

## Control of invasive hosts by generalist parasitoids

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This article was motivated by the invasion of leaf-mining microlepidopteron attacking horse chestnut trees in Europe and the need for a biological control. Following [Owen & Lewis \(2001, \*Bull. Math. Biol.\*, \*\*63\*\*, 655–684\)](#), we consider predation of leafminers by a generalist parasitoid with a Holling Type II functional response. We first identified six equilibrium points and discussed their stabilities in the non-spatial model. The model always predicts persistence of the parasitoid. Depending on the parameter values, the model may predict that the host persists and goes extinct or there is something like an Allee effect where the outcome depends on the initial host density. Special cases were also studied for small carrying capacities leading to complex dynamical behaviours. Then, numerical simulations of the spatial reaction–diffusion model enabled us to identify the conditions for which the leafminer’s advance can be stopped and reversed by parasitoids. Compared to the ordinary differential equation model, the incorporation of space, combined with the polyphagy of the parasitoid, leads to a decrease of the parameter domain of coexistence. This is in stark to several other models in which space promotes coexistence by enabling hosts to escape.

*Keywords:* ODE; PDE; invasion process; biological control; host–parasitoid system; generalist parasitoid; apparent competition.

### 1. Introduction

Propagation of invasive species has been studied both experimentally and theoretically for many years, starting with [Fisher \(1937\)](#) and [Skellam \(1951\)](#). Following [Fisher \(1937\)](#), many partial differential equation (PDE) models have been proposed to describe biological invasions. More recently, studies have focused on the estimation of the spatial spread ([Hastings, 2000](#)) and the parameters that determine it ([Snyder, 2003](#)). It is possible, on the basis of these works, to identify which parameters humans should concentrate on to stop invasions and even sometimes to reverse them. This can happen through the introduction of competitors, as shown, e.g. by [Okubo \*et al.\* \(1989\)](#), or predators.

Predators are able to stop or reverse invasions, as shown first by [Owen & Lewis \(2001\)](#). A slowdown of invasion can be obtained if the functional response is linear (Type I) and if the preys show a weak

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Allee effect in their growth. A strong Allee effect leads to either a full stop or even a reversal of the invasion process. Later results obtained by Fagan *et al.* (2002) confirm the importance of Type I functional response and the Allee effect in stopping or reversing the process for specialist predators. Generalist predators on logistically growing prey can slow down the invasion if they show a weak preference for the focal prey. A possible lack of control may be expected from a generalist already present in the ecosystem and preferring the alternative prey (Ehler, 1998; Madsen *et al.*, 2004; Koss & Snyder, 2005; van Baalen *et al.*, 2001). If the generalist has a strong preference for the focal prey, then the invasion process may be reversed and the prey finally eradicated. Thus, the control potential of a generalist predator depends on its preferences, as well as spatial and temporal scales at which the process is studied (Walde, 1994).

Our study is motivated by the invasion problem of lepidopteron, *Cameraria orchidella* (Lep. Gracilariidae). This moth started to invade the east of Europe in 1985 and invaded France in 1998. It attacks horse chestnut trees by mining their leaves. Infested chestnut trees turn completely yellow early summer and lose almost all leaves. The leafminer is attacked by several parasitoids; the most common one is *Minotetrastichus frontalis* (Hym. Eulophidae). We shall study the leafminer problem by using a reaction–diffusion host–parasitoid model. Using several countries to develop an *a priori* model of invasion in a newly invaded country, Gilbert *et al.* (2005) demonstrated that the best model in qualitative and quantitative terms was a stratified dispersal model taking into account human population density. It influences the probability of long-distance dispersal events (dispersal through cars, trucks, train and maybe planes). They conclude that little can be done to prevent or even slow down the spread. Their work was, however, not conducted in a multitrophic context.

Recent research on hosts and parasitoids (Godfray, 1994; Hawkins, 1994; Hassell, 2000) has contributed to advances in both the spatial ecology of predator–prey systems and the management of the biological control of invasions (Davis *et al.*, 2001; Hastings *et al.*, 2005; Hilker *et al.*, 2005; Kean & Barlow, 2001; King & Hastings, 2003; Huang *et al.*, 2003; Knops *et al.*, 1999; Korniss & Caraco, 2005; Lang, 2003; Lounibos *et al.*, 1997; Marsula & Wissel, 1994). There has been a considerable amount of research on spatial effects in host–parasitoid models. Much of it has been focused on the effects of parasitoid aggregation at relatively small spatial scales on the persistence and stability of host–parasitoid systems (see Briggs & Hoopes, 2004). One reason that there has been such concentration on the issue of stability is that the Nicholson–Bailey model for host–parasitoid interactions in discrete time is highly unstable, and researchers have been interested in the extent to which spatial effects can stabilize it. The Nicholson–Bailey model and its variants (Hassell, 2000) are discrete-time models for systems with non-overlapping generations and tight coupling between host and parasitoid densities. Host–parasitoid systems with overlapping generations or generalist parasitoids have also been modelled with Lotka–Volterra or MacArthur–Rosenzweig models (Hassell, 2000; Cronin & Reeve, 2005).

There has been some work on other aspects of the spatial ecology of host–parasitoid systems at small to medium scales, specifically the effects of spatial structure and heterogeneity on persistence in patchy landscapes (Cronin & Reeve, 2005) and the formation of spatial patterns (Hassell & Wilson, 1997; Maron & Harrison, 1997). The theoretical framework for these lines of research has typically used discrete spatial structures such as lattice models (Hassell & Wilson, 1997) or metapopulation models (Cronin & Reeve, 2005). However, the predictions on pattern formation in the lattice models of Hassell & Wilson (1997) are similar to what is seen in reaction–diffusion models (Murray, 1989), and Maron & Harrison (1997) specifically suggest that reaction–diffusion models could be a way to address questions of how patchy distributions of hosts and parasitoids might arise in continuous habitats. The problem we want to consider is the effect of a generalist parasitoid on the rate of spread of an invading host on a relatively large spatial scale. Since the parasitoid is a generalist, we cannot expect

tight coupling between either generations or densities of hosts and parasitoids. Since the spatial scale is relatively large, it is reasonable to approximate dispersal on a spatial lattice as in Hassell & Wilson (1997) with diffusion in continuous space. In fact, this approximation can be formalized, sometimes rigorously, via hydrodynamic limits or other forms of moment closure (see Cantrell & Cosner, 2004). Reaction–diffusion models are well suited to the study of invasion speeds (Okubo *et al.*, 1989; Andow *et al.*, 1990; Owen & Lewis, 2001). Even though they typically view space as homogeneous, which generally is not, they have been used successfully to predict invasion rates in actual systems (Skellam, 1951; Okubo *et al.*, 1989; Andow *et al.*, 1990). For these reasons, we have used a pair of reaction–diffusion equations to model our system. We believe that this approach could be used to gain insight into the general question of how the presence of generalist parasitoids or predators might influence biological invasions.

The PDEs for the host–parasitoid model we develop here are based on the ones proposed by Owen & Lewis (2001) and Fagan *et al.* (2002). Leafminers follow a logistic growth. They disperse through the homogeneous domain. The parasitoids are generalists already present in the domain of invasion, surviving on other leafminers. That is why parasitoids also follow a logistic growth without leafminers of horse chestnut trees. Like leafminers, parasitoids disperse homogeneously through the domain, and their diffusion rate is equal to that of the host. Our aim is to analyse this host–parasitoid system and give conditions under which leafminers can be controlled by parasitoids. We first concentrate on the non-spatial ordinary differential equations (ODEs) as this enables us to pinpoint the different dynamical aspects of the system through an analytical approach (Kooi & Kooijman, 2000; Ruan & Xiao, 2001; Zhu *et al.*, 2002). We also study special cases for small carrying capacities leading to particular dynamics. We then turn to study the spatial dynamics by numerically solving the PDE model (Kozlova *et al.*, 2002). The incorporation of space does change the dynamics of this system by increasing the range of conditions enabling host control by parasitoids.

## 2. Biological system

There are three generations of *Cameraria ohridella* per year from May to October (Tomiczek & Krehan, 1998) and the spatial spread was estimated to be around 60 km/year (Sefrova & Lastuvka, 2001). There are two ways of dispersion, a short- and a long-distance dispersion. For the short distance, *C. ohridella* can fly and cover a few hundred kilometres per generation (Gilbert *et al.*, 2003). Furthermore, it can be diffused passively by road or rail traffic or by wind, leading to a long-distance dispersion (Heitland *et al.*, 1999). *Cameraria ohridella* was observed for the first time in Macedonia in 1984 (Simova-Tošić & Filev, 1985; Deschka & Dimic, 1986). This pest was then observed in Bulgaria in 1988 (Pelov *et al.*, 1993), Romania in 1993 (Szaboky, 1997), Greece in 2001, Germany in 1993, (Butin & Fuhrer, 1994) and Italy in 1994 (Butin & Fuhrer, 1994). Since 1998, it was observed in Switzerland (Kenis & Forster, 1998), Belgium (De Prins & Puplesiene, 2000) and the Netherlands (Stigter *et al.*, 2000). The pest was observed for the first time in France in 2000 (Augustin & Reynaud, 2000).

The main host species of the leafminer is the horse chestnut tree, *Aesculus hippocastaneum* (Hippocastanaceae). Damages caused by *C. ohridella* on horse chestnut trees are mainly aesthetic. At low densities, leafminers cause a discolouration of leaves which become yellow or brown. At high densities, leaves fall in July (Guichard & Augustin, 2002). The exact effects on trees on the long run are unknown (Thalmann *et al.*, 2003). A solution in case of tree dying would be to replace the horse chestnut trees. However, a study showed that the hypothetical replacement of trees would cost 300 million euros for Berlin only (Balder & Jäckel, 2003). Thus, a method of control is needed.

There exist some insecticides to eradicate leafminers (Mertlik, 1999; Lohrer *et al.*, 2000), but we do not know the consequences for the environment and they are expensive. An ecological method is to remove leaves in which pupae overwinter (Deschka, 1993; Gilbert *et al.*, 2003; Kehrli & Bacher, 2003), a method which can be applied only locally. Even so, populations are able to rebuild rapidly even after a significant control (Gilbert *et al.*, 2003) and it takes only 2 or 3 years for this leafminer to reach its carrying capacity (Gilbert *et al.*, 2004).

A method of control was proposed by Bacher and colleagues (Kehrli *et al.*, 2005). This method is to increase the reservoir of parasitoids. The parasitism rate could be increased only to 17%, which is insufficient to control leafminers (Kehrli *et al.*, 2005). Parasitic wasps, pathogens and predators are the natural enemies (Heitland *et al.*, 1999; Backhaus *et al.*, 2002). Predation by birds is significant but not high enough to control the leafminers (Grabenweger *et al.*, 2005). Twenty different parasitoid species are known to develop on *C. ohridella* (Grabenweger, 2003). None of them are able to control the propagation of the leafminer, as the parasitism rate is generally very low, less than 5% (Heitland *et al.*, 1999; Freise *et al.*, 2002). Nevertheless, the method used by Bacher and colleagues and the lack of real alternative force us to carry on studying the potential use of parasitoids and identify the conditions under which they could be more effective.

### 3. Mathematical model

Let  $u(x, t)$  and  $v(x, t)$  denote the densities of leafminers (hosts) and parasitoids, respectively, at location  $x \in \mathfrak{R}$  and time  $t \geq 0$ . The model consists of two reaction–diffusion equations:

$$\begin{cases} u_t = Du_{xx} + r_1uf(u) - vp(u), \\ v_t = Dv_{xx} + \gamma vp(u) + r_2vg(v), \end{cases} \quad (3.1)$$

with  $f(u) = 1 - (u/K_1)$ ,  $p(u) = Eu/(1 + Ehu)$  and  $g(v) = 1 - v/K_2$ , where

- $D$  = diffusion rate,
- $r_1$  = growth rate of leafminers,
- $r_2$  = growth rate of parasitoids,
- $K_1$  = carrying capacity of leafminers,
- $K_2$  = carrying capacity of parasitoids in absence of focal hosts,
- $E$  = encounter rate,
- $h$  = harvesting time,
- $\gamma$  = conversion efficiency.

$D, r_1, r_2, K_1, K_2, E, h$  and  $\gamma$  are constant parameters.

The general structure of the model is typical of predator–prey models with diffusive dispersal. However, it has some special features because of the nature of the system we want it to describe. In the specific system that motivates the model, the parasitoid is a generalist that is already established in a region where the leafminers have been introduced and may spread. Because the parasitoid can persist at a positive density in the absence of the leafminers, its population dynamics in the absence of the leafminers are described by a logistic equation with a positive growth rate. This is different from standard predator–prey models, which usually envision the predator as a specialist that is strictly dependent on the prey species in the model and whose density is limited only by the availability of the prey species. The ultimate goal of the modelling process is to understand when the leafminers can or cannot invade a region where the generalist parasitoids are present, so we envision dispersal on a fairly large spatial

scale. At such a scale, diffusion gives a reasonable description of dispersal and provides a modelling framework that is well suited to the analysis of the speed of an invasion. We are interested in the rate of spread of the leafminers across a landscape as opposed to the effects of aggregation at small spatial scales on the host–parasitoid interaction (we plan to examine the issue of invasion speed in more detail in future work).

In our specific system, the leafminers and the parasitoids that attack them disperse at roughly the same rates, so it is reasonable to take the diffusion rates to be the same for the two species. The model is set in continuous time at the temporal scale of the establishment and spread of an invading population. Because we want to focus on the dynamics of the host–parasitoid system and how they interact with dispersal, we have used a relatively simple model where such an analysis is feasible. Because the model is formulated in continuous time, we do not consider distinct generations, so we cannot make a tight linkage between the number of hosts parasitized in one generation and the number of parasitoids present in the next, as is sometimes done in discrete-time models. Because of the scale at which the model is formulated, it is not essential for our purposes to include age structure, even though the organisms have life histories that involve distinct stages. Also, although we are motivated by a specific system, it is worth noting that there has been little work on the general question of what happens when a species is introduced to a region where there is already a generalist predator (or suite of predators). Thus, to understand our system, it is desirable to cast it in a fairly general form so that we can see how the behaviour of our system fits into the larger picture of the possible dynamics of systems with generalist predators. We will see that for some parameter ranges, such systems can have multiple equilibria or induce an Allee effect on the leafminers, among other things.

#### 4. The non-spatial model

We first study the associated ODE system:

$$\begin{cases} u_t = u (r_1 f(u) - \frac{v}{u} p(u)), \\ v_t = v (\gamma p(u) + r_2 g(v)). \end{cases} \quad (4.1)$$

##### 4.1 General analysis

We point out that there are at most six equilibria:  $(0, 0)$ ,  $(K_1, 0)$ ,  $(0, K_2)$ ,  $(u_1, v_1)$ ,  $(u_2, v_2)$  and  $(u_3, v_3)$ . Notice that the trivial equilibrium  $(0,0)$  and the semi-trivial equilibria  $(K_1, 0)$  and  $(0, K_2)$  always exist. For the three possible positive equilibrium points, the  $u$  component is the root of a third-degree equation:

$$u^3 + \left( \frac{2}{Eh} - K_1 \right) u^2 + \left[ \frac{K_1 K_2}{r_1 r_2 h^2} (\gamma + r_2 h) - 2 \frac{K_1}{Eh} + \frac{1}{E^2 h^2} \right] u + \frac{K_1}{E^2 h^2} \left( \frac{K_2 E}{r_1} - 1 \right) = 0$$

and the  $v$  component is given by the following equation:

$$v = \frac{r_1}{E} \left( 1 - \frac{u}{K_1} \right) (1 + Ehu).$$

Let

$$a = \frac{1}{3} \left( \frac{2}{Eh} - K_1 \right), \quad b = \frac{1}{3} \left[ \frac{K_1 K_2}{r_1 r_2 h^2} (\gamma + r_2 h) - 2 \frac{K_1}{Eh} + \frac{1}{E^2 h^2} \right] \quad \text{and} \quad c = \frac{K_1}{E^2 h^2} \left( \frac{K_2 E}{r_1} - 1 \right),$$

and denote

$$\alpha = a^2 - b \quad \text{and} \quad \beta = 2a^3 - 3ab + c.$$

The existence conditions of the positive equilibria are deduced by the conditions given by Murray (1989):

- If  $\alpha > 0$  and either  $\beta = 0$  or  $|\beta| \leq 2\alpha^{\frac{2}{3}}$ , we have zero, one, two or three non-trivial equilibria. This is a necessary but not sufficient condition to have three non-trivial equilibria.
- If  $\alpha > 0$  and  $|\beta| > 2\alpha^{\frac{2}{3}}$  or  $\alpha \leq 0$ , we have at most one non-trivial equilibrium.

We analyse the system in the phase plane by first calculating the nullcline equations and second studying the existence and the stability of equilibria.

Nullcline equations are for prey, ( $u' = 0$ )  $v = \frac{r_1}{EK_1}(K_1 - u)(1 + Ehu)$ , and predators, ( $v' = 0$ )  $v = K_2\left(1 + \frac{\gamma}{r_2} \frac{Eu}{1 + Ehu}\right)$ , which are shown in Fig. 1.

Intersections of nullclines give the different equilibria. We have three cases:

- (i) If  $K_2 > \frac{r_1}{E}$  and either  $\frac{r_1 h}{4K_1} \left(K_1 + \frac{1}{Eh}\right)^2 \leq K_2 \left(1 + \frac{\gamma}{hr_2} \frac{K_1 - \frac{1}{Eh}}{K_1 + \frac{1}{Eh}}\right)$  and  $K_1 > \frac{1}{Eh}$  or  $K_1 < \frac{1}{Eh}$ , there is no non-trivial equilibrium and the semi-trivial equilibrium  $(0, K_2)$  is stable (Fig. 2).

In Case (i), the leafminers always disappear; parasitoids control them. This condition includes the fact that if the parasitoid density is high enough and the host density is small enough, there is no establishment of leafminers.

- (ii) If  $K_2 > \frac{r_1}{E}$ ,  $\frac{r_1 h}{4K_1} \left(K_1 + \frac{1}{Eh}\right)^2 > K_2 \left(1 + \frac{\gamma}{hr_2} \frac{K_1 - \frac{1}{Eh}}{K_1 + \frac{1}{Eh}}\right)$  and  $K_1 > \frac{1}{Eh}$ , there are two non-trivial equilibria; one of them is a saddle point. The semi-trivial equilibrium  $(0, K_2)$  and the larger non-trivial equilibrium  $(u_2, v_2)$  are both locally stable and the outcome will depend on the initial conditions (Fig. 3).

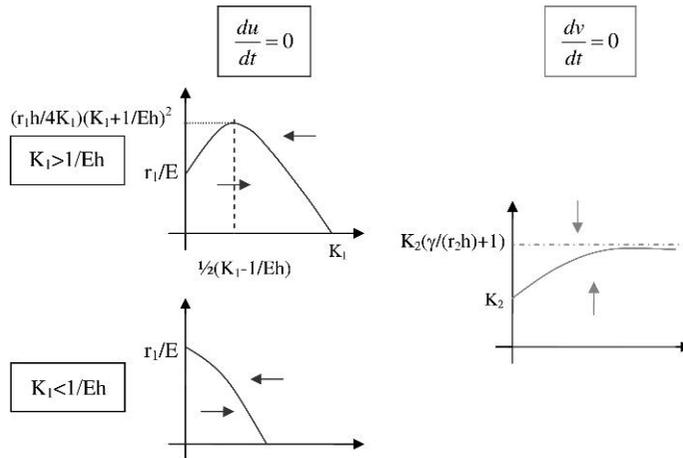


FIG. 1. Nullclines for leafminers (black) and parasitoids (grey).

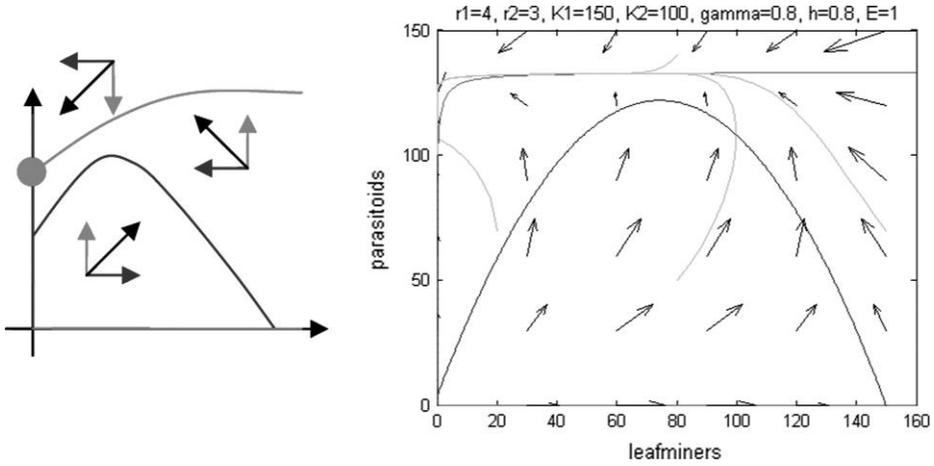


FIG. 2. Phase plane and the direction field for Case (i).

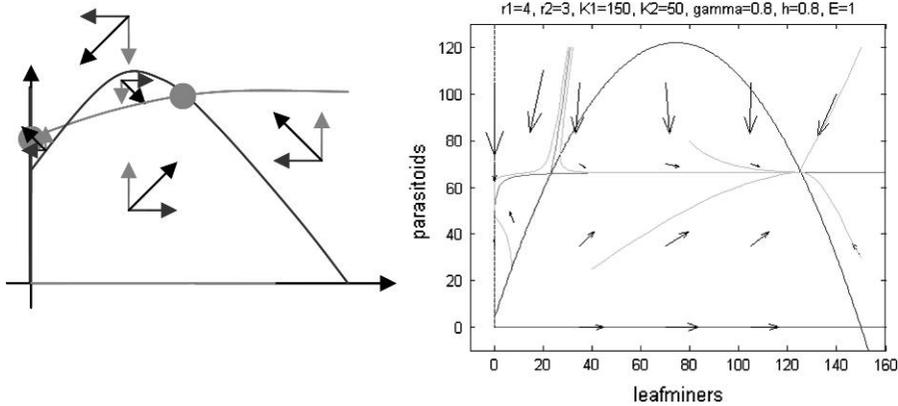


FIG. 3. Phase plane and the direction field for Case (ii).

In Case (ii), leafminers could survive. It depends on the initial conditions. If the initial leafminer density is high enough, they establish, but if that is not the case, they vanish. In this case, parasitoids induce an Allee effect.

REMARK If  $K_2 > \frac{r_1}{E}, \frac{r_1 h}{4K_1} (K_1 + \frac{1}{Eh})^2 = K_2 \left( 1 + \frac{\gamma}{hr_2} \frac{K_1 - \frac{1}{Eh}}{K_1 + \frac{1}{Eh}} \right)$  and  $K_1 > \frac{1}{Eh}$ , there is a unique non-trivial equilibrium which is a saddle-node (Fig. 4). In this case, the semi-trivial equilibrium  $(0, K_2)$  is stable.

This case is derived from the previous one when the saddle point and the stable non-trivial equilibrium join in one point to give a saddle-node. But, due to the very restrictive conditions, this case is for a particular set of parameters and occurs rarely. In this case, leafminers disappear.

(iii) If  $K_2 < \frac{r_1}{E}$ , we have one non-trivial equilibrium (Fig. 5a) or three non-trivial equilibria (Fig. 5b).

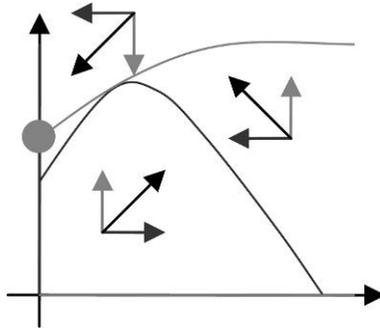


FIG. 4. Phase plane when there is a degenerate saddle-node.

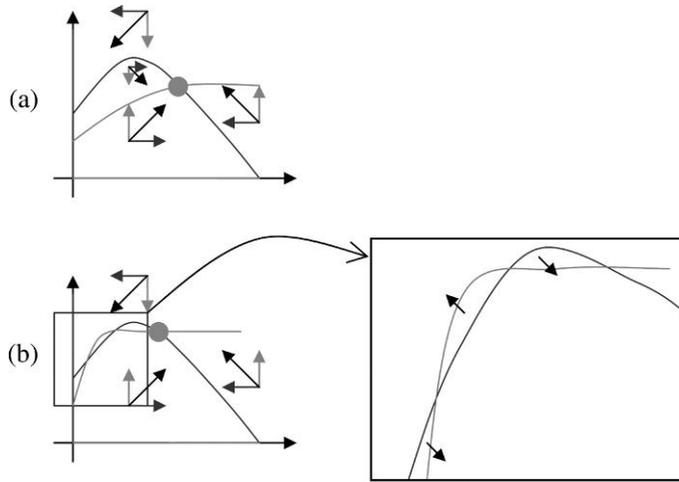


FIG. 5. Phase planes when (a) there is one non-trivial equilibrium and (b) there are three non-trivial equilibria.

In these two cases, there is a non-trivial equilibrium which is a stable point, so it corresponds to the establishment of leafminers. It could be explained by the fact that the condition implies a small parasitoid density, so parasitoids could not control leafminers.

To complement the graphical analysis, we study the Jacobian matrix of the ODE system.

For the trivial and semi-trivial equilibria, the Jacobian matrix is

$$\mathbf{J}(u, v) = \begin{pmatrix} r_1 - 2\frac{r_1}{K_1}u - \frac{Ev}{(1+Ehu)^2} & -\frac{Eu}{1+Ehu} \\ \gamma \frac{Ev}{(1+Ehu)^2} & \gamma \frac{Eu}{1+Ehu} + r_2 - 2\frac{r_2}{K_2}v \end{pmatrix}.$$

At the trivial equilibrium  $(0,0)$ , we have

$$\mathbf{J}(0, 0) = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 \end{pmatrix}.$$

So  $(0,0)$  is an unstable node. At the semi-trivial equilibrium  $(K_1, 0)$ , we have

$$\mathbf{J}(K_1, 0) = \begin{pmatrix} -r_1 & -\frac{EK_1}{1+Ek_1} \\ 0 & \gamma \frac{EK_1}{1+Ek_1} + r_2 \end{pmatrix}.$$

We can see that  $(K_1, 0)$  is a saddle point because there are two real roots, one is negative and the other one is positive. Similarly, at the semi-trivial equilibrium  $(0, K_2)$ , we have

$$\mathbf{J}(0, K_2) = \begin{pmatrix} r_1 - EK_2 & 0 \\ \gamma EK_2 & -r_2 \end{pmatrix}.$$

Thus,  $(0, K_2)$  is a stable node if  $r_1 - EK_2 > 0$ , i.e. if  $K_2 > r_1/E$ ; otherwise,  $(0, K_2)$  is a saddle point.

For the non-trivial equilibria  $(u^*, v^*)$ , the Jacobian matrix could be rewritten as:

$$\mathbf{J}(u^*, v^*) = \begin{pmatrix} u^* \left( -\frac{r_1}{K_1} + \frac{E^2hv^*}{(1+Ehu^*)^2} \right) & -\frac{Eu^*}{1+Ehu^*} \\ \gamma \frac{Ev^*}{(1+Ehu^*)^2} & -\frac{r_2}{K_2}v^* \end{pmatrix}.$$

One has

$$\text{Tr}\mathbf{J} = -\frac{r_1}{K_1}u^* - \frac{r_2}{K_2}v^* + \frac{E^2hu^*v^*}{(1+Ehu^*)^2},$$

$$\det \mathbf{J} = -\frac{r_2}{K_2} \left( -\frac{r_1}{K_1} + \frac{E^2hv^*}{(1+Ehu^*)^2} \right) u^*v^* + \gamma \frac{E^2u^*v^*}{(1+Ehu^*)^3}.$$

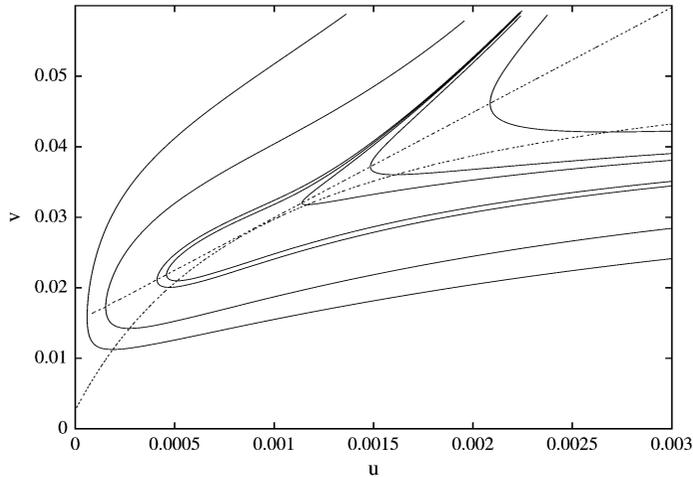


FIG. 6. Phase plane when  $r_1 = 3$ ,  $K_1 = 1$ ,  $E = 200.2$ ,  $h = 5$ ,  $r_2 = 0.1$ ,  $K_2 = 0.0027$  and  $\gamma = 10$ , there is a cusp, which is a unique degenerate positive equilibrium.

The stability of  $(u^*, v^*)$  depends on the sign of the trace and the determinant of the Jacobian matrix:

- (a) If  $\text{Tr}\mathbf{J} < 0$  and  $\det\mathbf{J} > 0$ , then  $(u^*, v^*)$  is a stable node or a stable spiral.
- (b) If  $\text{Tr}\mathbf{J} > 0$  and  $\det\mathbf{J} > 0$ , then  $(u^*, v^*)$  is an unstable node or an unstable spiral.
- (c) If  $\det\mathbf{J} < 0$ , then  $(u^*, v^*)$  is a saddle point.
- (d) If  $\text{Tr}\mathbf{J} = 0$ , then there are some limit cycles.

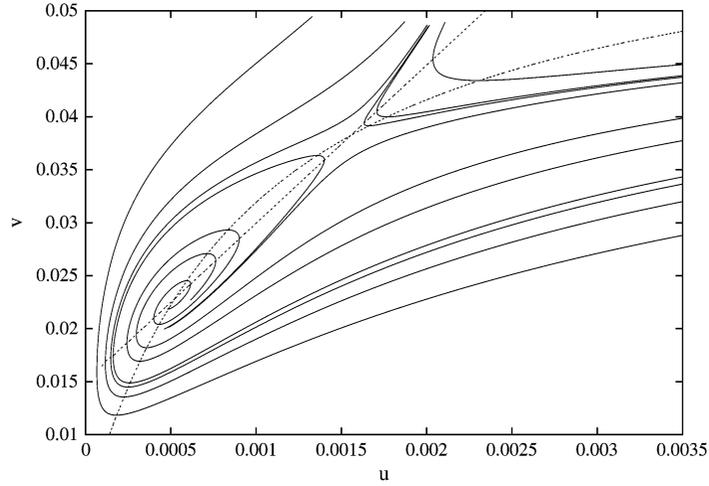


FIG. 7. Phase plane when  $r_1 = 3$ ,  $K_1 = 1$ ,  $E = 200.2$ ,  $h = 5$ ,  $r_2 = 0.1$ ,  $K_2 = 0.0029$  and  $\gamma = 10$ , there are two equilibria, an unstable focus and a saddle. From the phase portrait, we can see that there exist only two initial population densities such that the host and parasitoids coexist.

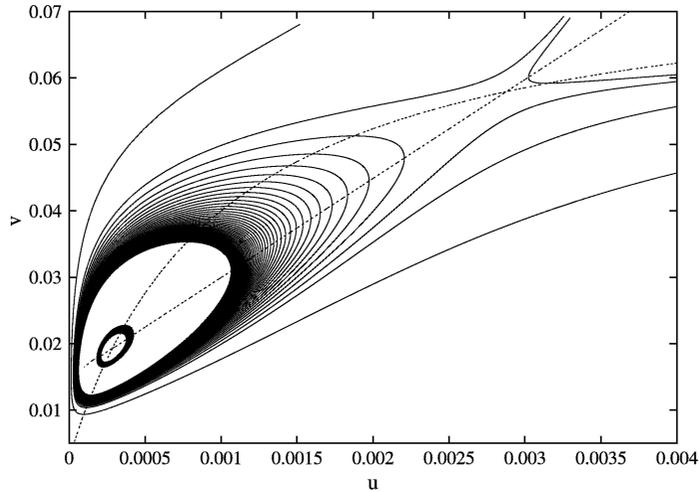


FIG. 8. Phase plane when  $r_1 = 3$ ,  $K_1 = 1$ ,  $E = 200.2$ ,  $h = 5$ ,  $r_2 = 0.1$ ,  $K_2 = 0.0029$  and  $\gamma = 12.7775$ , the unstable focus becomes stable and a Hopf bifurcation occurs, which gives an unstable limit cycle. Thus, there exists an open set of initial population densities such that both the host and the parasitoids populations tend to fluctuate.

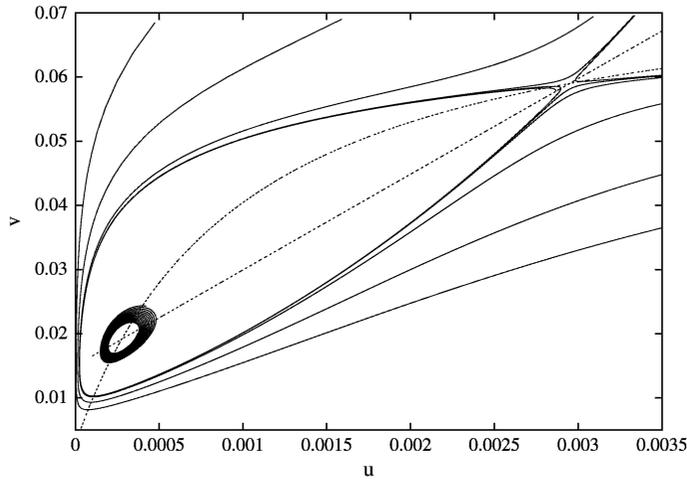


FIG. 9. Phase plane when  $r_1 = 3$ ,  $K_1 = 1$ ,  $E = 200.2$ ,  $h = 5$ ,  $r_2 = 0.1$ ,  $K_2 = 0.0029$  and  $\gamma = 12.9425$ , there is a homoclinic loop.

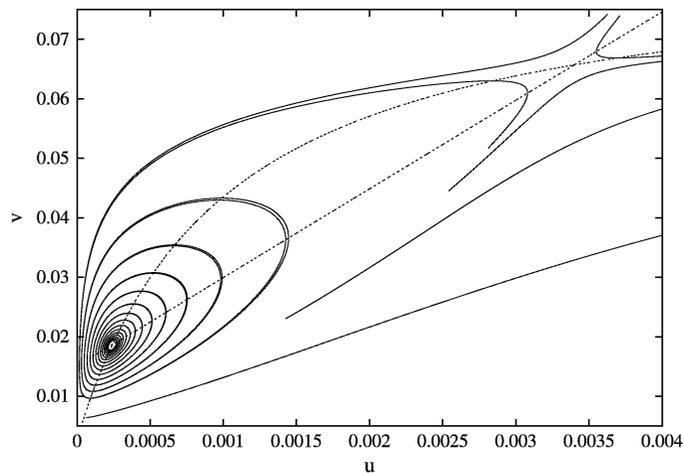


FIG. 10. Phase plane when  $r_1 = 3$ ,  $K_1 = 1$ ,  $E = 200.2$ ,  $h = 5$ ,  $r_2 = 0.1$ ,  $K_2 = 0.0029$  and  $\gamma = 14$ , there are two equilibria, a stable focus and a saddle. There exists an open set of initial population densities such that both host and parasitoids approach to steady-state values.

#### 4.2 Analysis for small carrying capacities

When there are three non-trivial equilibria, the dynamics of the model can be very complex and various types of bifurcations, including codimension-3 bifurcations, can occur (see, e.g. [Zhu et al., 2002](#)). In the following, by computer simulations we consider the dynamics and bifurcations at the two small non-trivial equilibria (which are very close to each other; see Figs. 6–10). By symmetry, similarly one can study the dynamics and bifurcations at the two large non-trivial equilibria (which are very far away from each other).

TABLE 1 *Control conditions*

$K_2 < r_1/E$	$K_2 > r_1/E$		
	$K_1 < 1/(Eh)$	$K_1 < 1/(Eh)$	
NO CONTROL	CONTROL	CONTROL	$A \leq B$
	CONTROL	POSSIBLE CONTROL	$A > B$

NO CONTROL: leafminers cannot be eradicated by parasitoids, and they settle; CONTROL: leafminers are eradicated, parasitoids go to their carrying capacity; POSSIBLE CONTROL: parasitoids could control leafminers if initial leafminers' density is small enough.

To do this, we fix some parameters as follows:  $r_1 = 3$ ,  $K_1 = 1$ ,  $E = 200.2$ ,  $h = 5$  and  $r_2 = 0.1$ . The analysis is run as function of  $K_2$  and  $\gamma$ . We set  $K_2$  to be small (Case iii) so that there is one or three non-trivial equilibria. When  $K_2 = 0.0027$  and  $\gamma = 10$ , there is a unique degenerate positive equilibrium which is a cusp (Fig. 6). The model is very sensitive to minute changes in this region. When  $K_2$  increases to 0.0029, the degenerate cusp bifurcates into two positive equilibria. One is an unstable focus and the other is a saddle (Fig. 7). When fixing  $K_2$  and increasing  $\gamma$  to 12.7775, the unstable focus becomes stable and a Hopf bifurcation occurs, which yields an unstable limit cycle surrounding the stable focus (Fig. 8). Increasing  $\gamma$  further to 12.9425, the limit cycle expands and reaches the stable and unstable manifolds of the saddle, forming a homoclinic loop (Fig. 9). When  $\gamma$  is further increased to 14, the focus regains its stability and the stable and unstable manifolds of the saddle interchange their positions (Fig. 10). One can also interpret these bifurcations backward by decreasing  $\gamma$ , the conversion efficiency parameter, and  $K_2$ , the carrying capacity of parasitoids. Similar and symmetric bifurcations occur at the two larger equilibrium points when another parameter varies. These indicate that the continuous host–parasitoid model (1) exhibits codimension-3 bifurcations.

### 4.3 Controlling leafminers

Now, we are interested in the case when the semi-trivial equilibrium  $(0, K_2)$  is stable, because it corresponds to the situation where leafminers are eradicated by parasitoids. Define

$$A = \frac{r_1 h}{4K_1} \left( K_1 + \frac{1}{Eh} \right)^2 \quad \text{and} \quad B = K_2 \left( 1 + \frac{\gamma}{hr_2} \frac{K_1 - \frac{1}{Eh}}{K_1 + \frac{1}{Eh}} \right).$$

We can express control conditions as a function of biological parameters (Table 1).

The cases that there is a control are the most desirable, but the case where control is possible is also interesting because if we can find a method to reduce the leafminer density, then the parasitoids could overtake them (Fig. 3).

Table 1 can also be represented on a graph which shows the different cases in terms of  $K_1$  and  $K_2$  (Fig. 11).

## 5. The spatial model

We explore now the dynamics of the model incorporating space. We use a 1D model. We suppose that parasitoids are present uniformly in the domain and leafminers arrive by one side. We take Neumann

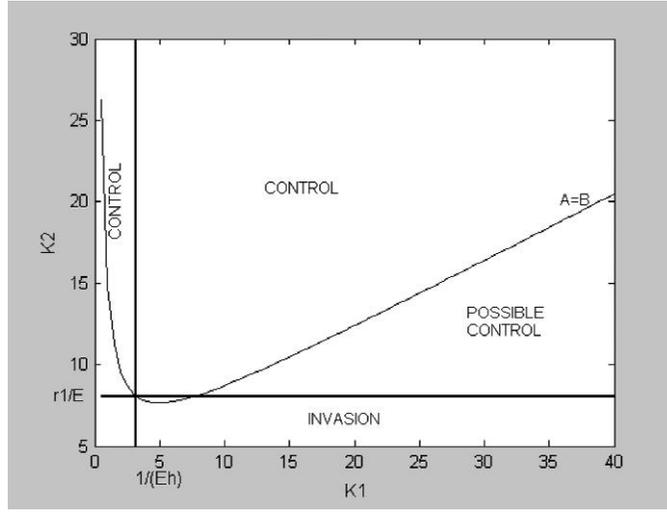


FIG. 11. Control zones of leafminers by parasitoids in terms of  $K_1$  (carrying capacity of leafminers) and  $K_2$  (carrying capacity of parasitoids). Parameters values are  $r_1 = 4$ ,  $r_2 = 3$ ,  $\gamma = 0.8$ ,  $h = 0.6$  and  $E = 0.5$ .

boundary conditions to represent a closed domain. The model with space is the following:

$$\begin{cases} u_t = Du_{xx} + r_1 u f(u) - v p(u) \\ v_t = Dv_{xx} + \gamma v p(u) + r_2 v g(v) \end{cases} \quad (5.1)$$

with

$$\frac{\partial u}{\partial x}(0, t) = \frac{\partial u}{\partial x}(40, t) = \frac{\partial v}{\partial x}(0, t) = \frac{\partial v}{\partial x}(40, t) = 0$$

and  $u(x, 0) = \varphi(x) \in L^1$  and  $v(x, 0) = \phi(x) \in L^1$ , with  $0 \leq \varphi(x) \leq C_1$  and  $0 \leq \phi(x) \leq C_2$  for  $x \in (0, 40)$ .  $\varphi(x)$  and  $\phi(x)$  are bounded functions.

The dynamics of the model are studied with numerical simulations. If there is no parasitoid, there is a travelling wave connecting the steady states  $u = 0$  and  $u = 1$  (the carrying capacity), which gives a transition zone from no leafminer to the saturation of leafminers. Thus, leafminers invade the domain with a constant speed which depends on the diffusion rate  $D$  (Fig. 12).

With parasitoids, we have chosen the same cases as in Section 4.1. With a small diffusion rate, we have observed the same possibilities: leafminers can settle (Fig. 13a), leafminers can be eradicated (Fig. 13b) or the issue depends on initial conditions. In Fig. 13(a), we can observe that the leafminers' density increases and that leafminers propagate to the right of the domain. At the same time, parasitoids' density decreases because the density of leafminers is too low. In Fig. 13(b), the initial density of leafminers is higher than in the previous case. Leafminers' density decreases and the leafminers are eliminated by the parasitoids. At the same time, parasitoids' density first increases but returns to the carrying capacity when all leafminers have disappeared.

Finally, we analyse the effect of the diffusion rate on the propagation speed of leafminers. When the diffusion rate increases, the propagation speed of leafminers increases too (Fig. 14). But when the rate

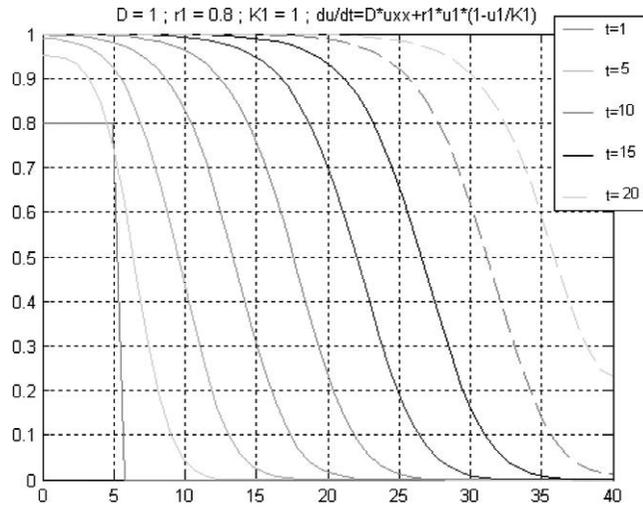


FIG. 12. Spatial propagation of leafminers without parasitoids.

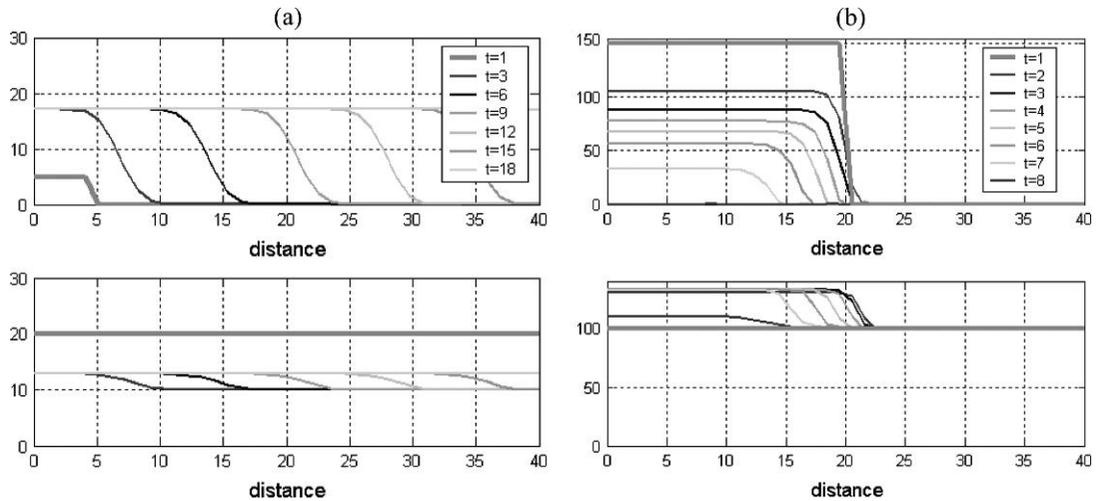


FIG. 13. Spatial propagation of leafminers (above) and parasitoids (below). Parameters of the simulations are (a)  $D = 1, r_1 = 6, r_2 = 3, K_1 = 20, K_2 = 10, E = 0.5, h = 0.8$  and  $\gamma = 0.8$  and (b)  $D = 1, r_1 = 4, r_2 = 3, K_1 = 150, K_2 = 100, E = 1, h = 0.8$  and  $\gamma = 0.8$ .

is too high, leafminers are eradicated (Fig. 14). This is because diffusion dilutes leafminers and then parasitoids take them over.

The curve in Fig. 14 corresponds to Case (ii) of Section 4.1. where the issue of the predation depends on the initial condition. In this case, predation induces an Allee effect. Indeed, if the initial leafminer density is not large enough, leafminers disappear.

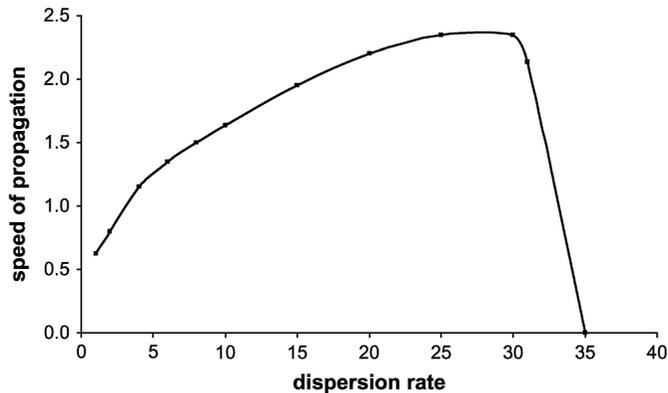


FIG. 14. The effect of the diffusion rate on the propagation speed of leafminers.

## 6. Discussion

The studied system has interesting and complex dynamics including the existence of multiple non-trivial equilibria and various types of bifurcations in the non-spatial model, even though their biological relevance may be minor, in particular at very low carrying capacity. Some similar analyses on predator–prey model were made by [Du & Lou \(2001\)](#) and [Du & Shi \(2006\)](#). We observed saddle-nodes reminiscent of [Greenman & Hudson \(1999, 2000\)](#). The existence of multiple attractors implies that the outcome of the interaction will often be a function of the initial conditions, as observed in [Miller \*et al.\* \(2004\)](#) and [Krivan & Sikder \(2003\)](#). Bifurcations in similar predator–prey systems have earlier been studied by [Hainzl \(1988, 1992\)](#). For some parameter ranges, the model predicts that a generalist parasitoid can induce something like an Allee effect on the leafminers, in the sense that small leafminer populations will go extinct, while larger ones persist. Allee effect and bistability in a spatially heterogeneous predator–prey model have been proved by [Du & Shi \(2007\)](#). For other parameter ranges, the equilibrium with no leafminer is unstable but there is a stable equilibrium where both parasitoids and leafminers are present. The coexistence of two equilibria, one being locally stable and the other locally unstable, is a strong hint towards the existence of travelling waves in the spatial model, which enable the system to switch from one state to the next. This analytical part will be developed in a further paper.

The mathematical analysis enabled us to understand the ‘control conditions’ using only three out of eight parameters: the carrying capacity for parasitoids ( $K_2$ ), the growth rate of the host ( $r_1$ ) and the encounter rate ( $E$ ). Indeed, these three parameters allow us to distinguish two cases: invasion when  $K_2 < r_1/E$  and a possible control when  $K_2 > r_1/E$  (Table 1). A method such as the augmentative method, targeting at increasing the carrying capacity for parasitoids ( $K_2$ ), proposed by Bacher and colleagues may be a good applied solution to the invasion of the leafminer ([Kehrli \*et al.\*, 2005](#)). Indeed, placing containers with leaves out of which only parasitoids can emerge below attacked trees is equivalent to an increase of the parasitoids’ carrying capacity. This idea did not work out in the study of [Kehrli \*et al.\* \(2005\)](#), but these authors did not take into account that the control cannot be immediate, as shown in Fig. 13. Thus, the potential for control of this leafminer using concepts and results from our work needs to be yet assessed, but represents so far the only hope for a biological solution to the problem.

Predator–prey systems have been widely studied, but most often with specialist predators ([Briggs & Hoopes, 2004](#); [Owen & Lewis, 2001](#)). Recent work focusing on generalist predators includes [Fagan \*et al.\* \(2002\)](#), [Ehler \(1998\)](#), [Liebhold \*et al.\* \(2000\)](#), [Schreiber \(1997\)](#), etc., while other authors focused on

generalist parasitoids (Dwyer *et al.*, 2004; Björkman *et al.*, 2000; Venzon *et al.*, 2002; Symondson *et al.*, 2002; Madsen *et al.*, 2004; Koss & Snyder, 2005). In most cases, generalism is studied while focusing on apparent competition, which is absent in our case, and in a non-analytical way because the dynamics of the system are often quite difficult. Nevertheless, there are some papers on apparent competition like Schreiber (2004) who gives some results on permanence and almost sure permanence in such system.

Generalists have two opposite impacts in our system. First, it is their capacity to survive on alternative hosts which enables parasitoids to be present in the ecosystem before the host arrival and to control it under specific conditions. This idea was also explored theoretically in the context of invasions by Krivan & Sikder (2003). It was confirmed experimentally by Namba *et al.* (1999) who observed good control by a predator dwelling at high density with alternate prey. Second, the same characteristic makes generalists inefficient, as they concentrate their attacks on several types of prey. The presence of alternative preferred prey may therefore reduce the control ability of generalists, as shown experimentally by Koss & Snyder (2005). This has been also confirmed theoretically by Krivan (1996) and Krivan & Sikder (1999, 2003), who demonstrate that the persistence of the system is increased with partial preference. Overall, generalist predators are a viable solution, as an overview of field trials by Symondson *et al.* (2002) revealed that they reduce their prey in 75% of the cases. In fact, the dynamical effects of partial preference compared to indifferent generalism are reminiscent of the differences obtained in metapopulation models of prey–predator interactions compared to models with continuous space. In continuous space, predators are everywhere, while metapopulation patterns enable prey to find safe spots. Similarly, generalist predators are everywhere, while specialist predators survive only in high-prey-density regions.

As expected, a moderate speed of invasion precludes any control. However, a control may be possible only if prey disperse quite rapidly. This counter-intuitive result is due to the dilution effect brought by rapid spreading, leading to small population. Generalists, already present on the spot, are able to control these tiny populations. This is an emergent property of our model, similar to an Allee effect. Under given parameter values, parasitoids kill the smallest populations and move on to larger ones, etc., leading to a reversal of the invasion. The incorporation of space reduces therefore the conditions for leafminer survival, in contrast to the first situation we analysed without spatial structure. This runs against the result of several metapopulation models of host–parasitoid populations, models in which coexistence is increased due to the possibility of the host to escape in space (Srinivasu & Gayatri, 2005; Abdul-Aziz, 1997; Newman *et al.*, 2002).

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