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Modelling the impact of an invasive insect,  
*Megastigmus schimitscheki*, 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 two-dimensional reaction-diffusion model to predict the expansion and impacts of this insect. Two main diffusion operators, of Fokker-Planck and Fickian types, are tested. We show that taking account of the dependence of the insects mobility with respect to spatial heterogeneity, and choosing the appropriate diffusion operator, are critical factors for obtaining good predictions.

**Keywords:** Insect dispersal; Reaction-diffusion model; Fickian diffusion; Fokker-Planck; Seed chalcid; Cedar;

## 1 Introduction

As a result of technological advances and of trade globalization, 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 (Liebhold et al., 1995). This is especially true for the insects infesting tree seeds, whose cryptic way of life does not usually allow a detection easier than using X-rays, the more as phytosanitary regulations are limited or non existent in many countries. 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 (Roques and Skrzypczynska, 2003). Modelling the expansion processes of such invasive species, and the related damages to forests and tree plantations, becomes a priority.

Fabre et al. (2003) 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 1990-1994, in the region of Mont-Ventoux. The study of Fabre et al. (2003), 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 area are rather similar to these of other *Megastigmus* seed chalcids which have been extensively studied in Europe, North America and Japan (e.g. Kamijo, 1962; Hedlin et al., 1980; Roques, 1983; Roques and Skrzypczynska, 2003). 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 colonized 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 (Roques and Skrzypczynska, 2003). However, *M. pinsapinis* seems dominated by *M. schimitscheki* (Fabre et al., 2003). 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 population dynamics models.

Reaction-diffusion models have proved themselves to be well adapted for describing some invasive species expansion in homogeneous and heterogeneous environments (Skellam, 1951; Shigesada and Kawasaki, 1997), especially when one cannot follow the movement of each organism independently (for review, see Shigesada and Kawasaki, 1997; Turchin, 1998; Murray, 2002; Okubo and Levin, 2002). In the present case of *M. schimitscheki*, however, standard approaches may fail. Indeed, the species life-cycle 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 of the previous years, 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, the methodology for coupling the ovo-larval stage time-discret model with a reaction-diffusion model for the adult stage, is not described in the existing literature. 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 seeds 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, is said to be more adapted than the Fickian one for modelling ecological processes in varying environments (Turchin, 1998). However, Fickian diffusion is more adapted for solving theoretical problems, and both are widely used in the ecological modelling literature (see e.g. Shigesada and Kawasaki (1997) for examples of Fickian diffusion, and Hannunen and Ekbom (2001) for an example of Fokker-Planck diffusion).

In Section 2, we propose a reaction-diffusion model for the adult stage, and a simple 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 seeds 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 (Turgeon et al., 1994); (ii) parthenogenesis (the females can reproduce without males Roques, 1983; Roques and Skrzypczynska, 2003). A simplified life cycle of *M. schimitscheki* is given in Fig. 1. The data obtained by Fabre et al. (2003) and Boivin (2006) 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 6-11-day period, with a quite constant rate (Fabre et al., 2003, Fig. 2). Similarly as in the related species, *Megastigmus spermotrophus*, the mean individual life expectancy is assumed to last 10 days (Jarry et al., 1997).

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 non or only a few cones 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 (Roques and Raimbault, 1998; Luik et al., 1999). 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 turbulences (Nathan et al, 2002).

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 model proposed below, the reaction part of the equation is not totally standard. Indeed, it does not have to take the reproduction into account, and thus differs from the classical logistic non-linearity  $u(\varepsilon - \nu u)$ . However, it has to take account of the insects progressive emergence and of the individuals mortality. As we mentioned in the introduction of this paper, two types of diffusion operators are considered, leading to two models. The model with a Fokker-Planck diffusion:

$$\frac{\partial u}{\partial t}(t, \mathbf{x}) = \nabla^2(D(\mathbf{x})u) - \frac{u}{\nu} + f(t, \mathbf{x}), \quad (2.1)$$

and the model with Fickian diffusion:

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

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  $D_0$ :

$$\frac{\partial u}{\partial t}(t, \mathbf{x}) = D\nabla^2 u - \frac{u}{\nu} + f(t, \mathbf{x}). \quad (2.3)$$

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  $\Omega$  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* (Turchin, 1998). The idea of considering such spatially-dependent motility and diffusivity coefficients was motivated by the biological observations (§ 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 (Nathan et al, 2002), 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. See Section 3 for a comparison between models (2.1), (2.2) and (2.3).

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

*Note:* The dispersion operators considered in these models are conservative. However, because of the mortality term,  $-u/\nu$ , 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

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

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

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

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

$$E_i = \varepsilon T_i \bar{U}_n, \quad (2.6)$$

where  $\varepsilon$  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:

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

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

$$E_i = \varepsilon \int_0^{N_d} \int_{P_i} u(t, \mathbf{x}) d\mathbf{x} dt. \quad (2.8)$$

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:

$$A_n(P_i) = \frac{\varepsilon}{F_n(P_i)} \int_0^{N_d} \int_{P_i} u(t, \mathbf{x}) dt d\mathbf{x}, \quad (2.9)$$

where  $F_n(P_i)$  corresponds to the fructification of year  $n$  (number of seeds) in plantation  $P_i$ . Note that, in practice,  $F_n(P_i)$  is generally measured in the course of year  $n + 1$ . Indeed, the attack occurs one year before the harvest takes place.

## 2.4 Model for the ovo-larval stage

Modelling this part of the insect life cycle does not require sophisticated mathematical tools. However, we briefly present a model here, for the sake of completeness. For each year  $k$ , the fructifications (number of seeds) and attack rates (percentage of seeds infested by *M. schimitscheki*) 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:

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

where  $\sigma_{n-k}$  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 § 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) and (2.2), numerical computations

As recalled in the introduction 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 insects 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 we are in a binary environment, and that the coefficient  $D(\mathbf{x})$  is 2 times differentiable and takes the constant values  $a > 0$  inside the plantations, and  $b > 0$  outside the plantations, with  $b > a$  from the observations of § 2.1. We have

$$\nabla^2(D(\mathbf{x})u) = \nabla(D(\mathbf{x})\nabla u) + u\nabla D(\mathbf{x}), \quad (3.11)$$

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  $\Omega$ , 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), (2.2) and (2.3), we carried out numerical simulations of the adult expansion and related attack rates, on an hypothetical landscape distribution. Most of the parameters values were deduced from previous empirical studies.

The landscape distribution that we considered is presented in Fig. 2. We considered a square domain  $\Omega$ , of sides 100 km, and including four cedar plantations of same circular shape, with a radius  $R = 0.5$  km. This lead to areas of 78 ha, which are 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  $U_n(P_i)$ ,  $i = 0 \dots 3$  was known. Namely, we took  $U_n(P_0) = 10^5$ , and  $U_n(P_i) = 0$  for  $i = 1 \dots 3$ . Thus  $P_0$  was assumed to be the “source” point of the insect expansion. Plantation  $P_1$  and  $P_2$  were placed at 5 km and 15 km, respectively, to the East of  $P_0$ . Plantation  $P_3$  was placed at 15km to the South of  $P_0$ . The fructification  $F_n(P_i)$ ,  $i = 0 \dots 3$ , was assumed to be the same in each plantation, and equal to  $10^6$  seeds, which is reasonable for plantations of this size (data obtained from the French National Forestry Office). The the initial ratio (emerging males+females)/(available seeds) is therefore of 0.2 in  $P_0$ .

The mortality rate,  $1/\nu$ , was directly computed, using a life expectancy,  $\nu$  of 10 days (Jarry et al., 1997). The mean laying rate  $\varepsilon = 1$  was obtained from previously conducted experiments on *M. schimitscheki* (Boivin, 2006). The length of the emergence period was set to  $N_{em} = 9$  days (cf. § 2.1), and  $N_d$  was set to 40 days. In models (2.1) and (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  $2R = 1$  km from the plantations centres. In the rings comprised between a distance  $R$  and  $2R$  from the plantations centres, we assumed that  $D(\mathbf{x})$  was radially increasing, from the centre of the closest plantation. More precisely, setting

$r(\mathbf{x}) =$  the distance between  $\mathbf{x}$  and the centre of the closest plantation,



we have:

$$\begin{cases} D(\mathbf{x}) = a \text{ if } r(\mathbf{x}) \leq R, \\ D(\mathbf{x}) = a + \frac{(b-a)(r(\mathbf{x})-R)^3}{R^5} (6r(\mathbf{x})^2 - 27r(\mathbf{x})R + 31R^2) \text{ if } R \leq r(\mathbf{x}) \leq 2R, \\ D(\mathbf{x}) = b \text{ if } r(\mathbf{x}) \geq 2R. \end{cases} \quad (3.12)$$

This function is depicted in Fig. 3.

In models (2.1) and (2.2), we assumed that the value of  $a$  was  $0.1 \text{ km}^2/\text{day}$ , corresponding to a low rate of movement inside the plantations (see Shigesada and Kawasaki, 1997, for some observed values of  $D$ , for different species). The value of  $b$  was set either to  $1 \text{ km}^2/\text{day}$  or to  $5 \text{ km}^2/\text{day}$ , corresponding respectively to intermediate, and high rates of movement. In the case of model (2.3), we set either  $D_0 = 0.1 \text{ km}^2/\text{day}$ ,  $D_0 = 1 \text{ km}^2/\text{day}$  or  $D_0 = 5 \text{ km}^2/\text{day}$ .

We solved the reaction-diffusion models using a finite elements method, using the Comsol<sup>®</sup> software.

### 3.1 Results

For each model, and each parameter value, we numerically obtained a population density  $u(t, \mathbf{x})$ , for  $t \in [0, N_d]$  and  $x \in \Omega$ . The corresponding attack rates  $A_n(P_i)$ , in plantations  $P_i$ ,  $i = 0 \dots 3$  were computed thanks to formula (2.9). In this section, we focus our analysis on the attack rates rather than on the population density, since, in practice, only the attack rates are measured. Fig. 4 gives 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), when  $a = 0.1$  and  $b = 1$ , the attack rates in plantations  $P_0$ ,  $P_1$ ,  $P_2$  and  $P_3$  at the end of the invasion are 19.78%, 1.18%, 0.02% and 0.02% respectively. When  $b = 5$ , these attack rates are 26.48%, 3.80%, 0.44% and 0.51% respectively (Fig. 5, (a)). The attack rates are larger for  $b = 5$ , even in the source plantation  $P_0$ . This phenomenon is probably the consequence of an higher convection coefficient, oriented inside the plantations, for large values of  $b$ . In both cases, the observed attack rates are consistent with what could be expected from a biological viewpoint. Note that the attack rates in plantations  $P_2$  are only slightly smaller than in  $P_3$ , which advocates for a low barrier effect played by the plantation  $P_1$ .

For model (2.2), when  $a = 0.1$  and  $b = 1$ , the attack rates are 7.67%, 0.21%, 0.00% and 0.00%, respectively in plantations  $P_i$ ,  $i = 0 \dots 3$ . For  $b = 5$ , we obtained 5.31%, 0.15%, 0.02% and 0.02% (Fig. 5, (b)). Thus, in the case of model (2.2), when  $b$  is increased, the plantations  $P_0$  and  $P_1$  have lower attack rates, and the plantations  $P_2$  and  $P_3$ , which are farther from the invasion source point, have slightly higher attack rates. In both cases, however, the attack rates are very small compared to model (2.1), and do not seem realistic from a biological viewpoint, basing ourselves on preliminary experiments conducted in the region of Mont-Ventoux. Indeed, these attack rates are too low to sustain an invasion (compare with the initial ratio (emerging males+females)/(available seeds) of 0.2 in  $P_0$ ).

Lastly, for model (2.3), when  $D_0 = 0.1$ , the attack rates are 15.21%, 0.04%, 0.00% and 0.00% respectively in  $P_i$ ,  $i = 0 \dots 3$ . When  $D_0 = 1$ , it gives 2.87%, 0.24%, 0.01% and 0.01%, and for  $D_0 = 5$ , 0.77%, 0.17%, 0.02% and 0.02% (Fig. 5, (c)). In all cases, the attack rates given by this model are smaller than those given by model (2.1). When  $D_0 = 0.1$ , the attack rate in  $P_0$  remains at a realistic level, but the other attack rates are very low, compared to what could be expected. For higher  $D$  values, the attack rate in the source point  $P_0$  either, is too low to sustain an invasion.

The model (2.1), seems better-adapted to our problem than the two other models. We also tested on this model the influence of the length of the emergence period on the attack rates. With  $b = 5$ , we obtained, taking  $N_{em} = 1$ , attacks rates of 25.73%, 3.72%, 0.44% and 0.51%, respectively in plantations  $P_i$ ,  $i = 0 \dots 3$ . Thus, in this case corresponding to a massive emergence of all the individuals in one day, the attack rates are very slightly decreased compared to the case of an emergence over a nine-day period.

## 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 Shigesada and Kawasaki, 1997; Turchin, 1998; Murray, 2002; Okubo and Levin, 2002, for review), we raised some questions which, to our knowledge, are not classical.

The first point was to relate the models for the ovo-larval stage and adult stage. To do so, we proposed a simple formula, in § 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 chose 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 with constant diffusion coefficient  $D$ . 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 are 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). The model (2.3), with constant coefficient  $D_0$ , predicted very low attack rates, except near the invasion source point for small  $D_0$  values. The comparison with model (2.1) showed that taking account of the effects of spatial heterogeneities on the individuals mobility, could have an important impact on the predicted attack rates. From our point of view, and basing ourselves on some preliminary observations made at Mont-Ventoux, model (2.1) gave more realistic results than the two others, for the species considered here. The model (2.2) tended to “homogenize” the population density, has it does for the solution of the heat equation. Indeed, as soon as the emergence period ends, almost no individual remains in the source plantation (see Fig. 4, (b)). To correct this, a drift term, oriented towards the region where  $D$  is smaller, should be added. This would lead to models close to (2.1). We would like to recall, however, that the “self-adjoint” nature of the Fickian diffusion operator considered in model (2.2) allows to obtain important theoretical results (see Cantrell and Cosner, 2003; Kinezaki et al., 2003; Berestycki et al., 2005a,b) and can be more realistic in other situations.

In order to fit the unknown coefficients  $a$  and  $b$ , and to assess the validity of the model (2.1), we are planning to obtain data from the region of Mont-Ventoux. The location of the cedar plantations in Southeastern France will be obtained from the French National Forestry Office (FNFO). On each plantation, the FNFO will give estimations of the annual seed production in each plantation. Then, standardized seeds samplings will be carried out. Immediately after being collected the seeds will be X-rayed in order to calculate the proportion of filled, empty and chalcid-infested seeds. However, *M. schimitscheki* cannot be separated from *M. pinsapinis* through observations of larvae on X-ray plates. Therefore, the infested seeds will 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*.

In this paper, we have explicitly modelled adults progressive emergence. We have seen in § 3.1 that, when the length of the emergence was shortened, the model (2.1) did not give dramatically different results. It is not surprising since no interaction between the individuals have been assumed. However, modelling this progressive emergence remains a very important question. Indeed, the domination of the competing species *M. pinsapinis* by *M. schimitscheki* seems to be linked to the earlier emergence of *M. schimitscheki* (Fabre et al., 2003). In a future work, we plan to build and analyse the competition between these two species through a system of reaction-diffusion. Much of the tools used in this paper could surely be adapted to this case. Taking account of the shape of the emergence function will probably be of crucial interest.

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

neous environments. For instance, individual based models (see e.g. Kareiva and Shigesada, 1983; Marsh and Jones, 1988; Gross et al., 1992), 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 (Mollison, 1977; Klein et al., 2006). 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 insects expansion and impacts in the framework of reaction-diffusion equations.

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## 5 Figure captions

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

**Fig. 2:** Hypothetical plantations 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). The boundary of the domain  $\Omega$ , whose center is assumed to be located in  $P_0$ , is not represented here.

**Fig. 3:** The function  $D(\mathbf{x})$ , defined by (3.12), near a circular plantation of radius  $R = 0.5$ , and centered in the point  $(0, 0)$ . In this plot, it is assumed that  $a = 0.1$  and  $b = 1$ .

**Fig. 4:** Mean population densities in plantations  $P_0$  (solid lines) and  $P_1$  (dashed lines), during the time-span  $[0, N_d]$ . (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  $D_0 = 1$ .

**Fig. 5:** Bar charts presenting the predicted attack rates, in each plantation. (a): Model (2.1); the black bars correspond to the case  $b = 1$ , and the white bars correspond to  $b = 5$ . (b): Model (2.2); the black bars correspond to the case  $b = 1$ , and the white bars correspond to  $b = 5$ . (c): Model (2.3); the black bars correspond to the case  $D_0 = 0.1$ , the gray bars correspond to  $D_0 = 1$ , and the white bars to  $D_0 = 5$ .

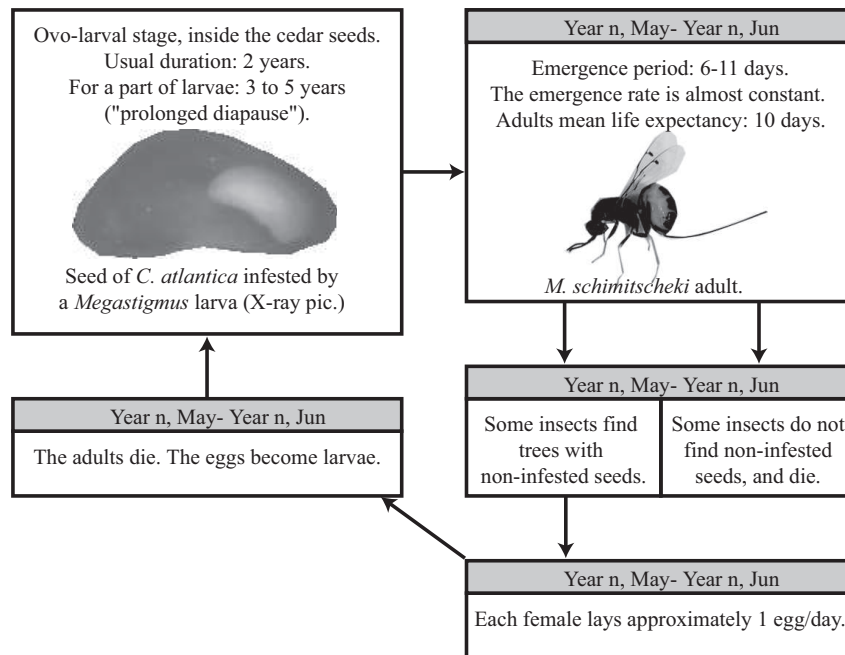


Figure 1:

## 6 Figures

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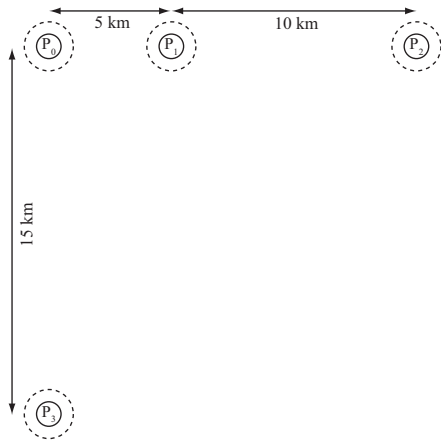


Figure 2:

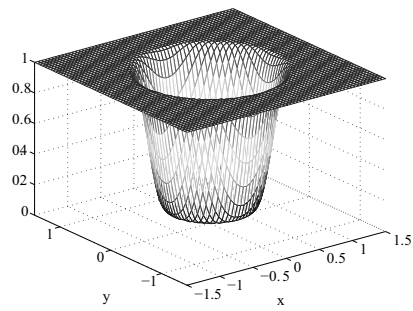


Figure 3:

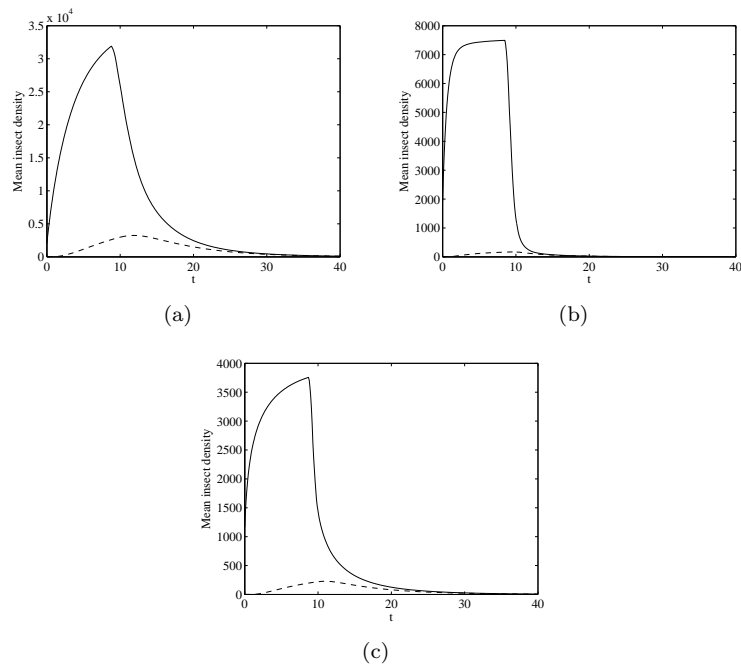


Figure 4:

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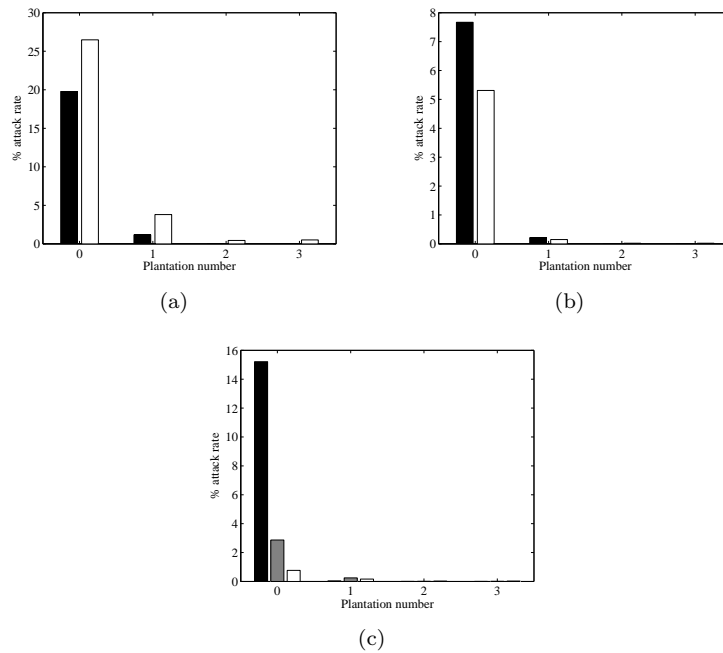


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