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# Bistability induced by generalist natural enemies can reverse pest invasions without the need for an Allee effect in prey dynamics

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**Abstract.** Reaction-diffusion analytical modeling of predator-prey systems has shown that specialist natural enemies can slow, stop and even reverse pest invasions, assuming that the prey population displays a strong Allee effect in its growth. Few additional analytical results have been obtained for other spatially distributed predator-prey systems, as traveling waves of non-monotonous systems are notoriously difficult to obtain. Traveling waves have indeed recently been shown to exist in predator-prey systems, but the direction of the wave, an essential item of information in the context of the control of biological invasions, is generally unknown. Preliminary numerical explorations have hinted that control by generalist predators might be possible for prey populations displaying logistic growth. We aimed to formalize the conditions in which spatial biological control can be achieved by generalists, through an analytical approach based on reaction-diffusion equations.

The population of the focal prey — the invader — is assumed to grow according to a logistic function. The predator has a type II functional response and is present everywhere in the domain, at its carrying capacity, on alternative hosts. Control, defined as the invader becoming extinct in the domain, may result from spatially independent demographic dynamics or from a spatial extinction wave. Using comparison principles, we obtain sufficient conditions for control and for invasion, based on scalar bistable partial differential equations (PDEs). The searching efficiency and functional response plateau of the predator are identified as the main parameters defining the parameter space for prey extinction and invasion. Numerical explorations are carried out in the region of those control parameters space between the super- and sub-solutions, in which no conclusion about controllability can be drawn on the basis of analytical solutions.

The ability of generalist predators to control prey populations with logistic growth lies in the bistable dynamics of the coupled system, rather than in the bistability of prey-only dynamics as observed for specialist predators attacking prey populations displaying Allee effects. The consideration of space in predator-prey systems involving generalist predators with a parabolic functional response is crucial. Analysis of the ordinary differential equations (ODEs) system identifies parameter regions with monostable (extinction) and bistable (extinction or invasion) dynamics. By contrast, analysis of the associated PDE system distinguishes different and additional regions of invasion and extinction. Depending on the relative positions of these different zones, four patterns of spatial dynamics can be identified : traveling waves of extinction and invasion, pulse waves of extinction and heterogeneous stationary positive solutions of the Turing type. As a consequence, prey control is predicted to be possible when space is considered in additional situations other than those identified without considering space. The reverse situation is also possible. None of these considerations apply to spatial predator-prey systems with specialist natural enemies.

# 1 Introduction

## 1.1 Modeling the biological control of invasive pests

Biological invasions are a major contemporary problem ([Pimentel (2011), Garnier et al. (2012), Mistro et al. (2012), Potapov & Rajakaryne (2013), Wang et al. (2013), Savage & Renton (2013)]) for which few solutions are available, all of which are very costly. The use of natural enemies for the biological control of invading insects is one of the most promising possibilities ([Moffat et al. (2013), Li et al. (2014), Ye et al. (2014), Basnet & Mukhopadhyay (2014)]). As invasion is essentially a spatial process, the potential of natural enemies to stop or even reverse an invasion is of particular interest. The fundamental analytical work of [Owen & Lewis (2001)] showed that *specialist* predators could potentially slow, stop or reverse the spread of invasive pests. The reversal of pest spread by specialist predation requires a strong Allee effect for the pest-only dynamics, defined as a negative growth rate for the prey population at low density. In the presence of a weak Allee effect, the predator can stop, but not reverse the wave of invasion. These conclusions have been confirmed in several other studies ([Cai et al. (2014), Boukal et al. (2007), Morozov & Petrovskii (2009)]).

Generalist predators can also control prey effectively ([Erbach et al. (2014), Chakraborty (2015)]). Their use could be promoted through conservation biological control programs without the need for exogenous specialist natural enemies. Unfortunately, the role of generalist predators in the spatial control of their prey has been much less studied than that of specialist predators, due to the intrinsic difficulties of having to work with a *system* of equations rather than with a *single* scalar equation. However, two important studies have been carried out in this area : the analytical and comprehensive study of [Du & Shi (2007)], and the preliminary simulation study of [Fagan et al. (2002)]. Both used the same model structure as we do here, with logistic growth for both prey and predator populations, and a type II functional response for predators. The convergence of these models was strengthened further by the in-depth analysis of [Magal et al. (2008)] in which space was not considered. It is difficult to use these models in a spatial context : the work of [Du & Shi (2007)] cannot deal with invasion and traveling waves, because it deals with a bounded space. The numerical simulations of [Fagan et al. (2002)] are restricted to a few parameter values. They are, however, valuable, because they suggest conditions in which a generalist predator might be able to stop, and even reverse the invasion wave of a pest population displaying logistic growth. Fagan *et al.* also reported the results of field studies indicating that predators with diffusion coefficients higher than those of their prey are poor control organisms. The authors provided an explanation for this finding founded on logical arguments, but without a firm mathematical foundation. This result has been confirmed by a few numerical simulations including space, as reported by [Magal et al. (2008)], revealing a strong dependence of system dynamics on the relative rates of diffusion of the prey and the predator. It is thus important to take space into account, by considering diffusion coefficients of both predator and prey. This conclusion accounts for the interest of scientists in questions of this type ([Lewis et al. (2013), Hastings (2000), De Roos et al. (1991), De Roos et al. (1998)]).

There are therefore hopes that it might be possible to extend the conditions for the control of invasive prey organisms to (i) generalist predators and (ii) prey populations displaying growth patterns not dependent on the restrictive assumption of Allee effects. Such control approaches would have a major impact in the field, given the high degree of generalism obtained. The aim of this study was, therefore, to formalize the conditions in which spatial biological control can be achieved by generalists, through an analytical approach based on traveling waves solutions of reaction-diffusion equations. We find that the conditions for control are very different from those for the system in which space is not considered.

The generalist predator-prey interaction used in the above studies, particularly in that by [Magal et al. (2008)], is as follows :

$$\begin{cases} u_t = r_1 u \left(1 - \frac{u}{K_1}\right) - \frac{Euv}{1+Ehu}, & t \in \mathbb{R}^+ \\ v_t = r_2 v \left(1 - \frac{v}{K_2}\right) + \gamma \frac{Euv}{1+Ehu}. \end{cases} \quad (1)$$

As prey survive in the absence of predators, the density  $u(t)$  of prey may decrease to zero only because of the presence of predators  $v(t)$ . In that case, the predators control the prey.

The analysis provided in [Magal et al. (2008)] gives conditions for this to happen, but this analysis was carried out largely without reference to space. Thus, we have extended system (1) by adding spatial diffusion, obtaining the following reaction-diffusion system

$$\begin{cases} u_t = D_u \Delta_x u + r_1 u \left(1 - \frac{u}{K_1}\right) - \frac{Euv}{1+Ehu}, & x \in \mathbb{R}, t \in \mathbb{R}^+ \\ v_t = D_v \Delta_x v + r_2 v \left(1 - \frac{v}{K_2}\right) + \gamma \frac{Euv}{1+Ehu}. \end{cases} \quad (2)$$

We distinguish two ways in which a predator can control the prey, one taking space into account and the other not considering this factor (mathematical definitions are provided in definition 1.1.1).

- The spatially *uniform extinction* results exclusively from *local* demographic processes and is independent of space.
- The *extinction wave* is due to both demographic and diffusive processes and may take various forms, from a traveling front to a pulse.

Conversely, invasion is defined as prey survival and we distinguish two ways in which the prey can invade.

- The spatially *uniform invasion*, which is independent of space.
- The *non-uniform invasion*, described by various *spatial* dynamics, from Turing phenomena to invasion waves.

**Definition 1.1.1.** Let  $(u_0(x), v_0(x))$  be an initial condition verifying (6) and  $(u(t, x), v(t, x))$  be the corresponding solution of (5).

- *Extinction of prey occurs if*

$$\forall x \in \mathbb{R}, \lim_{t \rightarrow +\infty} u(t, x) = 0.$$

- *Prey extinction is uniform if it is uniform with respect to  $x \in \mathbb{R}$ , that is, if there exists a map  $\phi(t)$  verifying*

$$\forall x \in \mathbb{R}, \forall t > t_0, 0 \leq u(t, x) \leq \phi(t) \text{ and } \lim_{t \rightarrow +\infty} \phi(t) = 0.$$

- *Prey extinction is non uniform if there is extinction but no uniform extinction.*
- *Invasion of prey occurs if there is no extinction, that is if*

$$\exists x \in \mathbb{R}, \limsup_{t \rightarrow +\infty} u(t, x) > 0$$

## 1.2 General context of traveling waves

In some cases, the long-term dynamics of a reaction-diffusion system as (2) is well described by that of the associated ODE system, as in our case (1). However, this is not always the case, and there may exist relevant solutions of (2) specific to the spatial structuration. One of the first examples of this type to be described is the well known Fisher-KPP system ([Fischer (1937), Kolmogorov et al. (1937)]) which describes a *single* population following a logistic equation and a diffusive process.

Depending on the initial conditions, the long-term dynamics of this equation is given by a large family of solutions, the so-called “traveling wave” solutions. A traveling wave is a solution of the system that can be written as

$$u(x, t) = U(x - ct). \quad (3)$$

This solution thus describes a constant profile  $U$  moving through space at a speed  $c$ . Such waves are often observed in nonlinear reaction-diffusion systems modeling various phenomena. They are particularly suitable for describing the propagation of invasive fronts. In systems modeling a single species, described by a *scalar* equation, this type of solution is very well understood (see [Volpert et al. (1994)] for a complete theory). Two particular classes of equation can be distinguished : monostable equations (like the Fisher-KPP equations) and bistable equations (often modeling the Allee effect). In monostable equations, there is a minimal wave speed  $c^*$  such that, for any  $c \geq c^*$ , a wave solution of the form (3) with speed  $c$  exists. In bistable equations traveling waves exist for a *unique* speed  $c^*$ . The sign of this speed  $c^*$  distinguishes between invasion or extinction of prey, which is a key property for our purposes.

For interactions of several species (described by a *multidimensional* system), the situation is much more complex. However, for some type of interaction, cooperation for instance, the system possesses a strong structural property, namely monotonicity. Essentially, this monotony makes it possible to use the comparison principle, which is always possible for one-dimensional systems, and the theory is then complete (see [Volpert et al. (1994)]). Unfortunately, our system, and prey-predator systems in general, do not have such a monotonous structure. This method is then unsuitable for monotonous systems and only a few results have been published. One of the key reasons for this is as follows : when we search for traveling wave solutions of form (3) for a system with  $N$  equations, we obtain a system of  $N$  second order ordinary equations that can be reformulated as a system of  $2N$  first order ordinary equations. In the scalar case ( $N = 1$ ) , it is therefore necessary to study trajectories in a plane, available using classical tools for two-dimensional dynamical systems. For several species ( $N > 1$ ), it is necessary to study trajectories in a  $2N$ -dimensional space, which may be very difficult.

Hence, the first rigorous results demonstrating the existence of traveling waves in prey-predator systems were based on a generalization, to the fourth dimension, of the classical shooting method in the phase plane ([Dunbar (1984a), Dunbar (1984b)]). This approach has since been generalised ([Huang et al. (2003), Xu & Weng (2012)]). However, all these studies simply investigate the mere *existence* of traveling waves. They do not determine the direction of the wave or the global dynamics for general initial conditions. Other methods have recently been developed in similar models ([Huang & Weng (2013), Ducrot & Langlais (2012)]), but they are subject to the same limitations. We therefore required another method.

### 1.3 Rationale

The conditions for prey extinction and invasion are discussed in terms of two essential parameters : the encounter rate  $E$  and the handling time  $h$ . Increasing  $E$  clearly increases predator pressure. Conversely, increasing  $h$  decreases predator pressure. The precise phenomena are as follows.

In the absence of prey, the predator population follows a simple logistic equation in which the global attractor is  $v = K_2$  : the predator carrying capacity. Hence,  $(0, K_2)$  is always a steady state of (2), called *the control solution*. We considered the system to be at equilibrium before prey invasion. The initial conditions are therefore of the form  $(u(x, 0), v(x, 0)) = (u_0(x), K_2)$ . If the control solution  $(0, K_2)$  is unstable for the ODE system (1), then it is also unstable for the PDE

system (2) and prey invasion occurs.

A necessary condition for the disappearance of the prey is thus that the control solution is stable for (1). A simple stability analysis shows this to be the case if, and only if the pressure of the predator is sufficiently large with respect to the rate of growth of the prey population, that is if  $EK_2 > r_1$ . This situation is similar to an Allee effect on the prey because, if the initial concentration  $(u_0(x), K_2)$  is close to  $(0, K_2)$ , then the prey disappears. Now, assuming that  $EK_2 > r_1$ , if  $h$  is small enough, then  $(0, K_2)$  is the only steady state of (2) and is a global attractor for (2). In this case prey extinction is observed, spatially uniform for low values of  $h$  and non-uniform for larger values of  $h$ . If  $h$  is greater than a critical value  $h^*(E, \alpha)$ , then there is a new stable positive homogeneous steady state  $(u^*, v^*)$  of (1) and of (2) as well.

We are now able to describe the dynamics of the systems (1) and (2). The description of (1) is easier since the initial concentration of prey  $u_0$  does not depend on  $x$ . If  $h > h^*$  is large enough, then the positive steady state  $(u^*, v^*)$  is stable. In this case the system (1) may be bistable and the long-term behavior of prey is dependent on the initial conditions : if  $u_0$  is close to 0 then prey disappears, whereas, if  $u_0$  is close to  $u^*$  then prey survive. In summary, we prove the following in theorem 2.1.

**For the system (1), prey invade if  $EK_2 < r_1$ . If  $EK_2 > r_1$ , there is extinction of prey if  $h$  is below a critical value  $h^*$  depending on other parameters, i. e. if  $h < h^*(E, \alpha)$ . There is invasion or extinction of prey, depending on the initial conditions, if  $h > h^*(E, \alpha)$ .**

For system (2) the initial condition  $u_0(x)$  may depend on space, resulting in a more complex situation. Indeed, there may exist traveling waves connecting the control solution  $(0, K_2)$  to the positive solution  $(u^*, v^*)$ . The direction of the wave, given by the sign of its speed  $c$ , determines whether (non-uniform) prey extinction (here, when  $c < 0$ ) or (non-uniform) prey invasion ( $c > 0$ ) occurs. Roughly speaking, all other parameters being fixed, this speed  $c$  is an increasing function of  $h$ . Hence, for low values of  $h$  there is extinction and for high values of  $h$  there is invasion. The main purpose of this work is to obtain a rigorous understanding of the sign of this speed  $c$  in term of the parameters. However, the non-monotonous structure of the system (2) generates three main difficulties :

1. The mere existence of traveling waves cannot be taken for granted in prey-predator systems.
2. Even if traveling waves are known to exist, the sign of their speed  $c$  is often unknown.
3. Similarly, even if the traveling wave is known to exist, it may not be stable and it is unclear whether it describes the global dynamics accurately.

We overcame these difficulties by using a sub- and super-solutions method making it possible to break the system down into *scalar* reaction-diffusion equations, each containing part of the information of the complete system. Traveling waves for such scalar equations are very well described, making it possible to obtain precise information about the speed  $c$  in term of the other parameters. In return, we lose some information about the full system, resulting in sufficient (but not necessary) conditions for extinction or invasion. In summary, in theorems 2.4 and 2.6, we prove the following.

**Let  $EK_2 > r_1$ . There exists  $h^-(E)$  and  $h^+(E, \alpha)$  such that there is extinction of prey for the system (2) if  $h < h^-(E)$  and invasion of prey if  $h > h^+(E, \alpha)$ .**

The paper is organized as follows. In section 2 we present the mathematical model and the main result of this work : theorem 2.1 describes invasion conditions for the ODE system (1) and the theorems 2.4 and 2.6 the invasion conditions for the PDE system (2). The dependence of the

critical values  $h^*$ ,  $h^-$  and  $h^+$  on the parameters  $E$  and  $\alpha$  are described by properties 2.2, 2.5 and 2.7 respectively. The mathematical results are completed by numerical simulations in section 3. The results are discussed in section 4. The final section 5 is devoted to the mathematical proofs.

## 2 Model and main results

### 2.1 Mathematical model

We analyze a system of partial differential equations for a prey population with logistic growth, and a generalist predator population with logistic growth on alternative prey in the absence of the invading host. The functional response is of Holling type II. The prey-predator interactions are modeled by the following partial differential equation system :

$$\begin{cases} u_t = D_u \Delta_x u + r_1 u \left(1 - \frac{u}{K_1}\right) - \frac{Euv}{1+Ehu}, \\ v_t = D_v \Delta_x v + r_2 v \left(1 - \frac{v}{K_2}\right) + \gamma \frac{Euv}{1+Ehu}, \\ u(x, 0) = u_0(x), \quad v(x, 0) = 1 \end{cases} \quad x \in \mathbb{R}, t \in \mathbb{R}^+ \quad (4)$$

with :

$u(t, x)$ = prey density at time $t$ and at point $x$ .	$v(t, x)$ = predator density at time $t$ and at point $x$ .
$D_u$ = diffusion rate of prey	$D_v$ = diffusion rate of predators
$r_1$ = growth rate of prey	$r_2$ = growth rate of predators
$K_1$ = carrying capacity of prey	$K_2$ = carrying capacity of predators in absence of focal prey
$E$ = encounter rate	$h$ = handling time
$\gamma$ = conversion efficiency	$u_0 \geq 0$ the initial concentration of prey,

$D_u, D_v, r_1, r_2, K_1, K_2, E, h$  and  $\gamma$  are positive constant parameters.

We carried out the following adimensionalization :

$$\begin{aligned} & \text{--- } t' = r_1 t; \quad x' = x \sqrt{\frac{r_1}{D_u}}; \quad u'(x', t') = u(t, x)/K_1; \quad v'(x', t') = v(t, x)/K_2 \\ & \text{--- } d' = D_v/D_u; \quad r' = r_2/r_1; \quad E' = EK_2/r_1; \quad h' = r_1 h K_1/K_2; \quad \gamma' = \gamma K_1/K_2; \quad \alpha = \frac{\gamma'}{r'}. \end{aligned}$$

Removing the sign ' to simplify the notation, system (2) reads

$$\begin{cases} u_t = \Delta_x u + u(1 - u) - \frac{Euv}{1+Ehu}, \\ v_t = d \Delta_x v + r(v(1 - v) + \alpha \frac{Euv}{1+Ehu}) \end{cases} \quad x \in \mathbb{R}, t \in \mathbb{R}^+ \quad (5)$$

with the initial conditions<sup>1</sup>

$$\begin{cases} u(0, x) = u_0(x) \in [0, 1]; \quad \lim_{x \rightarrow -\infty} u_0(x) = 1; \quad \lim_{x \rightarrow +\infty} u_0(x) = 0 \\ v(0, x) = 1. \end{cases} \quad (6)$$

### 2.2 Main results

#### 2.2.1 Analysis of the associated ODE system

If space is not taken into account, system (5) may be rewritten as follows.

$$\begin{cases} \frac{d}{dt} u = u(1 - u) - \frac{Euv}{1+Ehu}, \\ \frac{d}{dt} v = r(v(1 - v) + \alpha \frac{Euv}{1+Ehu}), \\ 0 < u(0) = u_0 \leq 1 \leq v(0) = v_0 \end{cases} \quad t \in \mathbb{R}^+ \quad (7)$$

---

1. All our results remain true for various different initial conditions. The essential being that solution of the scalar systems we consider converge to traveling wave solutions. In particular, compact support may be allowed for  $u_0$ . See [Fife (1979)] for a detailed discussion.

System (7) is well understood ([Magal et al. (2008)]). Indeed, it is clear that there are always three trivial stationary states :  $(0, 0)$  and  $(1, 0)$ , which are unstable and  $(0, 1)$ , which is asymptotically stable if, and only if,  $E > 1$ . Moreover, there are no more than three non-trivial positive steady states. We are interested principally in the case  $E > 1$ . In this case, there are either no or two stationary positive steady states. If the two steady states exist, denoted  $(u_1, v_1)$  and  $(u_2, v_2)$  with  $u_1 < u_2$  and  $v_1 < v_2$ , then  $(u_1, v_1)$  is unstable and  $(u_2, v_2)$  is stable. In this case, there are two stable nonnegative solutions,  $(0, 1)$  and  $(u_2, v_2)$  and the system is bistable.

We are interested principally in the conditions for prey extinction. If  $E < 1$ , then  $(0, 1)$  is unstable and no extinction occurs. We are therefore interested only in the case  $E > 1$ . Now, if  $E > 1$ , there are two possibilities. In the non bistable case,  $(0, 1)$  is globally stable and there is extinction. In the bistable case, provided that  $u$  is initially small enough, say  $u_0 < \mu_1$  for some  $0 < \mu_1 < 1$ , then  $u(t) \rightarrow 0$  as  $t \rightarrow +\infty$ . Conversely, if  $u$  is initially large enough, say  $0 < \mu_2 < u_0$ , then  $u(t) \rightarrow u_2$  as  $t \rightarrow +\infty$ . Thus, in this case, the outcome — extinction or invasion — depends on the initial conditions. The following result provides an explicit statement of the above in the parameter space  $(E ; h)$  and is proved in section 5.1.

**Theorem 2.1.** *Assume that  $E > 1$ .*

- (i) **Existence of positive solutions.** *There exists  $h^* = h^*(E, \alpha)$  such that*
  - *If  $h < h^*$  there is no positive stationary solution and there is extinction of prey for the ODE system.*
  - *If  $h > h^*(E, \alpha)$  then there exist two positive solutions for the ODE system  $(\hat{u}, \hat{v})$  and  $(u^*, v^*)$  with  $\hat{u} < u^*$ .*
- (ii) **Stability of the solutions.** *Let  $h > h^*(E, \alpha)$ . The solution  $(\hat{u}, \hat{v})$  is always unstable. Moreover, there exists  $h^{**}(E, \alpha) > h^*(E, \alpha)$  such that*
  - *If  $h > h^{**}(E, \alpha)$  then  $(u^*, v^*)$  is stable.*
  - *If  $h^*(E, \alpha) < h < h^{**}(E, \alpha)$  the stability of  $(u^*, v^*)$  depends on  $r$ . It is unstable if  $r$  is small enough and stable otherwise.*

**Remark 1.** *Our calculations show that the gap between  $h^*$  and  $h^{**}$  is very small, so, roughly speaking,  $(u^*, v^*)$  is stable whenever it exists. However, if  $h$  belongs to the conditional stability zone and  $r$  is very small, stability is lost and the system becomes excitable. This explains, in particular, the presence of pulses for small values of  $r$  when dealing with spatial interactions (see section 3).*

The map  $(E, \alpha) \mapsto h^*(E, \alpha)$  has the following properties, as proved in section 5.1.

**Properties 2.2.** *The maps  $E \mapsto h^*(E, \alpha)$  and  $\alpha \mapsto h^*(E, \alpha)$  are increasing.*

*Let  $\alpha \geq 0$  be fixed. One has the explicit limits :*

$$\lim_{E \rightarrow 1} h^*(E, \alpha) = \begin{cases} 1 + \alpha & \text{if } \alpha < 1 \\ 2\sqrt{\alpha} & \text{if } \alpha \geq 1 \end{cases} \quad \lim_{E \rightarrow +\infty} h^*(E, \alpha) = 2 + 2\sqrt{1 + \alpha}.$$

*Let  $E \geq 1$  be fixed. One has the explicit limits*

$$h^*(E, 0) = \frac{1}{E} \left( 2E - 1 + 2\sqrt{E(E-1)} \right) := h_1(E) \quad \text{and} \quad \lim_{\alpha \rightarrow +\infty} h^*(E, \alpha) = +\infty.$$

Figure 1 illustrates the maps  $h^*$  and  $h^{**}$  and the possible situations for system (7).

### 2.2.2 Analysis of the PDE system

We wish to identify the parameter conditions required to obtain prey extinction in the PDE system (5). A simple stability analysis shows that, if  $E < 1$ , then invasion occurs in the PDE system. If  $E > 1$ , then the situation for the PDE system is more complex. In this situation, the spatial



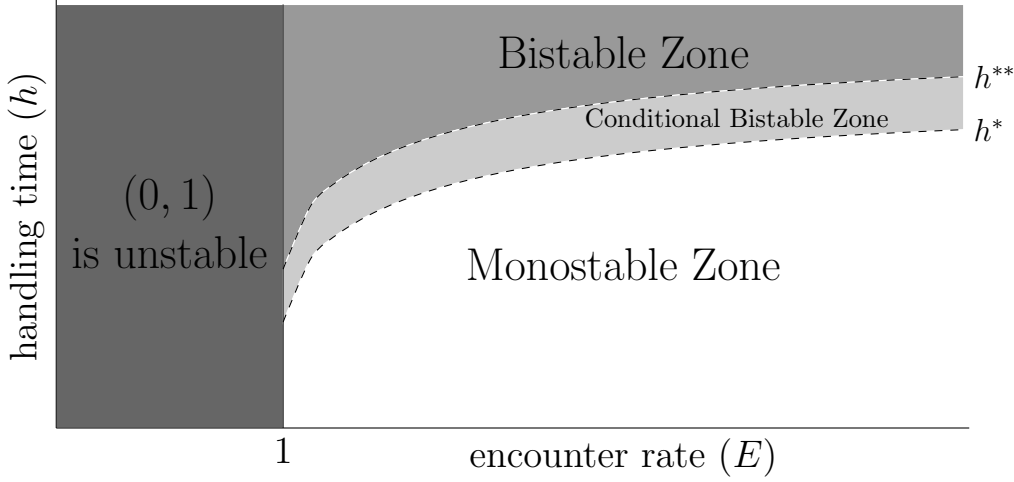


FIGURE 1: Description of the dynamics of the ODE system (7) in the  $E - h$  plane. If  $E < 1$ , the control solution  $(0, 1)$  is unstable. In this zone there exists at least one positive steady state and the prey never disappears entirely. If  $E > 1$ , then the control solution  $(0, 1)$  is always (locally) stable. Moreover, the  $E > 1$  zone is the union of three subzones. Below the  $h^*$  curve,  $(0, 1)$  is the only non-negative steady state and is a global attractor : this is a monostable zone. Above the  $h^*$  curve, there are two additional positive steady states, one of which is always unstable while the second, denoted  $(u^*, v^*)$ , may be stable or unstable. Above the  $h^{**}$  curve,  $(u^*, v^*)$  is always stable. In this subzone, the asymptotic behaviors depends only on the initial conditions : this is a bistable zone. Between the  $h^*$  and the  $h^{**}$  curves, the stability of  $(u^*, v^*)$  depends on other parameters : this is a conditional bistable zone. For illustration purpose, the size of this last subzone has been considerably increased on the figure.

structure and diffusion processes result in additional conditions for extinction. The rationale is explained in detail below.

Let us assume that there is a positive stable stationary solution of (5) denoted by  $(u^*, v^*)$  and that the initial condition  $u(x, 0)$  is close to  $u^*$  at some places  $x$  and close to 0 at other places. Since both  $u^*$  and 0 are stable, the demographic phenomena lead to an agregation near  $u^*$  and an agregation near 0. However, diffusion allows individuals to move around in space, so one of 0 or  $u^*$  may be the final global attractor. In other words, there may be a (stable) traveling wave joining  $u^*$  to 0. The direction of this wave, given by the sign of the speed of the wave, indicates whether extinction or invasion occurs. However, there are difficulties associated with this argument.

- There can be no homogeneous stationary solution of (5), only stable heterogeneous positive stationary solutions. In other words, it is possible that  $h < h^*(E, \alpha)$  without control occurring.
- Even in the case of bistability ( $h > h^*(E, \alpha)$ ), the bistable system (5) is neither competitive nor cooperative. Little theoretical knowledge is available concerning the occurrence of traveling waves in such systems, with even less known about the stability and direction of the wave.

Using super- and subsolutions, we show here how to obtain the conditions sufficient (but not necessary) for extinction and for invasion, based on well known *scalar* bistable PDEs. Roughly speaking, let  $(u(t, x), v(t, x))$  be the solution of (5). If we find a *positive constant*  $\underline{v}$  such that, for any<sup>2</sup>  $(t, x) \in \mathbb{R}^+ \times \mathbb{R}$ ,  $v(t, x) \geq \underline{v}$  then it comes

$$\partial_t u(t, x) - \Delta_x u(t, x) \leq u(t, x)(1 - u(t, x)) - \frac{Eu(t, x)}{1 + Ehu(t, x)}\underline{v}, \quad t > 0, x \in \mathbb{R}.$$

Let  $\bar{u}$  be the solution of

---

2. It suffices that this condition occurs for  $t > t_0$  for some  $t_0 > 0$ .

$$\begin{cases} \partial_t \bar{u}(t, x) - \Delta_x \bar{u}(t, x) = \bar{u}(t, x)(1 - \bar{u}(t, x)) - \frac{E\bar{u}(t, x)}{1 + E h \bar{u}(t, x)} \underline{v}, \\ \bar{u}(0, x) \geq u(0, x). \end{cases}$$

The comparison principle implies that  $\bar{u}(t, x) \geq u(t, x)$ . Now, if  $\bar{u}(x, t) \rightarrow 0$  when  $t \rightarrow +\infty$  then  $u(t, x) \rightarrow 0$  when  $t \rightarrow +\infty$  and extinction of prey occurs (see figure 2-(a)). Moreover, if  $\bar{u}(x, t) = \phi(t)$  does not depend on  $x$ , then there is aspatial control (see figure 2-(b)).

Conversly, if we can identify a *positive constant*  $\bar{v}$  such that  $v(x, t) \leq \bar{v}$ , then it comes

$$\partial_t u(t, x) - \Delta_x u(t, x) \geq u(t, x)(1 - u(t, x)) - \frac{Eu(t, x)}{1 + E h u(t, x)} \bar{v}, \quad t > 0, x \in \mathbb{R}.$$

Now, define  $\underline{u}(t, x)$  as the solution of

$$\begin{cases} \partial_t \underline{u}(t, x) - \Delta_x \underline{u}(t, x) = \underline{u}(t, x)(1 - \underline{u}(t, x)) - \frac{E\underline{u}(t, x)}{1 + E h \underline{u}(t, x)} \bar{v}, \\ \underline{u}(0, x) \leq u(0, x). \end{cases}$$

The comparison principle implies that  $\underline{u}(t, x) \leq u(t, x)$ . It follows that if for some  $x \in \mathbb{R}$ ,  $\limsup_{t \rightarrow +\infty} \underline{u}(x, t) > 0$  then  $\limsup_{t \rightarrow +\infty} u(t, x) > 0$  and there is (non uniform) invasion (see figure 3).

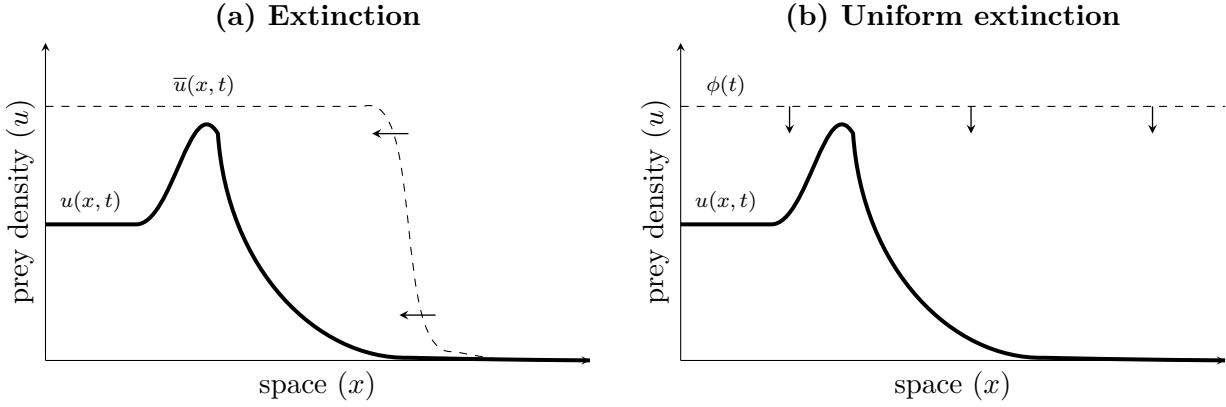


FIGURE 2: (a) Sufficient condition for extinction. The solution  $u(t, x)$  is majored by a supersolution  $\bar{u}(t, x)$ . If  $\lim_{t \rightarrow +\infty} \bar{u}(t, x) = 0$  then  $\lim_{t \rightarrow +\infty} u(t, x) = 0$  and there is extinction. (b) Sufficient condition for uniform extinction. The solution  $u(t, x)$  is majored by a supersolution  $\phi(t)$  which does not depend on  $x$ . If  $\lim_{t \rightarrow +\infty} \phi(t) = 0$  then  $\lim_{t \rightarrow +\infty} u(t, x) = 0$  uniformly in  $x$  and there is uniform extinction.

These arguments give rise to the following theorems yielding sufficient conditions, in terms of the parameters  $E$ ,  $\alpha$  and  $h$ , for extinction or invasion to occur. All theorems are proved in section 5. We begin with a sufficient condition for uniform extinction.

**Theorem 2.3.** *Let  $E > 1$  and define*

$$h_1(E) = \frac{1}{E} \left( 2E - 1 + 2\sqrt{E(E-1)} \right).$$

*If  $h < h_1(E)$  then there is uniform extinction. In other word, for any initial condition verifying (6), there exists  $\phi(t) \geq 0$  such that any solution  $(u(t, x), v(t, x))$  of (5) verifies*

$$\forall x \in \mathbb{R}, 0 \leq u(t, x) \leq \phi(t) \text{ and } \lim_{t \rightarrow +\infty} \phi(t) = 0.$$

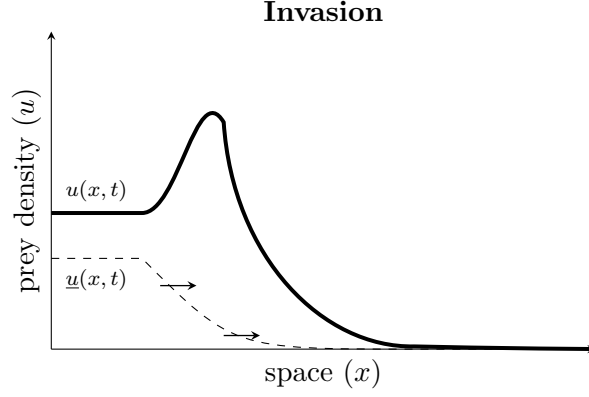


FIGURE 3: Sufficient condition for invasion. The solution  $u(t, x)$  is minored by a subsolution  $\underline{u}(t, x)$ . If  $\limsup_{t \rightarrow +\infty} \underline{u}(t, x) > 0$  then  $\limsup_{t \rightarrow +\infty} u(t, x) > 0$  and there is invasion.

If  $h > h_1(E)$  then there can be invasion or extinction. The following theorem give a sufficient condition for extinction to occur.

**Theorem 2.4.** *Assume that  $E > 1$ . There exists  $h^- = h^-(E) > h_1(E)$ , such that if  $h < h^-(E)$  then there is extinction of prey. In other words, for any initial condition verifying (6) and for any  $x \in \mathbb{R}$ ,  $\lim_{t \rightarrow +\infty} u(t, x) = 0$ .*

The map  $E \mapsto h^-(E)$  verifies the following properties proved in section 5.3.

**Properties 2.5.** *The map  $E \mapsto h^-(E)$  is increasing and admits the following explicit limits :*

$$\lim_{E \rightarrow 1} h^-(E) = 1 \quad ; \quad \lim_{E \rightarrow +\infty} h^-(E) = \frac{16}{3}.$$

Our last result gives a sufficient condition for invasion to occur.

**Theorem 2.6.** *For any  $E > 1$  and  $\alpha \geq 0$ , there exists  $h^+ = h^+(E, \alpha)$  verifying  $h^+(E, \alpha) > h^-(E)$  and  $h^+(E, \alpha) > h^*(E, \alpha)$  such that, if  $h > h^+(E, \alpha)$  then prey invasion occurs. More precisely, for any  $x$ ,  $\limsup_{t \rightarrow +\infty} u(t, x) > 0$ .*

Finally, the following result specifies the behavior of the map  $h^+$ .

**Properties 2.7.** *The maps  $E \mapsto h^+(E, \alpha)$  and  $\alpha \mapsto h^+(E, \alpha)$  are increasing. For any  $E > 1$ ,  $h^+(E, 0) = h^-(E)$  and  $\lim_{\alpha \rightarrow +\infty} h^+(E, \alpha) = +\infty$ . Finally,  $\alpha \geq 0$  being fixed, one has the explicit limit*

$$\lim_{E \rightarrow +\infty} h^+(E, \alpha) = \frac{8}{3} \left( 1 + \sqrt{1 + \frac{3}{4}\alpha} \right).$$

The results above are summarized in figure 4. In the domain  $\{(E, h), E > 1, h^-(E) < h < h^+(E, \alpha)\}$ , which we will refer to as the ‘transition zone’, it is not possible to draw any conclusions concerning whether prey invasion or extinction is likely to occur. Indeed, this zone can be separated into two subzones, according to the parameter values :

$$\text{Zone I} = \{(E, h), E > 1, \max(h^*(E, \alpha), h^-(E)) < h < h^+(E, \alpha)\},$$

$$\text{Zone II} = \{(E, h), E > 1, h^-(E) < h < h^*(E, \alpha)\}.$$

In the Zone I, our numerical simulations show non-monotonous traveling waves. In the zone II, simulations show various types of behavior including pulse and even heterogeneous positive stationary solutions. This phenomena are discussed in the section 3.

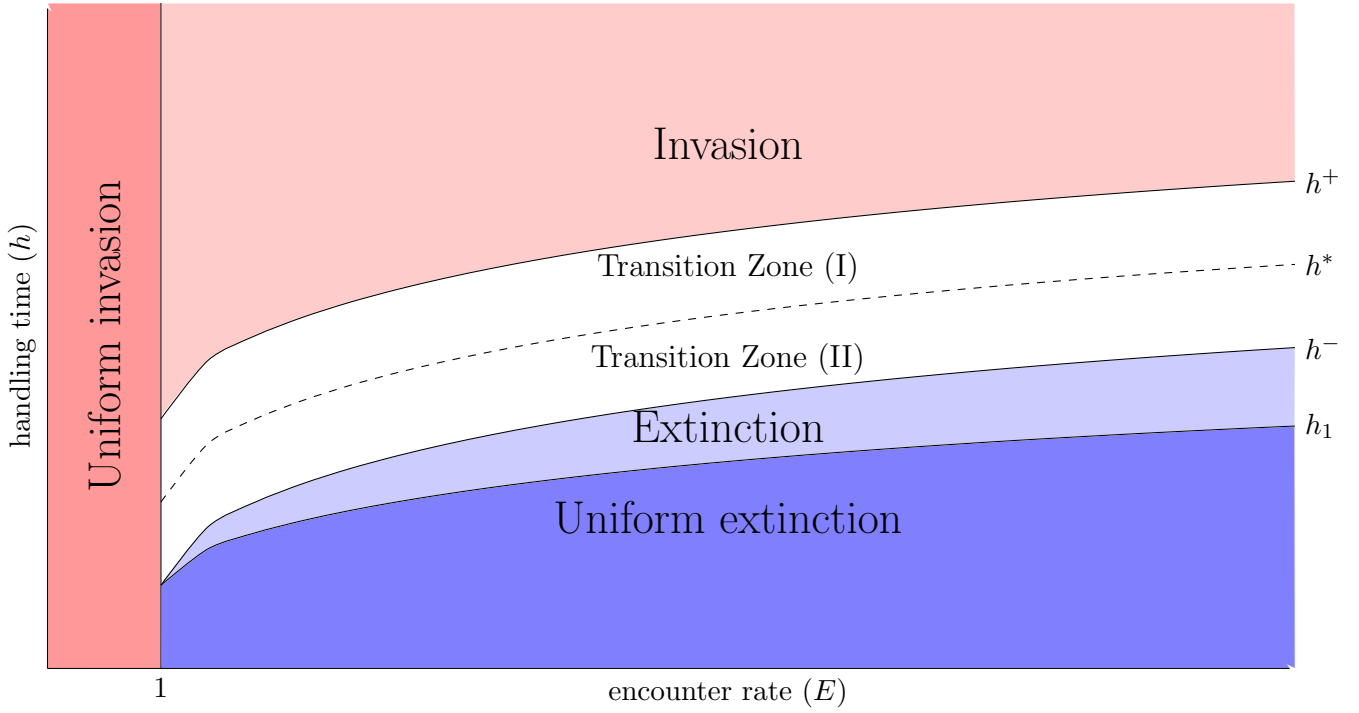


FIGURE 4: Description of the dynamic of the PDE system (5) in the  $E - H$  plan. If  $E < 1$  there is always invasion. If  $E > 1$  there is a uniform extinction for  $h < h_1(E)$ , extinction for  $h_1(E) < h < h^-(E)$  and invasion for  $h^+(E, \alpha) < h$ . The zone between  $h^-$  and  $h^+$  is called the transition zone. This transition zone is splitted into two subzones : Zone I and Zone II, separated by the  $h^*$  curve. In these two zones, both extinction or invasion of prey may occur due to various spatial phenomena.

### 3 Numerical study of the transition zone

#### 3.1 Influence of $\alpha$ .

The mathematical results above demonstrate the influence of the parameters  $E$  and  $h$ , and, indirectly, that of the conversion rate  $\alpha$ , on the long-term behavior of the system.

In summary, we have demonstrated the following phenomena :

- An increase in the rate of encounter  $E$  increases predator efficacy and, thus, the chances of prey extinction.
- An increase in the handling rate  $h$  decreases predator efficacy and, thus, increases the risk of prey invasion.

More precisely, when  $E > 1$ , prey extinction or invasion may occur, depending on the value of  $h$ . Indeed, we can define two values  $h^- = h^-(E) < h^+ = h^+(E, \alpha)$  (see theorems 2.4 and 2.6). Extinction occurs if  $h < h^-$  and invasion occurs if  $h > h^+$ . When  $h \in (h^-, h^+)$  we observe richer dynamics, which may depend on other factors. We refer to this zone as the **transition zone**. Note that, as  $h^-$  is not dependent on  $\alpha$  and  $h^+$  is an increasing function of  $\alpha$  (proposition 2.7), the size of this transition zone increases with increasing  $\alpha$ .

A first clue to the possible dynamics in the transition zone is provided by an understanding of the dynamics of the ODE system (7) described in the theorem 2.1. The dynamic of (7) is essentially dependent<sup>3</sup> on the position of  $h$  relative to  $h^* = h^*(E, \alpha)$ . When  $h < h^*$ , there is no positive stationary solution, whereas, for  $h > h^*$  there are two positive stationary solutions, one

3. The dynamics generally also depends on a quantity  $h^{**}$ , defined in the theorem 2.1, slightly greater than  $h^*$  that is not taken into account here for the sake of simplicity.

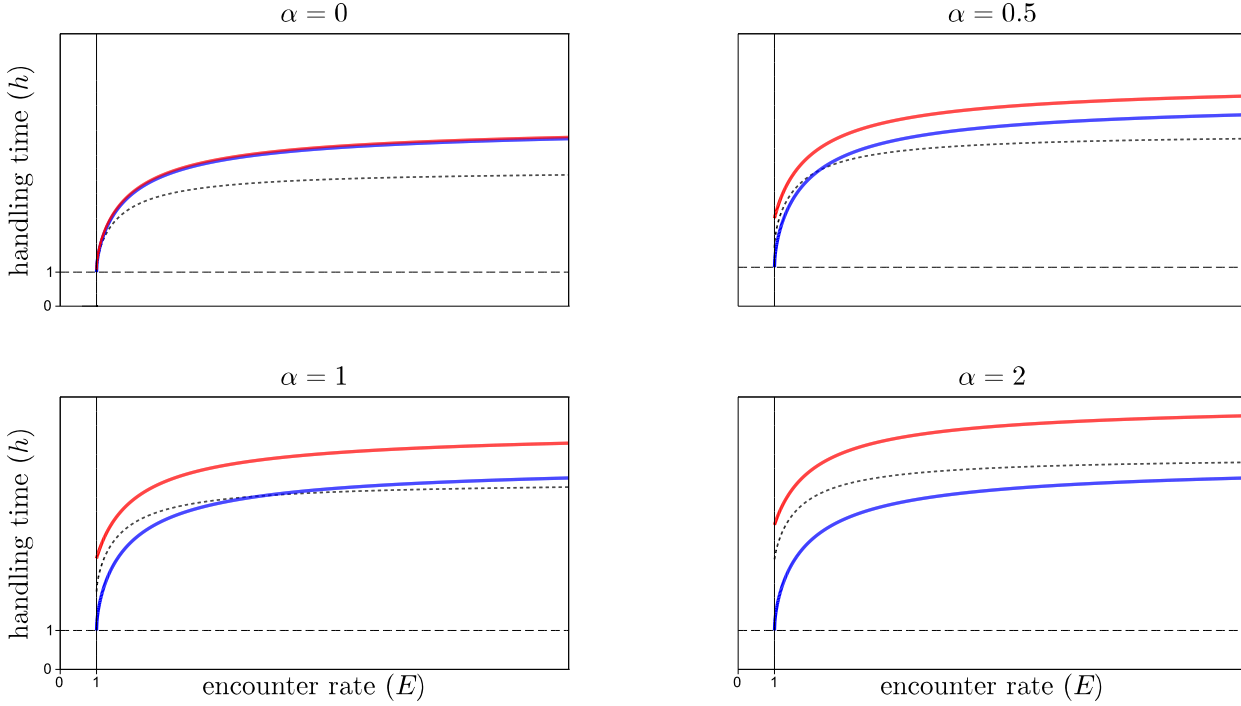


FIGURE 5: Computation of  $h^*(E, \alpha)$ ,  $h^-(E)$  and  $h^+(E, \alpha)$  for four values of  $\alpha$ . The so-called transition zone lies between the red curve  $h^+$  and the blue curve  $h^-$ . The transition zone increases within increasing  $\alpha$ . This transition zone can be split into two subzones separated by  $h^*$  (black line).

of which, the larger of the two, is (nearly always) stable.

The position of  $h^*$  relative to  $h^-$  and  $h^+$  provides a first description of the transition zone. By virtue of proposition 2.2, one gets the following. We always have  $h^* < h^+$ , but the position of  $h^*$  relative to  $h^-$  is dependent on  $\alpha$ . On the one hand, from the facts that  $h^*(1, \alpha) > h^-(1)$  for  $\alpha > 0$  and  $h^*(E, 0) = h_1(E) < h^-(E)$  for  $E > 1$ , we deduce that  $h^- > h^*$  for large enough values of  $E$  and small enough values of  $\alpha$ . On the other hand,  $h^*$  is an increasing function of  $\alpha$  tending to  $+\infty$  and, thus, one has  $h^*(E, \alpha) > h^-(E)$  for large values of  $\alpha$  and any  $E > 1$ .

**Remark 2.** When  $h^- > h^*$ , which may occur for sufficiently small values of  $\alpha$ , we see that taking space into account automatically increases the potential of extinction of preys.

The transition zone can thus be separated into two subzones : one in which  $h < h^*$  (Zone II) and one in which  $h > h^*$  (Zone I). Figure 5 sums up this discussion on the transition zone. As we will see below, both extinction and invasion are possible in each of these zones, but the phenomena at work differ considerably, according to whether  $h < h^*$  or  $h > h^*$ . These phenomena are studied in more detail below, using a numerical approach.

### 3.2 Extinction or invasion : influence of $r$ and $d$ .

Our numerical analysis shows that both invasion and extinction are possible in the transition zone. When space is taken into account we see that  $h^*$  does not separate the zone of invasion from that of extinction. These two zones are, indeed, separated by a new critical value of the handling time denoted  $h_{crit} \in (h^-, h^+)$ , which is dependent on  $E$  and  $\alpha$ , of course, but also on the relative rates of growth ( $r$ ) and diffusion ( $d$ ) of the predator population :

$$h_{crit} = h_{crit}(E, \alpha, r, d).$$

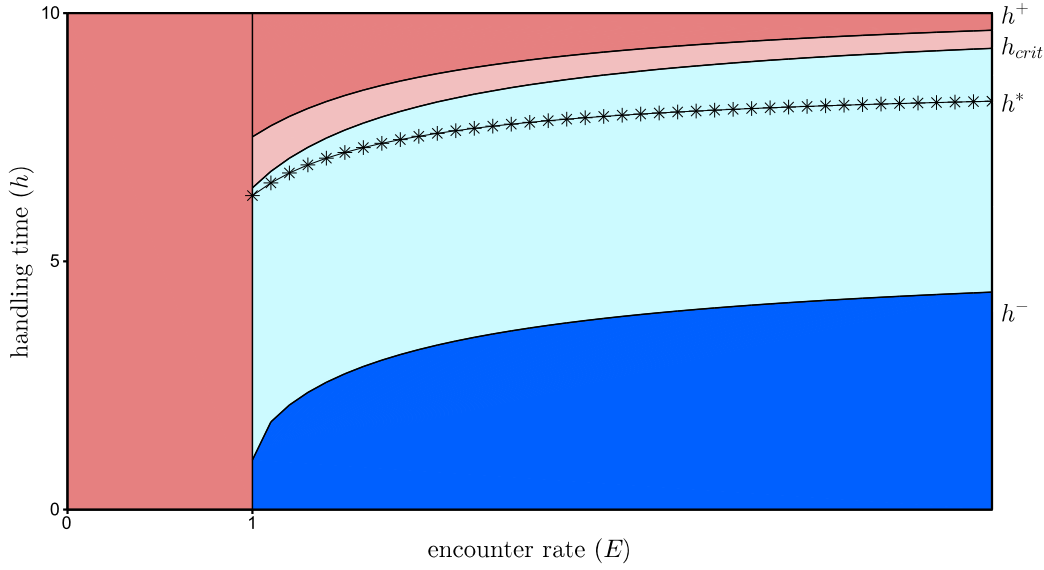


FIGURE 6: Numerical computation of  $h_{crit}$  in the  $E - h$  plan for fixed values of  $\alpha$ ,  $d$  and  $r$ . The transition zone  $h \in (h^-, h^+)$  is split into two subzones separated by  $h_{crit}$ . Extinction occurs below  $h_{crit}$  and invasion occurs above.

As expected, when  $h > h_{crit}$ , prey invasion is observed, whereas extinction is observed when  $h < h_{crit}$ . Thus, higher values of  $h_{crit}$  are associated with more effective predation and thus with less effective invasion by the prey.

Figure 6 completes the theoretical scheme represented in figure 4, by presenting an example of the curve for a particular selection of values for the parameters  $\alpha$ ,  $r$  and  $d$  in the  $E - h$  plan.

Like  $h^*$  and  $h^+$ ,  $h_{crit}$  increases with both  $E$  and  $\alpha$ . This naturally translates the facts that, higher values of  $E$  increases the chance of meeting between predators and prey and that at higher  $\alpha$  values, the predator is able to make greater use of the prey and can therefore eliminate it.

Given the multiple dependence of  $h_{crit}$  on different parameters, figure 6 can only represent a particular case, chosen for its simplicity. Figure 7 shows the relationships between  $h_{crit}$  and  $d$  for fixed values of  $E$  and  $\alpha$  and for various values of  $r$ . We see that  $h_{crit}$  increases with  $r$ . This translates the fact that for small values of  $r$ , the predators growth rate is small and their effectiveness reduced. Conversely,  $h_{crit}$  (essentially) decreases with increasing  $d$ . This is due to the fact that for large  $d$ , predators spread into a zone in which prey are not present, resulting in a weakening predation.

**Remark 3.** For small values of  $r$  and intermediate values of  $d$ , predators may increase their effectiveness by increasing  $d$ . In that case, the predators growth rate being small, predators density remains high for a long time even if prey are absent. Now, if  $d$  is large enough but not large, predators may spread into a zone in which prey are not present and remain there at a high density and long enough to stop the prey to invade. This phenomenon may enable predators to form a barrier to prey's movement, preventing thereby prey propagation. For too large values of  $d$ , the loss in predators effectiveness due to movement is too strong and the above phenomenon does not happen any more. This explains why, for small values of  $r$ ,  $h_{crit}$  first increase and then decreases with increasing  $d$ .

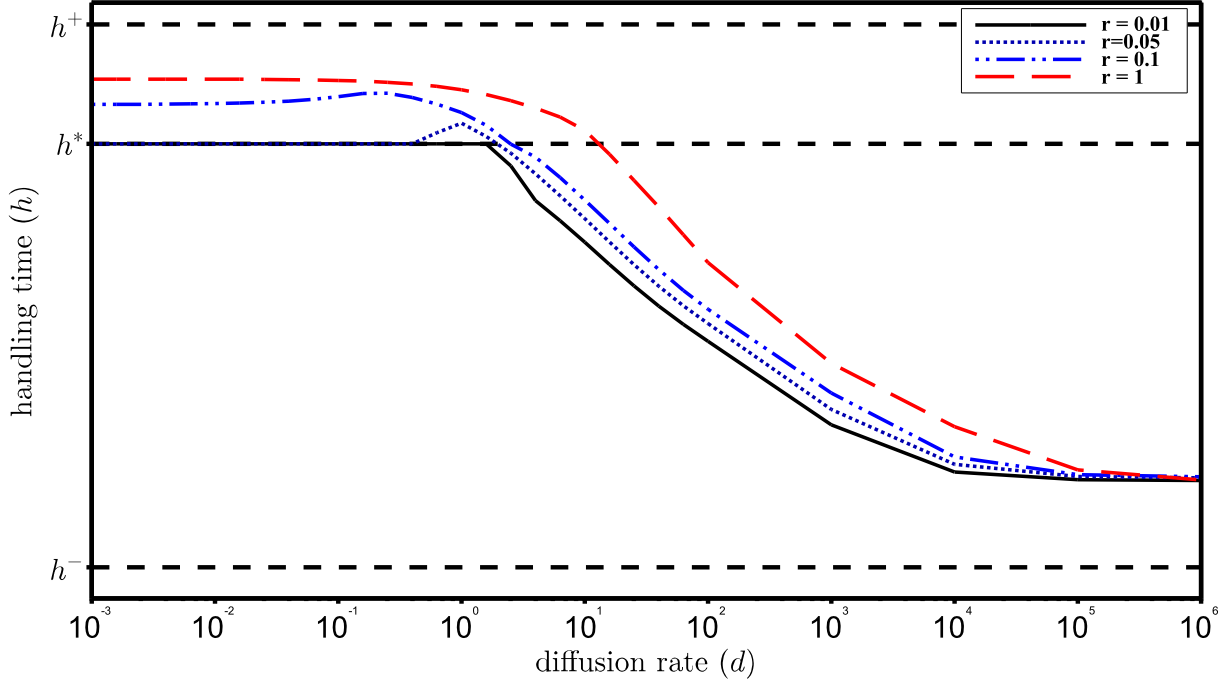


FIGURE 7: Numerical computation of  $h_{crit}$  with respect to  $d$  for four values of  $r$  with  $E = 2$  and  $\alpha = 4$ . For a given value of the parameters, there is invasion of prey if  $h > h_{crit}$  and extinction if  $h < h_{crit}$ . Therefore, the larger  $h_{crit}$  is, the greater is the potential for extinction of prey. We see that  $h_{crit}$  is increasing in  $r$  and (essentially) decreasing in  $d$ . Thus, an increase of  $d$  or a decrease of  $r$  decrease the impact of the predation on invasive prey.

### 3.3 Dynamics of the system in the transition zone

We know that extinction occurs when  $h < h_{crit}$ , whereas invasion occurs when  $h > h_{crit}$ . It should be borne in mind that the existence or absence of non-trivial solutions that are homogeneous over space is dependent on the position of  $h$  with respect to  $h^*$ . Consequently, the processes at work during extinction or invasion are highly dependent on the position of  $h$  with respect to  $h^*$ .

We will now describe the different dynamics occurring in the transition zone, summarized in table 1. See section 2.2 for a precise definition of the various quantities described here.

#### A] Invasion ( $h > h_{crit}$ )

- **Turing instabilities (TI)** :  $h < h^*$  and  $d \gg 1$ . As  $d$  increases, predators spread out, moving into areas from which the prey is absent, leading to a decrease in the size of the predator population. This phenomenon leads to a decrease in predator density throughout the space occupied by the predator, allowing the prey to survive in certain zones. We thus obtain a periodic distribution in space and a constant distribution over time of the densities of the prey and predator. Mathematically, this phenomenon is described by a Turing bifurcation.
- **Invasion traveling waves (ITW)** :  $h > h^*$ . The invasion is described simply by an invasion traveling wave : a wave of propagation linking the two stable solutions  $(u^*, v^*)$  and  $(0, 1)$  in the direction of the positive solution  $(u^*, v^*)$ . When  $r$  is large this traveling wave is monotone. By contrast, when  $r \ll 1$  it displays a rich dynamics. When  $r \ll 1$  and  $d$  is not too large, we observe that  $h_{crit}$  is approximately equal to  $h^*$  (see figure 7). This

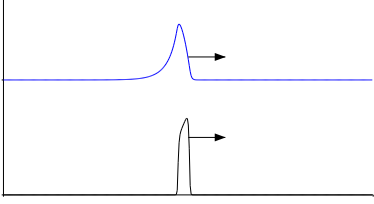
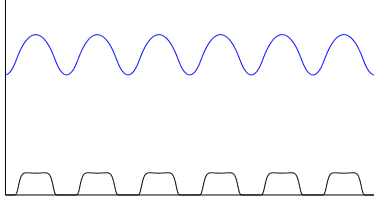
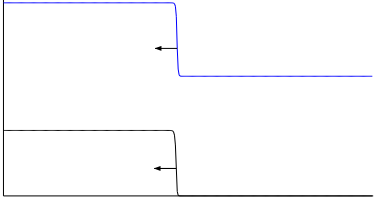
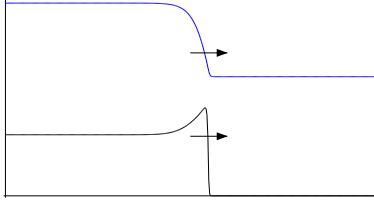
	$h < h_{crit} : \text{Extinction}$	$h > h_{crit} : \text{Invasion}$
$h < h^* : \text{Zone II}$	<p>PULSE (<math>r \ll 1</math>)</p> 	<p>TURING (<math>d \gg 1</math>)</p> 
$h > h^* : \text{Zone I}$	<p>ETW</p> 	<p>ITW</p> 

TABLE 1: Summary of the four different situations involving space in the transition zone. The X axis represent space and the Y axis the concentration of species. The blue curve (above) represent the concentration of predators in space while the black curve (below) is the concentration of prey. Extinction and Invasion Traveling Waves are abbreviated ETW and ITW respectively.

indicates that there is an invasion traveling wave if a positive solution exists. In this case, ahead of the front,  $v = 1$  and, since  $r \ll 1$ , the predator population increases very slowly. Besides, as  $h > h^-$  the prey invades the space when the predator is at concentration 1. This leads to the front advancing. Behind the front, the predator has had sufficient time to increase the size of its population and, therefore, to decrease the size of the prey population. As  $h > h^*$ , the population of the prey decreases towards the positive solution  $u^*$  and we see a non-monotonous invasive traveling wave.

#### B] Extinction ( $h < h_{crit}$ )

- **Pulse** :  $h \in [h^-, h^*]$  and  $r \ll 1$  Since  $r \ll 1$ , The front of the wave is similar to the ITW described above. However, as  $h < h^*$ , here is no homogeneous positive solution  $u^*$ . The prey population therefore decreases to zero behind the front, whereas it continues to advance in front of the front. We thus obtain a pulse.
- **Extinction traveling wave (ETW)** :  $h > h^*$  This corresponds to the simplest case described above. We observe a propagation wave linking the two stable solutions  $(u^*, v^*)$  and  $(0, 1)$  in the direction of the control solution  $(0, 1)$ .

Finally, figure 8 presents the map in the  $E - h$  plane for fixed values of  $\alpha$ ,  $d$  and  $r$  and specifies the possible dynamics in each zone.



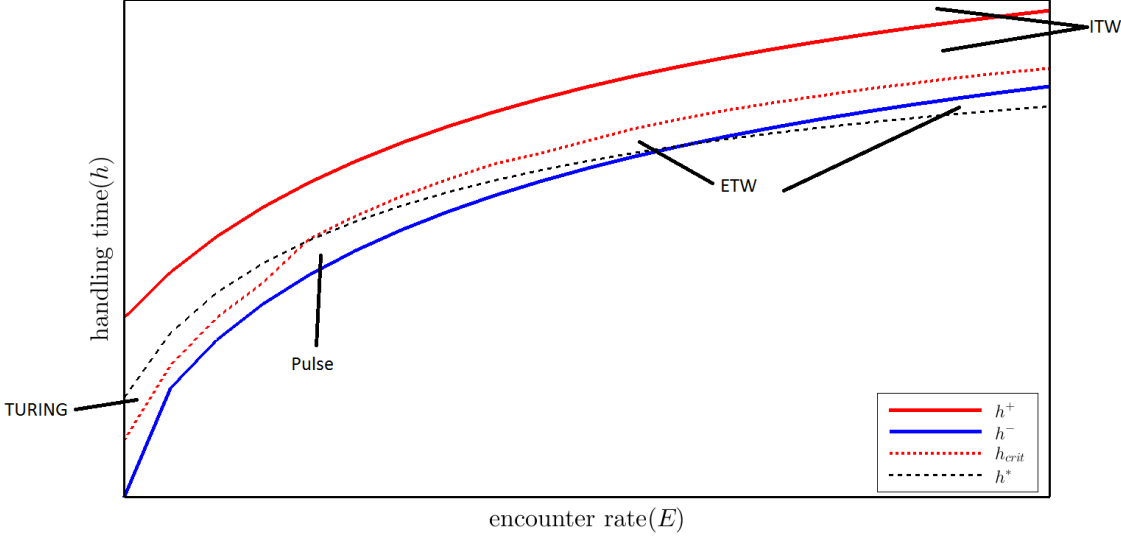


FIGURE 8: Different spatial dynamics in the transition zone. To ensure that all possible situations are represented, we chose  $\alpha = 0.5$ ,  $r = 0.01$  and  $d = 10$ . Note that traveling waves of extinction (ETW) and traveling waves of invasion (ITW) may be obtained outside the transition zone

## 4 Conclusion and discussion

### 4.1 Summary of the results

We have shown that invasion occurs if  $E < 1$ . If predators do not encounter their prey they cannot control them. If  $E > 1$ , then extinction or invasion can occur, depending on the parameters  $h$ ,  $E$  and  $\alpha$ . Uniform extinction occurs for  $h < h_1(E)$  and extinction occurs for  $h_1(E) < h < h^-(E)$ . Invasion occurs for  $h^+(E, \alpha) < h$ . Thus, if  $h$  increases, we move from a zone of extinction without a consideration of space to a zone of extinction requiring a consideration of spatial aspects and then to a zone of invasion. For intermediate values of  $E$ , the zones of extinction increase with increasing  $E$  resulting in a higher potential of extinction, as  $h_1, h^*, h^-$  are increasing functions of  $E$ . When  $E$  is large, the zones of control do not depend on  $E$  any more because  $h_1, h^-, h^+$  have finite limits when  $E \rightarrow +\infty$ . Thus,  $E$  can only play a role in prey control if it takes intermediate values and if  $h$  is not too large. In summary, for low values of  $E$  ( $E < 1$ ) or high values of  $E$  or  $h$ , the outcome of the interaction (extinction or invasion) is independent of  $E$ .

There is furthermore a transition zone splitted in two subzones, Zone I and Zone II, with various spatio-temporal phenomena and wherein both extinction and invasion can occur. The size of this transition zone greatly increases when the conversion rate  $\alpha$  increases. Depending on the relative positions of these two zones with regard to the zone of extinction and the zone of invasion, four spatial dynamics were identified : extinction and invasion traveling waves, extinction pulse waves and heterogeneous stationary positive solutions of the Turing type.

### 4.2 Biological interpretation of the main results

We have shown that an increase in  $E$  increases the potential of extinction while an increase in  $h$  increases the potential of invasion. This translates the fact that a highly effective predator does have a high encounter rate and a small handling time. Furthermore, since  $h^+$  is an increasing

function of  $\alpha$ , an increase in  $\alpha$  decreases the potential of invasion and increases the size of the transition zone, which in turn increases the potential for the system to have complex dynamics. Finally, an increase of the diffusion rate  $d$  and a decrease of the amplitude of the predators growth rate  $r$  both increase the potential of invasion of prey. Thus, a generalist predator loses its effectiveness to exterminate invasive prey if it diffuses too fast or if it has a too slow dynamics.

The above results are stated in term of adimensionalized parameters (see section 2.1). By choosing the appropriate spatio-temporal variables, we may define  $D_u = r_1 = 1$ . Thus, the biological interpretations of  $d$  and  $r$  are accurate. Conversely, the definitions of the searching efficiency,  $E = EK_2$ , the handling time  $h = h \frac{K_1}{K_2}$  and the conversion rate  $\alpha = \frac{\gamma}{r}$  complicate the biological interpretation of this three parameters. Thus, in addition to the above discussion about the influence of  $E$  and  $h$ , we now discuss our results in terms of the other biological variables :  $K_1$ ,  $K_2$ ,  $\gamma$  and  $r$ . The parameter  $h$  being increasing in the carrying capacity  $K_1$  of prey, prey with high carrying capacity show a high risk of being invasive. Conversely,  $h$  and  $E$  are respectively decreasing and increasing in the carrying capacity of predators  $K_2$ . Thus, predators with high carrying capacity have a high potential to control prey invasion. Otherwise  $\gamma < 1$  means that predators growth is mostly due to alternative prey while  $\gamma > 1$  implies that predators growth is due to consumption of the focal prey. Finally, an increase in  $\gamma$  and a decrease in the amplitude of the predators growth rate  $r$  yield an increase of  $\alpha$ . Therefore, predators with a preference for focal prey or predator with a slow dynamics potentially lead to a high potential of complex dynamics. In particular, the likelihood of the system to exhibit a pulse wave is then important.

### 4.3 The consideration of space often, but not always, increases the potential for control of pest invasion

The model analyzed here was studied without taking space into account, except for a numerical exploration in the discussion, in an article by [Magal et al. (2008)]. As explained in the introduction, models of identical structure have been proposed independently by [Fagan et al. (2002)] and [Chakraborty (2015)]. We will now discuss our results in the context of these previous studies. Adding a spatial component to predator-prey systems makes any prediction about the controllability of the system difficult, as it then depends on the values of several parameters. The comparison between situations with and without the consideration of space is epitomized by the distinction between  $h^*$ , separating parameter regions of mono- and bistability in the ODE system, and  $h_{crit}$ , separating parameter regions of invasion and extinction in the PDE system. We will now focus on the case of  $E > 1$ , as values of  $E < 1$  do not promote control, predators encountering prey too infrequently.

If space is not taken into account, control occurs if  $h < h^*$ , as 0 is a global attractor. This is still true in situations in which space is taken into account, if  $h < h_1$  where  $h_1$  is smaller than  $h^*$ . When  $h$  is between  $h_1$  and  $h^*$ , 0 is only a local attractor, so it is not possible to state that control is always attained. In this respect, adding consideration of space decreases the potential for control. Furthermore, when space is not taken into account, there is either extinction or invasion when  $h > h^*(E, \alpha)$ , depending on initial conditions. Incorporating consideration of space changes the invasion region into  $h > h^+(E, \alpha)$ , with  $h^+ > h^*$ . Thus, the consideration of space reduces the size of the invasion zone and is detrimental to the invading prey. Finally, the relative levels of predator and prey diffusion also determine the potential for control. Our model shows that control is increased by predators being less mobile than prey. If predator mobility levels are too high, the predators become too thinly spread on the ground. For similar reasons, too high a level of prey mobility leaves the prey vulnerable to predators. This is entirely consistent with the experimental findings of [Fagan et al. (2002)]. In conclusion, taking space into account can lead to an increase or a decrease in the controllability of invading prey by predators; the addition of space to the model has no generic implication for considerations of predator-prey dynamics (see also [Lam & Ni (2012), Braverman et al. (2015)]).

## 4.4 How can generalist predators reverse invasion by pest ?

The originality of this study lies in its consideration of a generalist predator in a spatial context. When studying generalist predators, it is common practice to assume that the functional response is of type III, due to switching between prey species ([Erbach et al. (2014), van Leuven et al. (2007), van Leuven et al. (2013), Morozov & Petrovskii (2013)]). However, this approach is not mandatory, and other works ([Basnet & Mukhopadhyay (2014), Krivan & Eisner (2006), Hoyle & Bowers (2007)]) have considered a type II functional response. Altering our model to include a type III functional response would be very costly in terms of understanding, because such responses lead to a loss of bistability. Its derivative would be null without prey, so some of our demonstration would fail and the analytical complexity would be greatly increased. However, traveling waves for *specialist* predator with type III functional response is known to exist ([Li & Wu (2008)]) which indicates that our result may be extended to this case.

The complexity of analytical studies of spatial predator-prey interactions lies in the reaction terms being of alternative signs in the equations, making the study of the *systems* of equations essential ([Dunbar (1984b), Huang et al. (2003), Huang & Weng (2013)]). Other interactions, such as competition of two species (all negative) and symbiosis (all positive), are simpler, as their studies are similar to the study of a single equation ([Volpert et al. (1994), Alzahrani et al. (2012)]). This accounts for the slow scientific progress in this otherwise highly relevant topic. However, several major results have been obtained in recent decades, including those of the fundamental work of [Owen & Lewis (2001)]. The finding of Owen and Lewis that predators can slow, stop, and even reverse invasion by their prey was based on the bistability of the prey-only dynamics of systems consisting of specialist predators attacking prey populations displaying Allee effects. By contrast, our work shows that the ability of generalist predators to control prey populations with logistic growth lies in the bistable dynamics of the *coupled* system. We also observe pseudo-Allee effects in our system, but their physics is quite different. An analysis of the ODE system identified parameter regions of monostable (extinction) and bistable (extinction or invasion) dynamics, but analysis of the associated PDE was able to distinguish different and additional regions of invasion and extinction. As a consequence, prey control was predicted to be possible when space was considered in additional situations other than those identified without considering space. The reverse situation was also possible. None of these considerations apply to spatial predator-prey systems with specialist natural enemies.

## 5 Proofs

### 5.1 Proof of Theorem 2.1

Let  $E > 1$  and assume that there exists a positive solution  $(u, v)$ . Therefore, one gets

$$v = \frac{1}{E}(1 - u)(1 + Ehu) := f(E, h, u)$$

and

$$v = 1 + \alpha \frac{Eu}{1 + Ehu} := g(E, h, \alpha, u).$$

It follows that there exist a positive solution if and only if  $f(E, h, u) = g(E, h, \alpha, u)$  for some  $u \in [0, 1]$ . Since  $E > 1$ , one gets  $f(E, h, 0) = \frac{1}{E} < g(E, h, \alpha, 0) = 1$ . Moreover, since  $g$  is increasing in  $u$  and  $f$  is a parabola, it is necessary for a solution to exist that  $\frac{\partial f}{\partial u}(E, h, 0) > 0$  which reads  $h > \frac{1}{E}$  (see the figure 9).

Define  $H(E, h, \alpha, u) = g(E, h, \alpha, u) - f(E, h, u)$ . There exists a positive solution if and only if  $\min_{u \in [0, 1]} (H(E, h, \alpha, u)) < 0$ .

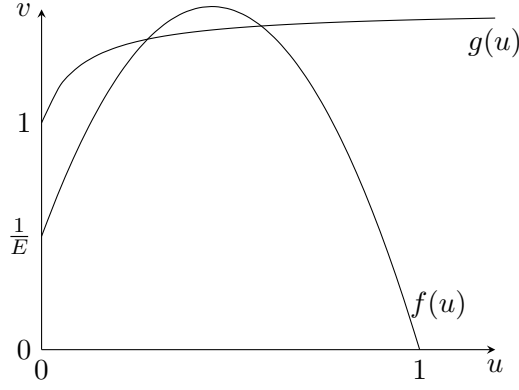


FIGURE 9: with  $E = 2$ ,  $h = 5$ ,  $\alpha = 0.1$

Since  $H(E, h, \alpha, 0) > 0$  and  $H(E, h, \alpha, 1) > 0$ , for positive solution to exist, it is necessary that there exists (at least one)  $u^* \in ]0, 1[$  such that  $u^*$  is a local minima of the map  $H : u \mapsto H(E, h, \alpha, u)$ . The following lemma give a precise condition on  $h$  for such a local minima does exist.

**Lemma 5.1.** *Let  $E > 1$  and  $\alpha \geq 0$  be fixed and define*

$$\bar{h} = \frac{1}{E}(\alpha E^2 + 1) \text{ and } \underline{h} = \begin{cases} \bar{h} & \text{if } \alpha E^2 \leq 1 \\ \frac{1}{E} \left( 3\sqrt[3]{\alpha E^2} - 1 \right) & \text{if } \alpha E^2 > 1 \end{cases}.$$

*If  $0 \leq h < \underline{h}$  then  $H$  is increasing on  $(0, 1)$ .*

*If  $h > \bar{h}$  then there exists  $u^*(h) \in (0, 1)$  such that  $H$  is decreasing on  $(0, u^*(h))$  and increasing on  $(u^*(h), 1)$ .*

*If  $\underline{h} < h < \bar{h}$  then there exists  $u^*(h) \in (0, 1)$  and  $\hat{u}(h) \in (0, u^*(h))$  such that  $H$  is increasing on  $(0, \hat{u}(h)) \cup (u^*(h), 1)$  and decreasing on  $(\hat{u}(h), u^*(h))$ .*

**Proof of lemma 5.1 :** Let  $E > 1$  and  $\alpha \geq 0$  being fixed. For simplicity of notation, we do not explicitly write the dependence of the following functions in this two variables.

If  $u^*$  exists, one has  $\partial_u H(h, u^*) = 0$  that is  $\partial_u f(h, u^*) = \partial_u g(h, u^*)$ . One gets  $\partial_u f(h, u) = \frac{1}{E}(-2Ehu + Eh - 1)$  and  $\partial_u g(h, u) = \alpha \frac{E}{(1+Ehu)^2}$  so that

$\partial_u f(h, 0) = \frac{Eh-1}{E}$  and  $\partial_u g(h, 0) = \alpha E$  does not depend on  $h$ . By convexity of  $u \mapsto \partial_u g(h, u)$  two cases are possible (see figure 10).

- Either  $\partial_u f(h, 0) \geq \partial_u g(h, 0)$  and there is exactly one intersection point  $u^*$
- or  $\partial_u f(h, 0) < \partial_u g(h, 0)$ . In this second case, there is either no solution or two solution  $u_1 < u_2$ , where  $u_1$  is a local maxima of  $u \mapsto H(h, u)$  and  $u_2 = u^*$  a local minima of  $u \mapsto H(h, u)$ .

For any  $u \in [0, 1/2[$ , the map  $h \mapsto \partial_u f(E, h, u)$  is increasing while the map  $h \mapsto \partial_u g(E, \alpha, h, u)$  is decreasing. It follows that for any  $u \in [0, 1/2[$ , there exists  $\underline{h}(u)$  such that for all  $h < \underline{h}(u)$  one gets  $g'(u) > f'(u)$  and for all  $h > \underline{h}(u)$  one gets  $g'(u) < f'(u)$ . Denote  $\underline{h} = \inf_u \underline{h}(u)$ . Therefore, for any  $h < \underline{h}$  one has  $g'(u) < f'(u)$  for each  $u$ , and for any  $h > \underline{h}$  there is exactly one local minima  $u^*$  of  $H$  in  $]0, 1[$ . The map  $u^* : [\underline{h}, +\infty) \longrightarrow [0, 1[$   $h \mapsto u^*(h)$  is clearly continuously differentiable.

The value  $\underline{h}$  depends on  $E$  and  $\alpha$  and may be computed explicitly

- If  $\alpha E^2 \leq 1$ , one gets  $-2hE := f''(0) \leq g''(0) := -2\alpha Eh$ , so the curves meet at  $u^*(\underline{h}) = 0$  for the value  $\underline{h} = \frac{1}{E}(\alpha E^2 + 1)$ .

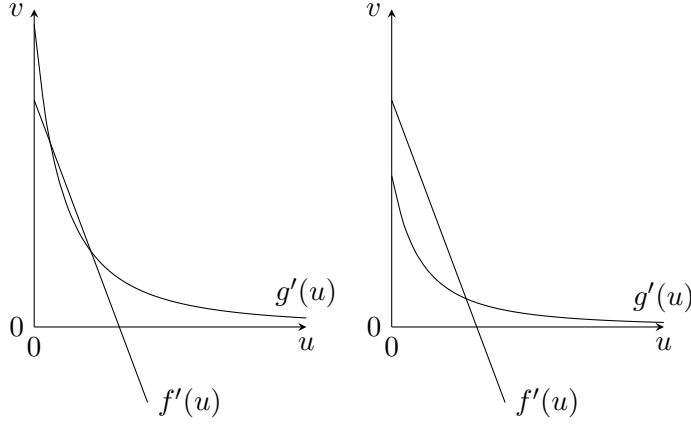


FIGURE 10: First :  $f'(0) < g'(0)$ . Second :  $f'(0) > g'(0)$

- If  $\alpha E^2 > 1$ , one gets  $-2hE := f''(0) > g''(0) := -2\alpha E^2 h$ , so the curves meet at some  $u^* > 0$ . At this point, one gets  $H'(u^*) = H''(u^*) = 0$ . from  $H''(u^*) = 0$  one deduce  $(1 + Ehu^*)^3 = \alpha E^2$  and plugging this into  $H'(u^*) = 0$ , one gets  $\underline{h} = \frac{1}{E} \left( 3\sqrt[3]{\alpha E^2} - 1 \right)$  and we deduce  $u^*(\underline{h}) = \frac{\sqrt[3]{\alpha E^2} - 1}{3\sqrt[3]{\alpha E^2} - 1}$ .

This end the proof of the lemma.  $\square$

**Proof of the Existence** For now,  $E > 1$  and  $\alpha \geq 0$  being fixed, the lemma 5.1 allows to define the  $C^1$  map

$$\begin{aligned} m_{E,\alpha} : [\underline{h}, +\infty) &\rightarrow [0, 1[ \\ h &\mapsto m_{E,\alpha}(h) = H(E, \alpha, u^*(h)). \end{aligned} \quad (8)$$

One gets  $m_{E,\alpha}(\underline{h}) > 0$  and  $m_{E,\alpha}(+\infty) = -\infty$ . Moreover, for each  $h > \underline{h}$ , one gets

$$\frac{d}{dh} m_{E,\alpha}(h) = \frac{\partial u^*}{\partial h}(h) \cdot \frac{\partial H}{\partial u}(E, h, \alpha, u^*) + \frac{\partial H}{\partial h}(E, h, \alpha, u^*).$$

By definition of  $u^*$ , one have  $\partial_u H(E, h, \alpha, u^*) = 0$  which leads to

$$\frac{d}{dh} m_{E,\alpha}(h) = \frac{\partial H}{\partial h}(E, h, \alpha, u^*) = -\frac{\alpha(Eu^*)^2}{(1 + Ehu^*)^2} - u^*(1 - u^*) < 0 \quad (9)$$

It follows that  $m_{E,\alpha}$  is decreasing so there exists a unique  $h^* := h^*(E, \alpha)$  such that  $m_{E,\alpha}(h^*) = 0$  and  $m_{E,\alpha}(h) < 0$  if and only if  $h > h^*$ .  $\square$

**Proof of the stability** Let  $H(E, h, \alpha, u) = g(E, h, \alpha, u) - f(E, h, u) := H(u)$ . Take  $E > 1$  and  $h > h^*(E, \alpha)$ . From the lemma 5.1, one knows that there exists  $u^* \in (0, 1)$  such that  $u \mapsto H(u)$  decreases on  $(0, u^*)$  and increases on  $(u^*, 1)$  and is negative at  $u^*$ . It follows that there exists two solutions  $u_1 < u^* < u_2$  and moreover  $\partial_u g(u_1) < \partial_u f(u_1)$  and  $\partial_u g(u_2) > \partial_u f(u_2)$ .

Define  $\Theta(u) = \frac{Eu}{1 + Ehu}$ . The system reads

$$\begin{cases} \frac{d}{dt} u = \Theta(u)(f(u) - v) \\ \frac{d}{dt} v = rv(g(u) - v). \end{cases}$$

Therefore, the Jacobien at a positive steady-state  $(u_i, v_i)$  reads

$$J(u_i, v_i) = \begin{bmatrix} \Theta(u_i)f'(u_i) & -\Theta(u_i) \\ rv_i g'(u_i) & -rv_i \end{bmatrix}.$$

One gets  $\det(J(u_i, v_i)) = r\Theta(u_i)v_i(g'(u_i) - f'(u_i))$ .

On a first hand, from  $g'(u_1) < f'(u_1)$ , it follows that  $\det(J(u_1, v_1)) < 0$  thus  $(u_1, v_1)$  is always unstable.

On the other hand, since  $g'(u_2) > f'(u_2)$ , the stability of  $(u_2, v_2)$  depends on the sign of the trace of the Jacobian  $T = \Theta(u_2)f'(u_2) - rv_2$ .

If  $f'(u_2) \leq 0$ , then  $T < 0$  and  $(u_2, v_2)$  is stable. This happens exactly when  $u_2 > \operatorname{argmax} f(u) = \frac{Eh-1}{2Eh} := u^{**}$ .

Now, define  $h^{**}(E, \alpha)$  the only solution of  $H(E, \alpha, h^{**}, u^{**}) = 0$ . One gets clearly  $h^{**} > h^*$ .

If  $h \in (h^*, h^{**})$  then  $u_2 \in (0, \frac{Eh-1}{2Eh})$  and  $f'(u_2) > 0$ . Therefore, using  $v_2 = f(u_2)$ , one obtains

— The steady state  $(u_2, v_2)$  is stable if  $T > 0$  that is if

$$r > \frac{\Theta(u_2)f'(u_2)}{f(u_2)}$$

— The steady state  $(u_2, v_2)$  is unstable if  $T < 0$  that is if

$$r < \frac{\Theta(u_2)f'(u_2)}{f(u_2)} \leq 1$$

Note that it can be show that  $h^{**} - h^*$  is a (positive) decreasing function of  $E$  going to 0 as  $E \rightarrow +\infty$  and that  $h^{**}(1, \alpha) - h^*(1, \alpha)$  is maximum for  $\alpha = 3/4$  and take the value  $h^{**}(1, 3/4) - h^*(1, 3/4) = 1/4$ . Therefore  $h^{**} - h^* \in [0, 1/4]$ .

## Proofs of properties 2.2

— **Growth of  $E \mapsto h^*(E, \alpha)$  and  $\alpha \mapsto h^*(E, \alpha)$ .**

Recall that the function  $h^*(E, \alpha)$  is characterized by

$$m_{E,\alpha}(h^*(E, \alpha)) = 0. \quad (10)$$

where  $m_{E,\alpha}$  is defined in (8).

By the implicit function theorem, the fact that  $(E, \alpha) \mapsto m_{E,\alpha}(h)$  is a  $C^1$  function implies that  $(E, \alpha) \mapsto h^*(E, \alpha)$  is a  $C^1$  function. Derivating (10) with respect to  $E$  gives

$$\partial_E h^*(E, \alpha) \cdot \partial_h m_{E,\alpha}(h^*(E, \alpha)) + \partial_E m_{E,\alpha}(h^*(E, \alpha)) = 0. \quad (11)$$

One a first hand, by (9) one knows that  $\partial_h m_{E,\alpha}(h^*(E, \alpha)) < 0$ . On an other hand, recall that the definition of  $m_{E,\alpha}$  reads  $m_{E,\alpha}(h) = H(E, h, \alpha, u^*(E, h, \alpha))$  and from  $\partial_u H(E, h, \alpha, u^*(E, h, \alpha)) = 0$  we deduce

$$\partial_E m_{E,\alpha}(h) = \partial_E H(E, h, \alpha, u^*(E, h, \alpha)).$$

A direct computation shows, for any  $u \in [0, 1]$ ,

$$\partial_E H(E, h, \alpha, u) = \frac{(1-u)}{E^2} + \alpha \frac{u}{(1+Ehu)^2} > 0.$$

And then, by (11), one obtains

$$\partial_E h^*(E, \alpha) > 0.$$

A similar computation shows that  $\partial_\alpha h^*(E, \alpha) > 0$ . □

— **Computation of  $\lim_{E \rightarrow 1} h^*(E, \alpha)$ .**

Recall that, for any  $E > 1$  and  $\alpha \geq 0$ ,  $h^*(E, \alpha)$  is characterized by the property that for any  $h > h^*(E, \alpha)$ , there exists two positive solutions of

$$f_{E,h,\alpha}(u) = g_{E,h,\alpha}(u) \quad (12)$$

where  $f_{E,h,\alpha}(u) = \frac{1}{E}(1-u)(1+Ehu)$  and  $g_{E,h,\alpha}(u) = 1 + \alpha \frac{Eu}{1+Ehu}$ . Define the polynome

$$P_{E,h,\alpha}(u) = \frac{1}{E}(1-u)(1+Ehu)^2 - (1+Ehu) - \alpha Eu.$$

It follows that  $h^*(E, \alpha)$  is characterized by the minimal value of  $h$  such that  $P_{E,h,\alpha}$  admits a nonnegative roots  $u^* = u^*(E, \alpha)$  of multiplicity (at least) two, that is

$$P_{E,h,\alpha}(u^*) = P'_{E,h,\alpha}(u^*) = 0. \quad (13)$$

Since  $h^*(\cdot, \alpha)$  is increasing and positive on  $(1, +\infty)$ , there exists a nonnegative scalar  $h^*(\alpha)$  such that  $h^*(E, \alpha) \rightarrow h^*(\alpha)$  as  $E \rightarrow 1$ . As  $E \rightarrow 1$ , one gets

$$P_{1,h,\alpha}(u) = u(h^2u^2 + h(2-h)u + \alpha + 1 - h).$$

It follows that  $h^*(\alpha)$  is the minimal value of  $h$  such that there exists  $u^* \geq 0$  verifying

$$P_{1,h,\alpha}(u^*) = P'_{1,h,\alpha}(u^*) = 0.$$

For  $h = 1 + \alpha$ ,  $u^* = 0$  is always a nonnegative double<sup>4</sup> root of  $P_{1,1+\alpha,\alpha}$ .

For  $h = 2\sqrt{\alpha}$ ,  $u^* = 1 - \frac{1}{\sqrt{\alpha}}$  is a double roots of  $P_{1,1+\alpha,\alpha}$  and is nonnegative if and only if  $\alpha \geq 1$ .

Since  $2\sqrt{\alpha} \leq 1 + \alpha$  for  $\alpha \geq 1$ , it follows that

$$h^*(\alpha) = \begin{cases} 1 + \alpha & \text{if } \alpha \leq 1 \\ 2\sqrt{\alpha} & \text{if } \alpha \geq 1. \end{cases} \quad (14)$$

Remark that  $h^*(\alpha)$  is a  $C^1$  function of  $\alpha$ . □

— **Computation of  $\lim_{E \rightarrow +\infty} h^*(E, \alpha)$ .**

Since  $h^*(\cdot, \alpha)$  is increasing, one has

$$\lim_{E \rightarrow +\infty} h^*(E, \alpha) = \frac{1}{\ell_\alpha}$$

for some nonnegative number  $\ell_\alpha$  (wherein we have note  $\frac{1}{0} = +\infty$ ).

On an other hand, since  $u^*(E, \alpha)$  is bounded, up to a subsequence again denoted by  $E$ , one has  $u^*(E, \alpha) \rightarrow u^*$  for some positive number  $u^*$  (eventually depending on  $\alpha$ ).

Divide (13) by  $E$  and passing to the limit  $E \rightarrow +\infty$  in the second equation lead to  $u^* = 1/2$  and the first equation gives

$$\frac{1}{\ell_\alpha^2} = \frac{2}{\ell_\alpha} + 2\alpha$$

so that ( $\ell_\alpha$  being nonnegative)

$$\frac{1}{\ell_\alpha} = 2 + 2\sqrt{1 + \alpha};$$

□

---

4. Indeed, for  $\alpha = 1$ , 0 is a triple roots of  $P_{1,2,1}$ .

— **Computation of  $h^*(E, 0)$ .**

If  $\alpha = 0$  then, one gets

$$P_{E,h,0}(u) = \frac{1}{E}(1 + Ehu) (-Ehu^2 + u(Eh - 1) + 1 - E).$$

It can be proven (see step 2 of section 5.2) that  $P_{E,h,0}$  admits a nonnegative roots if and only if  $h > \frac{1}{E}(2E - 1 + \sqrt{E(E - 1)}) := h_1(E)$  which shows that  $h^*(E, 0) = h_1(E)$ .  $\square$

— **Computation of  $\lim_{\alpha \rightarrow +\infty} h^*(E, \alpha)$ .**

Since  $E \mapsto h^*(E, \alpha)$  is increasing one gets for any  $E \geq 1$ ,  $h^*(E, \alpha) \geq h^*(\alpha)$ . The explicit expression (14) of  $h^*(\alpha)$  shows that

$$\lim_{\alpha \rightarrow +\infty} h^*(E, \alpha) = +\infty.$$

$\square$

## 5.2 Proof of the Theorem 2.3.

Let  $E > 1$  be fixed and  $(u(t, x), v(t, x))$  be a solution to (5) with initial condition  $(u_0(x), v_0(x))$  verifying (6).

The proof is done in two steps. Firstly, one shows that  $0 \leq u(t, x) \leq \phi(t)$  for some function  $\phi(t)$  verifying an *ordinary differential equation* depending on  $E$  and  $h$ .

Secondly, one shows that  $\lim_{t \rightarrow +\infty} \phi(t) = 0$  if and only if  $h < h_1(E)$  where  $h_1(E)$  is an (explicit) positive valued function of  $E$ .

**Step 1.** Let  $(u, v)(t, x)$  be a solution of (5). It is clear that  $u(t, x) \geq 0$  for any  $t > 0$  which implies

$$\partial_t v(t, x) - d\Delta v(t, x) \geq rv(t, x)(1 - v(t, x)) \quad t > 0, \quad x \in \mathbb{R}.$$

From this, using the comparison principle, we deduce that  $v(t, x) \geq 1$  for any  $t \geq 0$  and  $x \in \mathbb{R}$ . It follows that

$$\partial_t u(t, x) - \Delta u(t, x) \leq u(t, x)(1 - u(t, x)) - \frac{Eu(t, x)}{1 + Ehu(t, x)} \quad t > 0, \quad x \in \mathbb{R}.$$

By the comparison principle, any solution  $\bar{u}$  of

$$\partial_t \bar{u}(t, x) - \Delta \bar{u}(t, x) = \bar{u}(t, x)(1 - \bar{u}(t, x)) - \frac{E\bar{u}(t, x)}{1 + Eh\bar{u}(t, x)}, \quad t > 0, \quad x \in \mathbb{R} \quad (15)$$

verifying  $\bar{u}(0, x) \geq u_0(x)$  for any  $x \in \mathbb{R}$  satisfies

$$\forall t > 0, \quad \forall x \in \mathbb{R}, \quad u(t, x) \leq \bar{u}(t, x).$$

Now let  $\phi(t)$  be the solution of the ordinary differential equation

$$\frac{d}{dt} \phi(t) = \phi(t)(1 - \phi(t)) - \frac{E\phi(t)}{1 + Eh\phi(t)}, \quad t > 0 \quad (16)$$

satisfying  $\phi(0) = 1$ .

Clearly,  $\phi$  is a homogeneous solution of (15) and from  $u(0, x) \leq 1 = \phi(0)$  one deduces by the comparison principle

$$\forall t > 0, \quad \forall x \in \mathbb{R}, \quad 0 \leq u(t, x) \leq \phi(t).$$



**Step 2.** Let us study the equation (16). It is clear that  $\phi = 0$  is always a stationary solution of this equation and is asymptotically stable for  $E > 1$ .

Now, let  $\phi_0 > 0$  be a positive steady state of (16). One has

$$(1 - \phi_0) - \frac{E}{1 + Eh\phi_0} = 0.$$

Therefore

$$Eh\phi_0^2 + (1 - Eh)\phi_0 + E - 1 = 0$$

This equation has two real solutions  $u^-(E, h) \leq u^+(E, h)$  if and only if

$$\Delta = (1 - Eh)^2 - 4(E - 1)Eh \geq 0. \quad (17)$$

Define

$$h_0 := \frac{1}{E} \left( 2E - 1 - 2\sqrt{E(E - 1)} \right) \text{ and } h_1 := \frac{1}{E} \left( 2E - 1 + 2\sqrt{E(E - 1)} \right).$$

One verifies that  $0 < h_0 < h_1$  and the inequality (17) holds true iff

$$h \in (0, h_0] \cup [h_1, +\infty)$$

and in that case, one has two solutions

$$u^-(E, h) = \frac{Eh - 1 - \sqrt{(1 - Eh)^2 - 4(E - 1)Eh}}{2Eh} \text{ and } u^+(E, h) = \frac{Eh - 1 + \sqrt{(1 - Eh)^2 - 4(E - 1)Eh}}{2Eh}.$$

since  $E - 1 > 0$ ,  $u^-(E, h)$  and  $u^+(E, h)$  have the same sign. Finally, if  $h \leq h_0$  then  $u^-(E, h) \leq u^+(E, h) < 0$  and (16) has no positive stationary solution. and, if  $h \geq h_1$  then  $0 < u^- \leq u^+$  and (16) has two positive stationary solutions.

A linear analysis shows that  $u^-$  is unstable and  $u^+$  is (asymptotically) stable.

Indeed, one may shows that  $\phi(t) \rightarrow u^+(E, h)$  if  $h > h_1(E)$  and  $\phi(t) \rightarrow 0$  when  $h < h_1(E)$  which end the proof of the theorem.  $\square$

### 5.3 Proof of the Theorem 2.4.

Let  $E > 1$  be fixed and  $(u(t, x), v(t, x))$  be a solution to (5) with initial condition  $(u_0(x), v_0(x))$  verifying (6).

By the argument of the proof 5.2, one already knows that

$$u(t, x) \leq \bar{u}(t, x)$$

where  $\bar{u}(t, x)$  is a solution of (15) with  $\bar{u}(0, x) = u_0(x)$ . One also known that, if  $h > h_1(E)$  then the equation (15) is *bistable* since it admits two stable nonnegative stationary solutions  $u = 0$  and  $u = u^+(E, h) < 1$ .

Now, we show that, in that case, there exists a traveling waves connecting 0 to  $u^+$  at a negative speed if and only if  $h < h^-(E)$  for some (implicit) number  $h^-(E) > h_1(E)$ .

This will implies that for any  $x \in \mathbb{R}$ ,  $\bar{u}(t, x) \rightarrow 0$  if  $h < h^-(E)$  which proves the theorem.

Fixe  $h > h_1(E)$ . It can be proven (see [Fife (1979)], [Volpert et al. (1994)] and the reference therein) that there exists a (stable) traveling wave of speed  $c = c(h, E)$  joining  $u^+$  to 0, says  $U(x - ct) = u(x, t)$  with  $U(-\infty) = u^+$ ,  $U(+\infty) = 0$  and  $U'(\pm\infty) = 0$ . Moreover (see [Fife (1979)])

this traveling wave describes the asymptotic behavior of all solutions provided the initial condition (6) are verified.

It follows that there is extinction of prey for equation (15) if  $c < 0$  and the prey is invasive for equation (15) if  $c > 0$ .

The theorem will be proved by showing that there exists  $h^-(E)$  such that  $c(E, h) < 0$  when  $h < h^-(E)$  and  $c(E, h) > 0$  when  $h > h^-(E)$ . This result is obtained by the two following lemma which are proven below. The first lemma give a carактерisation of the sign of  $c$  by an explicit function (see figure 11).

**Lemma 5.2.** *Define*

$$W(E, h, u) = \int_0^u \left( s(1-s) - \frac{Es}{1+Ehs} \right) ds.$$

Then  $\text{sign}(c(E, h)) = \text{sign}(W(E, h, u^+))$  where  $u^+ := u^+(E, h)$ .

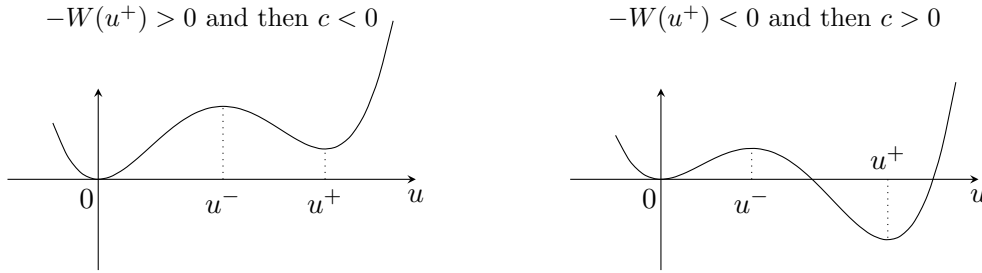


FIGURE 11: Figure of  $u \mapsto -W(E, h, u)$ . The steady states 0,  $u^-$  and  $u^+$  correspondent to critical points of the potential  $-W$ . A stable solution is a local minima of  $W$  and an unstable one is a local maxima.

One see that 0 and  $u^+$  are two stable steady states, the sign of  $c$  says which of them is the final global attractor : if  $c < 0$  then 0 is the global attractor while if  $c > 0$  then  $u^+$  is the global attractor.

Roughly speaking, the deeper the potential well of a stable solution is, the more stable the solution is. Hence, the final global attractor correspond to the deeper potential well.

The second lemma gives finally the existence of the searching number  $h^-(E)$ .

**Lemma 5.3.** *For any  $E > 1$ , there exists (an unique)  $h^-(E) > h_1(E)$  such that*

$$\text{sign}(W(E, h, u^+(E, h))) = \text{sign}(h - h^-(E)).$$

Now, lemma 5.2 and 5.3 show that

- There is invasion of prey for (15) ( $c > 0$ ) if  $h \in (h^-(E), +\infty)$ .
- There is extinction of prey for (15) ( $c < 0$ ) if  $h \in [h_1(E), h^-(E))$ .
- There is a uniform extinction of prey for (15) if  $h < h_1(E)$ .

Since the solution of (15) control the real solution of (5), the theorem is proven.  $\square$

It remains to prove the lemma 5.2 and 5.3.

**Proof of lemma 5.2.** Denote  $c = c(E, h)$  and let  $Z = x - ct$  and  $U(Z) = u(x, t)$  with  $U(-\infty) = u^+$ ,  $U(+\infty) = 0$  and  $U'(\pm\infty) = 0$ . It comes

$$-cU' = U'' + U(1-U) - \frac{EU}{1+EU} = U'' + \frac{\partial W}{\partial U}(E, h, U).$$

Multiplying by  $U'$  and integrating over  $\mathbb{R}$  one gets

$$\begin{aligned} -c \int_{-\infty}^{+\infty} (U')^2 dZ &= \int_{-\infty}^{+\infty} \left( U(1-U) - \frac{EU}{1+UhU} \right) U' dZ \\ &= \int_{u^+}^0 \frac{\partial W}{\partial U}(E, h, U) dU = -W(E, h, u^+) \end{aligned}$$

and  $\text{sign}(c) = \text{sign}(W(E, h, u^+(E, h)))$  follows.  $\square$

**Proof of lemma 5.3.** Define  $H(E, h) = W(E, h, u^+(E, h))$ . The previous lemma shows that  $\text{sign}(c) = \text{sign}(H(E, h))$ . Now, we show that there exists  $h^-(E) > h_1(E)$  such that  $\text{sign}(H(E, h)) = \text{sign}(h - h^-(E))$ .

Derivating  $H$  with respect to  $h$  gives

$$\partial_h H(E, h) = \partial_h W(E, h, u^+(E, h)) + \partial_u W(E, h, u^+(E, h)) \partial_h u^+(E, h).$$

By the very definition of  $W$  and  $u^+$ , one has

$$\partial_u W(E, h, u^+(E, h)) = 0$$

and it follows

$$\partial_h H(E, h) = \partial_h W(E, h, u^+(E, h)).$$

Explicit calculations show that

$$W(E, h, u) = \frac{u^2}{2} - \frac{u^3}{3} - \frac{u}{h} + \frac{1}{Eh^2} \ln(1 + Ehu).$$

Derivating this expression with respect to  $h$  and denoting  $x = Ehu^+(E, h)$ , it comes

$$\partial_h W(E, h, u^+(E, h)) = \frac{1}{Eh^3} \left( x - 2 \ln(1+x) + \frac{x}{1+x} \right).$$

A standard analysis shows that the map  $x \mapsto x - 2 \ln(1+x) + \frac{x}{1+x}$  takes positive values for  $x > 0$  from which we deduce that  $H(E, \cdot)$  is an increasing function. One verifies that  $u^+(E, h) \rightarrow 1$  as  $h \rightarrow +\infty$  and therefore  $H(E, +\infty) = 1/2 - 1/3 = 1/6 > 0$ .

It remains to show that  $H(E, h_1(E)) = W(E, h_1(E), u^+(E, h_1(E))) := g(E)$  is negative for any  $E > 1$ .

First, remark that the explicit expression of  $u^+(E, h)$  together with the fact that

$$h_1(E) = \frac{1}{E} \left( 2E - 1 + 2\sqrt{E(E-1)} \right)$$

is such that  $\Delta = 0$  in (17), implies

$$u^+(E, h_1(E)) = \frac{1}{2} \left( 1 - \frac{1}{Eh_1(E)} \right) = 1 - E + \sqrt{E(E-1)}.$$

On a first hand, we see that  $h_1(1) = 1$  and  $u^+(1, 1) = 0$  so that  $g(1) = 0$ .

On an other hand, one gets

$$g'(E) = \partial_E W(E, h_1(E), u^+(E, h_1(E))) + \partial_h W(E, h_1(E), u^+(E, h_1(E))) \cdot h_1'(E).$$

Straightforward calculations give

$$h'_1(E) = \frac{1}{E^2} \left( \sqrt{\frac{E}{E-1}} + 1 \right),$$

$$\partial_h W(E, h_1(E), u^+(E, h_1(E))) = \frac{1}{E(h_1(E))^3} \left( x + \frac{x}{1+x} - 2 \ln(1+x) \right).$$

Denote

$$x = E h_1(E) u^+(E, h_1(E)) = E - 1 + \sqrt{E(E-1)} = \sqrt{E-1} (\sqrt{E} + \sqrt{E-1}),$$

one verifies that  $\sqrt{\frac{E}{E-1}} = 1 + \frac{1}{x}$  and  $E h_1(E) = 2x + 1$  so that

$$\partial_h W(E, h_1(E), u^+(E, h_1(E))) \cdot h'_1(E) = \left( \frac{1}{E h_1(E)} \right)^2 \left( 1 + \frac{1}{1+x} - \frac{2}{x} \ln(1+x) \right).$$

Finally, one has

$$\partial_E W(E, h_1(E), u^+(E, h_1(E))) = \left( \frac{1}{E h_1(E)} \right)^2 \left( \frac{x}{1+x} - \ln(1+x) \right)$$

and it comes

$$g'(E) = \left( \frac{1}{E h_1(E)} \right)^2 \left[ 2 - \ln(1+x) \left( 1 + \frac{2}{x} \right) \right].$$

A standard analysis shows that  $2 \frac{x}{x+2} < \ln(1+x)$  for any  $x > 0$  and so  $g'(E) < 0$  for any  $E > 1$ .

It follows that  $g(E) < 0$  if  $E > 1$ .

Therefore  $H(E, \cdot)$  is an increasing function verifying  $H(E, +\infty) = 1/6$  and  $H(E, h_1(E)) < 0$ .

So, for any  $E > 1$ , there exists a unique  $h^- = h^-(E) \in (h_1(E), +\infty)$  such that  $\text{sign}(W(E, h, u^+)) = \text{sign}(h - h^-(E))$  which end the proof of the lemma.  $\square$

**Proofs of properties 2.5.** Let  $E > 1$  be fixed.

— **Growth of  $h^-(\cdot)$ .**

Recall that  $h^-(E)$  is characterize by

$$W(E, h^-(E), u^+(E, h^-(E))) = 0 \tag{18}$$

where

$$W(E, h, u) = \frac{u^2}{2} - \frac{u^3}{3} - \frac{u}{h} + \frac{1}{Eh} \ln(1 + Ehu)$$

and

$$u^+(E, h) = \frac{1}{2} \left( 1 - \frac{1}{Eh} + \sqrt{\left( 1 - \frac{1}{Eh} \right)^2 - 4 \frac{E-1}{Eh}} \right) > 0.$$

By definition of  $W$ , one has

$$\partial_u W(E, h^-(E), u^+(E, h^-(E))) = 0,$$

it comes

$$\partial_E W(E, h^-(E), u^+(E, h^-(E))) + \frac{dh^-}{dE}(E) \cdot \partial_h W(E, h^-(E), u^+(E, h^-(E))) = 0.$$

The explicit computation of  $\partial_E W$  and  $\partial_h W$  is done in the proof 5.3 and one gets

$$\partial_E W(E, h^-(E), u^+(E, h^-(E))) < 0 \text{ and } \partial_h W(E, h^-(E), u^+(E, h^-(E))) > 0$$

so that

$$\frac{dh^-}{dE}(E) = -\frac{\partial_E W(E, h^-(E), u^+(E, h^-(E)))}{\partial_h W(E, h^-(E), u^+(E, h^-(E)))} > 0$$

as needed. □

— **Limit of  $h^-(E)$  as  $E \rightarrow 1$ .**

Let  $E > 1$  and (re)define

$$u^-(E, h) = \frac{1}{2} \left( 1 - \frac{1}{Eh} - \sqrt{\left(1 - \frac{1}{Eh}\right)^2 - 4\frac{E-1}{Eh}} \right) > 0.$$

The necessary existence and positivity of  $u^\pm(E, h)$  implies (see the proof (5.2))

$$h^-(E) > h_1(E) := \frac{1}{E} \left( 2E - 1 + 2\sqrt{E(E-1)} \right).$$

On a first hand, since  $h^-(\cdot)$  is positive and increasing on  $(1, +\infty)$ ,  $h^-(E)$  admits a limit  $h^-$  as  $E \rightarrow 1$  and from  $h_1(1) = 1$  one obtains

$$h^- \geq 1$$

and then

$$u^-(1, h^-) = 0 \text{ and } u^+(1, h^-) = \frac{1 - h^-}{h^-}.$$

Assume that  $u^+(1, h^-) > 0$ . then, for any  $h \geq 1$  and  $0 < u < u^+(h, 1)$ ,

$$\partial_u W(1, h, u) = u(1 - u) - \frac{1}{1 + hu} > 0 \text{ and } W(1, h, 0) = 0.$$

which implies  $W(1, h^-, u^+(1, h^-)) < 0$ , a contradiction with the fact that  $h^-$  verifies  $W(1, h^-, u^+(1, h^-)) = 0$ .

It follows that  $u^+(1, h^-) = 0$  so  $h^- = 1$  which reads

$$\lim_{E \rightarrow 1} h^-(E) = 1.$$

□

— **Limit of  $h^-(E)$  as  $E \rightarrow +\infty$ .**

One knows that  $h^-(E)$  is increasing so that there is some  $\ell \geq 0$  such that  $\lim_{E \rightarrow +\infty} h^-(E) = \frac{1}{\ell}$  (wherein we have note  $\frac{1}{\infty} = 0$ ). Passing to the limits in the expression of  $u^+(E, h^-(E))$  gives

$$\lim_{E \rightarrow +\infty} u^+(E, h^-(E)) = u_\ell := \frac{1}{2}(1 + \sqrt{1 - 4\ell}) > 0.$$

and then, by passing to the limit in (18),

$$\frac{u_\ell^2}{2} - \frac{u_\ell^3}{3} - \frac{u_\ell}{\ell} = 0$$

from which one obtains

$$\sqrt{1 - 4\ell} = 8\ell - 1$$

so that

$$\ell = \frac{3}{16}$$

and finally

$$\lim_{E \rightarrow +\infty} h^-(E) = \frac{16}{3}.$$

## 5.4 Invasion conditions, proof of Theorem 2.6

Like in the proof 5.3, we start by showing that  $0 \leq \underline{u}(t, x) \leq u(t, x)$  for some function  $\underline{u}$  verifying a *scalar* reaction-diffusion equation (19) depending on  $E$ ,  $h$  and  $\alpha$ . Next, we show that there exists  $h^+(E, \alpha)$  such that  $\liminf_{t \rightarrow +\infty} \underline{u}(t, x) > 0$  when  $h > h^+(E, \alpha)$ . This step is done by using the proof of Theorem 2.4 together with an appropriate change of variable.

Finally, in the last step, we proof that the two maps  $h^+(E, \cdot)$  and  $h^+(\cdot, \alpha)$  are increasing.

**Step 1** Fixe  $E > 1$ . In general, using that  $0 \leq u \leq 1$ , one has  $1 \leq v \leq \bar{v}$  with

$$\bar{v} := \bar{v}(E, h, \alpha) = 1 + \alpha \frac{E}{1 + Eh}.$$

Now, using the estimate  $v \leq \bar{v}$ , one has  $\underline{u}(t, x) \leq u(t, x)$  where  $\underline{u}$  verifies the following equation

$$\partial_t u = \Delta_x u + u(1 - u) - \frac{E\bar{v}u}{1 + Eh} \quad t > 0, \quad x \in \mathbb{R}. \quad (19)$$

Denoting  $\tilde{E} = E\bar{v}$  and  $\tilde{h} = \frac{h}{\bar{v}}$ , this equation writes simply

$$\partial_t u = \Delta_x u + u(1 - u) - \frac{\tilde{E}u}{1 + \tilde{E}h} \quad t > 0, \quad x \in \mathbb{R}. \quad (20)$$

Remark that, removing the  $\tilde{\cdot}$ , this equation is nothing but (15). As a consequence, the proof of the theorem 2.4 implies the following result on (20).

**Lemma 5.4.** *Let  $\tilde{u}(t, x)$  be a solution of (20) verifying the initial condition (6). There exists  $h^-(\tilde{E}) > h_1(\tilde{E})$  such that*

- *if  $\tilde{h} < h^-(\tilde{E})$  then for any  $x \in \mathbb{R}$ ,  $\lim_{t \rightarrow +\infty} \tilde{u}(t, x) = 0$  (extinction),*
- *if  $\tilde{h} > h^-(\tilde{E})$  then for any  $x \in \mathbb{R}$ ,  $\limsup_{t \rightarrow +\infty} \tilde{u}(t, x) > 0$  (invasion).*

**Step 2.** Recall that  $\tilde{E} = E\bar{v}(E, h, \alpha)$  and  $\tilde{h} = \frac{h}{\bar{v}(E, h, \alpha)}$  do depend on  $h$ , the previous proposition gives the following implicit condition on  $h$  for invasion to occur :

There is invasion for (19) if

$$h > \bar{v}(E, h, \alpha)h^-(E\bar{v}(E, h, \alpha)). \quad (21)$$

The following lemma give an equivalent condition for this implicit condition to occur.

**Lemma 5.5.** *for any  $E > 1$  and  $\alpha \geq 0$ , there exists (an unique)  $h^+(E, \alpha) > h^-(E)$  such that (21) holds true if and only if  $h > h^+(E, \alpha)$ .*

**Proof of lemma 5.5 :** Let  $E > 1$  and  $\alpha \geq 0$  be fixed and define the function

$$f_{E, \alpha}(h) = h - \bar{v}(E, h, \alpha)h^-(E\bar{v}(E, h, \alpha)). \quad (22)$$

By the construction of  $h^-$  via the implicit function theorem, one knows that  $f_{E, \alpha}(\cdot)$  is a  $C^1$  function. Moreover, since  $h^-$  is bounded, one gets  $f_{E, \alpha}(+\infty) = +\infty$  and

$$f_{E, \alpha}(0) = -\bar{v}(E, 0, \alpha)h^-(E\bar{v}(E, 0, \alpha)) = -(1 + \alpha E)h^-(E(1 + \alpha E)) < 0.$$

Therefore, it suffices to show that  $f_{E, \alpha}$  is strictly increasing.

One has

$$f'_{E, \alpha}(h) = 1 - \partial_h \bar{v}(E, h, \alpha) \left( h^-(E\bar{v}) + \bar{v} \frac{\partial h^-}{\partial E} \right).$$

By the expression of  $\bar{v}$ , one has  $\partial_h \bar{v} < 0$  and one already known that  $\partial_E h^- > 0$ . It follows that  $f'_{E, \alpha}(h) > 0$  which end the proof of the theorem.  $\square$

**Proofs of properties 2.7.**

— **Proof of the growth of  $h^+(E, \cdot)$  and  $h^+(\cdot, \alpha)$ .**

$h^+(E, \alpha)$  is characterized by an equality in (21) that is,

$$f_{E,\alpha}(h^+(E, \alpha)) = 0 \quad (23)$$

where  $f_{E,\alpha}$  is defined in (22).

Differentiating (23) with respect to  $E$  gives

$$\partial_E h^+(E, \alpha) \cdot f'_{E,\alpha}(h^+(E, \alpha)) + \partial_E f_{E,\alpha}(h^+(E, \alpha)) = 0$$

and then

$$\partial_E h^+(E, \alpha) \cdot f'_{E,\alpha}(h^+(E, \alpha)) = [(E\bar{v} + h^-)\partial_E \bar{v} + \bar{v}^2] \cdot (h^-)'(E\bar{v}).$$

with the obvious notations

$$h^- = h^-(E\bar{v}(E, h^+(E, \alpha), \alpha)), \quad \bar{v} = \bar{v}(E, h^+(E, \alpha), \alpha) \text{ and } \partial_E \bar{v} = \partial_E \bar{v}(E, h^+(E, \alpha), \alpha).$$

One already knows that  $f'_{E,\alpha}(h^+(E, \alpha)) > 0$  and that  $(h^-)' > 0$ . A direct computation shows that  $\partial_E \bar{v} > 0$  which leads to  $\partial_E h^+(E, \alpha) > 0$  as needed.

Similarly, differentiating (23) with respect to  $\alpha$  gives, with the obvious notations,

$$\partial_\alpha h^+(E, \alpha) \cdot f'_{E,\alpha}(h^+(E, \alpha)) = \partial_\alpha \bar{v} \cdot (h^- + E(h^-)'),$$

and since  $\partial_\alpha \bar{v} > 0$ , one obtains  $\partial_\alpha h^+(E, \alpha) > 0$ .

— **Limit of  $h^+(E, \alpha)$  as  $\alpha \rightarrow 0$  and  $\alpha \rightarrow +\infty$ .**

From  $\bar{v}(E, h, 0) = 1$  we deduce  $h^+(E, 0) = h^-(E)$ .

Now, it is clear from the construction of  $h^+$  that  $h^+(E, \alpha) \geq h^*(E, \alpha)$  and from the properties 2.2 we obtain  $h^+(E, \alpha) \rightarrow +\infty$  as  $\alpha \rightarrow +\infty$ .  $\square$

— **Limit of  $h^+(E, \alpha)$  as  $E \rightarrow +\infty$ .**

First, recall that  $h^+(E, \alpha)$  is characterized by (23) which reads

$$h^+(E, \alpha) = \left(1 + \alpha \frac{E}{1 + Eh^+(E, \alpha)}\right) \cdot h^- \left(E + \alpha \frac{E^2}{1 + Eh^+(E, \alpha)}\right). \quad (24)$$

Since  $h^+(\cdot, \alpha)$  is increasing, there exists  $\ell_\alpha \geq 0$  such that

$$\lim_{E \rightarrow +\infty} h^+(E, \alpha) = \frac{1}{\ell_\alpha}.$$

Passing to the limit  $E \rightarrow +\infty$  in (24) and using that  $h^-(E) \rightarrow \frac{16}{3}$ , one obtains

$$\frac{1}{\ell_\alpha} = \frac{16}{3} \cdot (1 + \alpha \ell_\alpha)$$

therefore

$$\ell_\alpha = \frac{-1 + \sqrt{1 + \frac{3\alpha}{4}}}{2\alpha}$$

and finally

$$\lim_{E \rightarrow +\infty} h^+(E, \alpha) = \frac{8}{3} \left(1 + \sqrt{1 + \frac{3\alpha}{4}}\right).$$

$\square$

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