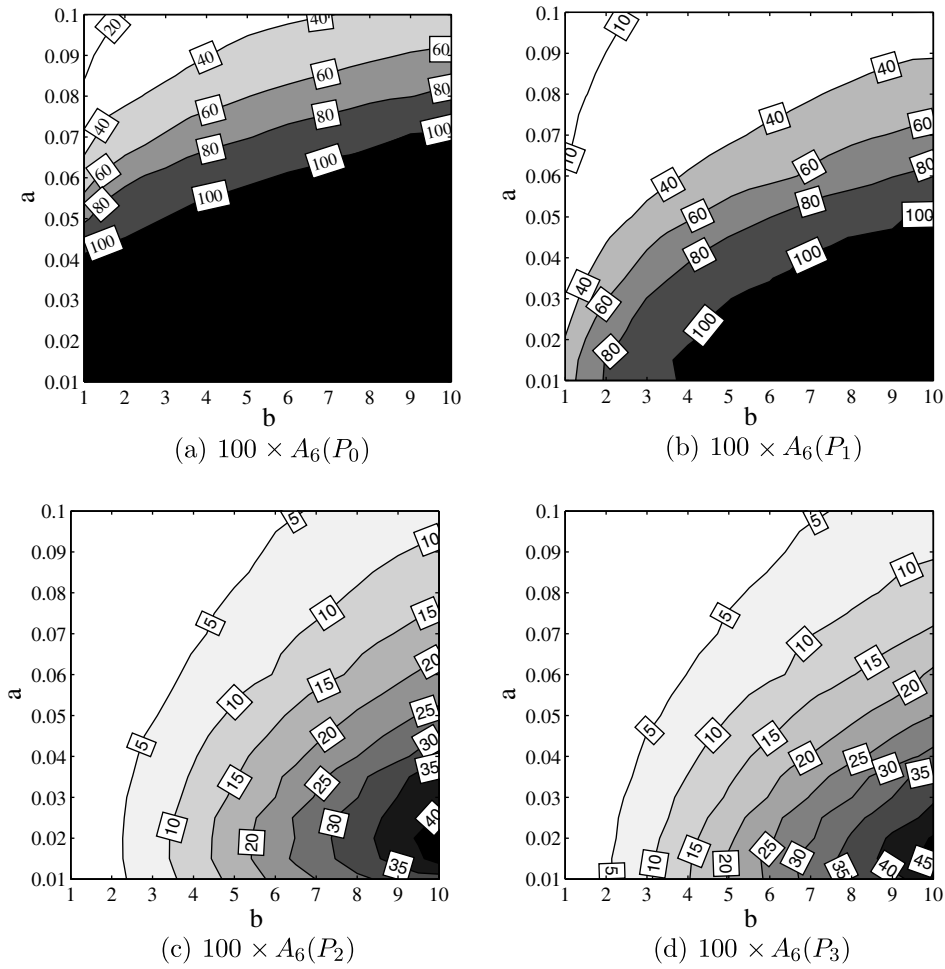
(a) $100 \times A_6(P_0)$

(b) $100 \times A_6(P_1)$

(c) $100 \times A_6(P_2)$

(d) $100 \times A_6(P_3)$

Fig. 8. Contour lines of the attack rates $100 \times A_6(P_i)$, obtained after 7 years, in each plantation P_i, $i = 0,\ldots,3$, when adult dispersal is modelled by (2.1).

2-years diapause and 20% of 3-years diapause (see Fig. 1), and no larval mortality.

Because of the minimal diapause duration of 2 years, and since the invasion is assumed to begin at year $n = 0$, no adult emerge during year 1. Thus, in each plantation P_i, $U_1(P_i) = 0$ (see formula (2.9)). As a consequence, the attack rates $A_1(P_i)$ are equal to 0. Furthermore, the number of female adults that emerge during year 2 in each plantation is $U_2(P_i) = \sigma_2 A_0(P_i)/2$, whereas during year 3,

$U_3(P_i) = \sigma_3 A_0(P_i)/2$. Thus, because most of the adults emerge after 2 years (indeed, $\sigma_2 = 4\sigma_3$), $U_2(P_i) = 4U_3(P_i)$ in each plantation. This leads to higher values of the attack rates during the even years compared to odd years. This is illustrated in Fig. 7, in the case of an adult dispersal modelled with (2.1).

The attack rates $100 \times A_6(P_i)$, $i = 0,\ldots,3$, obtained after 7 years when adult dispersal is modelled with (2.1) are presented in Fig. 8. They range from 13.2% to 100% in P_0, from 3.0% to 100% in
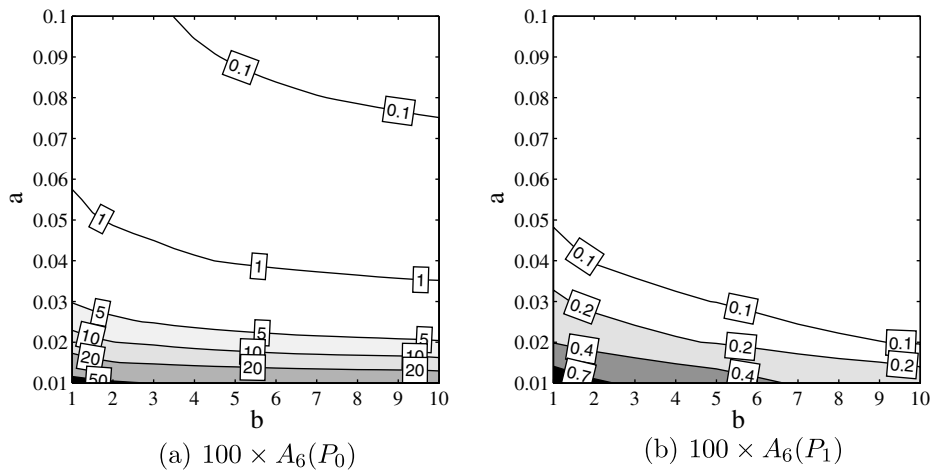

(a) $100 \times A_6(P_0)$

(b) $100 \times A_6(P_1)$

Fig. 9. Contour lines of the attack rates $100 \times A_6(P_i)$, obtained after 7 years, in plantation P_1 and P_2, when adult dispersal is modelled by (2.2).

P_1, from 0.1% to 42.6% in P_2, and from 0.0% to 47.6% in P_3. Subtracting the results presented in Fig. 8(d) to those of Fig. 8(c), we observed that, contrarily to what happened at the beginning of the invasion (Section 3.1.1), the attack rates in P_2 after 7 years are now slightly higher than in P_3, for values of a larger than 0.03. However, for $a < 0.03$, the attack rates in P_3 remain higher than in P_2, after 7 years.

The attack rates in plantations P_0 and P_1, obtained after 7 years when the adult dispersal was modelled by (2.2), are presented in Fig. 9. They range from 0.1% to 61.5% and from 0.0% to 0.9%, respectively, in P_0 and P_1. The attack rates in P_2 and P_3 are both of 0.0%.

Lastly, when adult dispersal is modelled by (2.3), with $D_0 \in [0.01,5]$, the attack rate $100 \times A_6(P_0)$ decreases with D_0 and ranges from 0.0% when $D_0 \in [0.7,5]$ to 100.0% when $D_0 \in [0.01,0.02]$. In the other plantations, all the attack rates remain at 0.0%, whatever D_0.

Thus, contrary to what has been obtained with model (2.1), modelling adult dispersal by (2.2) or (2.3) leads to population extinction for a large range of parameter values, and in any case leads to very low attack rates in plantations other than the source one, which can be interpreted as an invasion failure.

4. Discussion

In this work, we have proposed models to describe the expansion of an invasive insect, and its impact on cedar plantations. The life-cycle of the insect consisted in two distinct stages: ovo-larval and adult stages. Modelling the ovo-larval stage of the insect did not require sophisticated mathematical tools. On the other hand, the insect expansion, occurring during the adult stage was modelled with a two-dimensional reaction-diffusion equation. Though reaction-diffusion models are very common in the literature related to insect dispersal (see the books [8–11], for review), we raised some questions which are not classical.

The first point was to relate the models for the ovo-larval and adult stages. To do so, we proposed a simple formula, in Section 2.3, linking the adult population density, solution of a reaction-diffusion model, with a seed attack rate, corresponding to the new laid eggs at the end of the seasonal invasion (Fig. 1). The idea behind this formula is that the attack rate in each plantation is proportional to the mean time spent by the individuals inside this plantation.

The second point was to choose the appropriate diffusion operator. We considered the three most common diffusion operators found in the reaction-diffusion literature. The corresponding models were (2.1), with Fokker–Planck diffusion, (2.2) with Fickian diffusion, and the model (2.3) with constant diffusion coefficient. The wind effects were not modelled through an additional advection term, since, at the scale considered here, winds may vary greatly in time and space, and cannot therefore be measured precisely. We chose rather to incorporate them in the random diffusion term. We assumed, in models (2.1) and (2.2), that the mobility was smaller inside the plantations. This assumption was consistent with previous empirical observations, since *Megastigmus* fly at lower altitudes inside the plantations, and is therefore subject to lower winds.

Writing the Fokker–Planck diffusion operator of model (2.1) in a different form, we observed that the main difference with model (2.2), and also with model (2.3), was a convection term, pushing the individuals situated at the interface of the plantations into these plantations. Numerical computations confirmed this observation. With the same coefficient $D(\mathbf{x})$, model (2.1) predicted higher attack rates than model (2.2).

Previous experimental observations show that the results obtained when adult dispersal is modelled by (2.2) or (2.3) are not realistic. Indeed, measures of the attack rates conducted in the region of Mont-Ventoux during the period following the insect introduction show that, in 1999 (i.e. 6–9 years after the introduction of the insect), *M. schimitscheki* has colonised an area of diameter at least 15 km [3, Table 1]. Several plantations, situated at opposite points of this area, exhibit attack rates above 50%, and up to 86.8% [3, Table 2]. Such attack rates could not be obtained with models (2.2) and (2.3), which tend to "homogenise" the population density, as they do for the solution of the heat equation. Indeed, our numerical results show that these models lead to very low attack rates in plantations other than the source one, and finally to extinction or, at least, invasion failure.

On the other hand, model (2.1) gave more realistic results than the two others, with attack rates reaching 100% in the source plantation, and more than 40% in plantations situated 15 km away from this source, 7 years after the beginning of the invasion. From a qualitative viewpoint, these values are not far from the above-mentioned observations of [3].

Thus, our study shows that taking account of the dependence of the insect mobility with respect to spatial heterogeneity is critical for obtaining good predictions of the insect impact. Moreover, it confirms the previous observations that Fokker–Planck diffusion is more adapted than Fickian diffusion for modelling such ecological processes. We would like to recall, however, that the "self-adjoint" nature of the Fickian diffusion operator allows to obtain important theoretical results (see [21–24]) and can be more realistic in other situations.

In order to fit the unknown coefficients a and b, and to further assess the validity of our model, we should be planing to obtain new data from the region of Mont-Ventoux. The location of the cedar plantations in Southeastern France, as well as estimates of the annual seed production in each plantation, can be obtained from the French National Forestry Office (FNFO). Standardised seeds samplings should be carried out. Immediately after being collected the seeds should be X-rayed in order to calculate the proportion of filled, empty and chalcid-infested seeds. Since *M. schimitscheki* cannot be separated from *M. pinsapinis* through observations of larvae on X-ray plates, the infested seeds should be placed in emergence boxes until adult emergence in order to know the proportion of each species, and to estimate the specific damage that can be attributed to *M. schimitscheki*. It is noteworthy that attack rates could be largely modulated by spatiotemporal changes in the fructification parameters $F_n(P_i)$, which therefore need to be carefully evaluated. Fitting the model to the data may also require to investigate the dependence of the width ρ of the interface where $D(\mathbf{x})$ is not constant, with respect to the plantation sizes.

If the validity of our model was confirmed, it could lead to qualitative results regarding the influence of biological and environmental parameters. For instance, comparing the attack rates in our hypothetical plantations P_2 and P_3, we observed that the presence of an intermediate plantation (P_1) between the invasion source point and the considered plantation can slow down invasion during the first years ("barrier effect"), and then facilitate it ("intermediate step effect"). We also observed that a shortening of the emergence period N_{em}, in model (2.1), had almost no effect on attack rates. It is not surprising since no interaction between the individuals have been assumed. However, modelling this progressive emergence can be crucial under different hypotheses. For instance, the domination of the competing species *M. pinsapinis* by *M. schimitscheki* seems to be linked to the earlier emergence of *M. schimitscheki* [3]. In a future work, we plan to build and analyse the competition between these two species through a similar model. The effects of prolonged diapause, especially for time-varying fructification parameters, could also be investigated.

Lastly, we would like to emphasise that other types of models exist and are efficient in practice for modelling such dispersion

phenomena in heterogeneous environments. For instance, individual based models (see e.g. [25–27]), where each individual interacts with its environment, and simulations are run until a general behaviour of the population can be observed. Integro-difference or dispersal kernel models can also be useful, especially when long distance dispersal is a key factor of the expansion [28,29]. However, our aim in this paper was precisely to compare some dispersion operators used in practice in reaction-diffusion models, and to give a clear approach of the modelling of insect expansion and impact in the framework of reaction-diffusion equations.

Acknowledgments

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