Propagation phenomena of fungal plant parasites, by coupling of spatial diffusion and sexual reproduction

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Phénomènes de propagation de champignons parasites de plantes, par couplage de diffusion spatiale et de reproduction sexuée

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Introduction

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1.1 Motivations biologiques

Cette introduction s'inspire des articles [HCD+16] et [RLW+17].

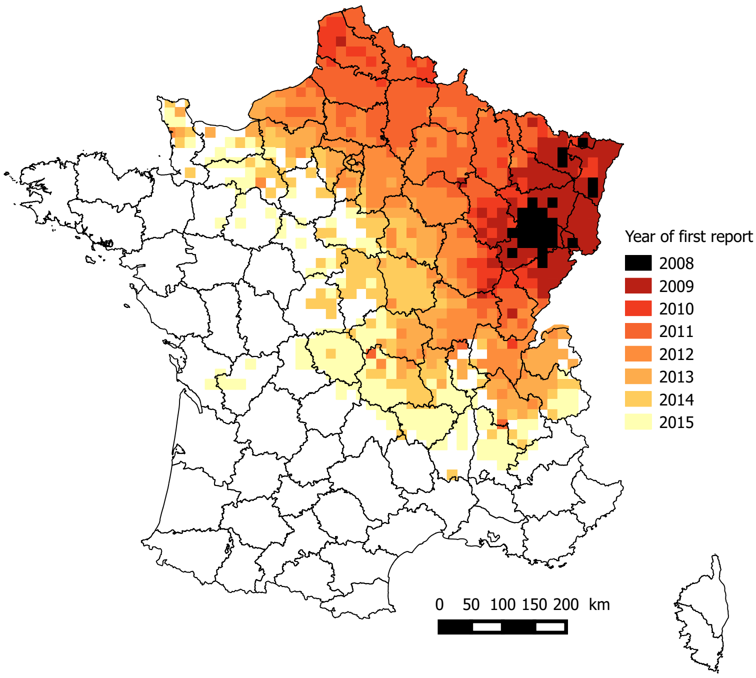
Les champignons parasites de plantes (phytopathogènes) représentent une menace croissante pour la sécurité alimentaire mondiale [P+10], [FHB+12], [RLW+17]. La plupart des champignons combinent la faculté de produire des spores infectieuses par voies sexuée et asexuée. Les épidémies sont ainsi propagées par deux types de spores à partir des mêmes hôtes. Les spores sexuées et asexuées[1] diffèrent généralement par leurs formes, leurs tailles, et par conséquent leurs capacités à se disperser. Les spores produites via reproduction sexuée ont souvent de plus grandes capacités de propagation en termes de dispersion et/ou de survie [Bon58], [Wil75]. Chez beaucoup d'espèces, la fusion effective des gamètes peut uniquement se produire entre individus haploïdes portant des allèles de types sexuels différents (+ et −). Ce phénomène se nomme *hétérothallisme* [BLVD+11]. Chez les champignons hétérothalliques haploïdes, la production de spores sexuées résulte alors obligatoirement de l'intéraction de deux individus de types sexuels compatibles (+ et −).

De nombreux champignons phytopathogènes, dont certains sont considérés comme des menaces majeures pour la sécurité alimentaire mondiale, sont hétérothalliques. L'exemple le plus connu concerne le mildiou de la pomme de terre, qui a été à l'origine de la Grande Famine de 1845 en Irlande et qui sévit encore aujourd'hui partout sur la planète [RP16]. Cette maladie est causée par *Phytophthora infestans*, un oomycète hétérothallique. Un autre exemple notable concerne la maladie sud-américaine des feuilles de l'hévéa, qui est historiquement connue pour avoir ruiné la production industrielle en latex de Ford au Brésil dans les années 1940. Cette maladie est causée par le champignon *Microcyclus ulei*, présumé hétérothallique [WFA+02]. Plus récemment, l'agent responsable de la chalarose du frêne, *Hymenoscyphus fraxineus*, est un champignon hétérothallique. Cette maladie mortelle du frêne envahit actuellement l'Europe à une vitesse de 75 km/an [GHP+14]. La figure 1.1 montre l'avancée du front de propagation de la maladie en France entre 2008 et 2012. Avec l'avènement des études génomiques, de plus en plus d'espèces auparavant classées comme asexuées sont à présent reconnues capables de reproduction

1. Dorénavant, on dénomme les spores produites par reproductions sexuée et asexuée comme des spores "sexuées" et "asexuées", ce qui constitue un petit abus de langage.

sexuée et dans certains cas possèdent des gènes d'hétérothallisme opérationnels [EB14].

Fig. 1.1 – *Propagation de la chalarose du frêne*



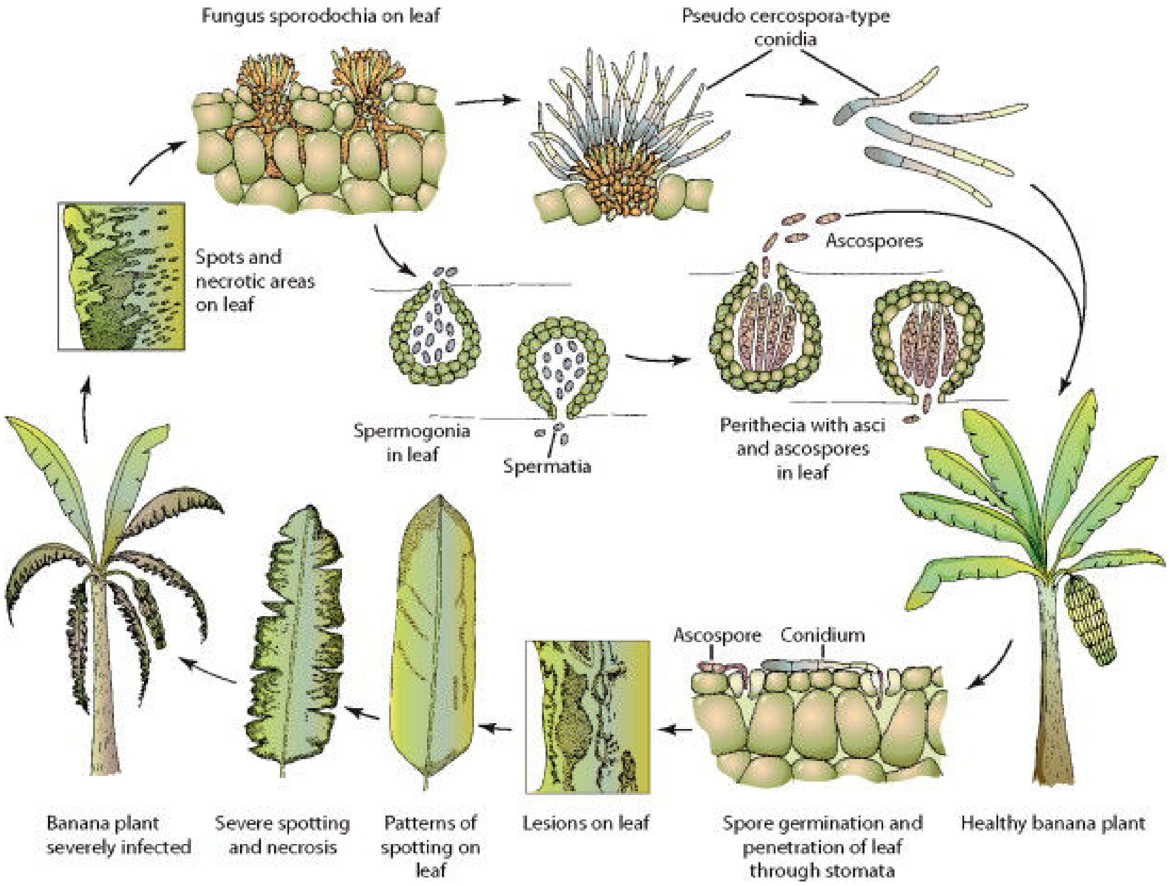
Chez les champignons hétérothalliques haploïdes, la reproduction sexuée nécessite de trouver un partenaire, ce qui peut s'avérer compliqué pour une population de faible densité. La production de spores via reproduction sexuée requiert ainsi une densité suffisante de parasites pour qu'il y ait effectivement rencontre et appariemment de deux individus sexuellement compatibles. Une telle corrélation positive entre une composante du taux de croissance *per capita* (reproduction sexuée) et de la densité de population est appelée effet Allee [APE+49]. La limitation en partenaire a été reportée comme étant le mécanisme le plus commun conduisant à un effet Allee [GBGC09]. Les effets Allee peuvent donner lieu à des densités critiques en-dessous desquelles la population peut s'éteindre, ce qui correspond à un effet Allee dit fort [TH05]. Par ailleurs, les effets Allee sont connus pour influencer la vitesse de propagation d'espèces invasives à la fois négativement (*critical initial area*, [LK93]) et positivement : [RGHK12] ont montré qu'avec un effet Allee, la population se propage comme un front poussé, ce qui empêche l'érosion de la diversité génétique. A l'inverse des fronts tirés qui sont entraînés par l'extrêmité du front, les fronts poussés sont entraînés par la totalité du front. Par conséquent, la découverte d'un partenaire sexuel comme un prérequis à la reproduction et à la dispersion mérite une attention particulière.

En dépit de l'importance de ces espèces pour le bien-être de l'homme, il y a très peu d'études sur l'effet de la reproduction sexuée en épidémiologie végétale [CMA+14]. Les dynamiques épidémiologiques font traditionnellement l'hypothèse de la reproduction aséxuée ou clonale du parasite. Il n'y a, à l'heure actuelle, aucun modèle épidémiologique générique pour des espèces capables de produire des spores sexuées et asexuées distinctes à partir du même hôte. Ceci limite notre compréhension de ces épidémies et leur contrôle.

Les cercosporioses jaunes et noires du bananier (causées respectivement par *Mycosphaerella musicola* et *Mycosphaerella fijiensis*) sont un bon exemple de maladies où une meilleure appréhension de l'impact épidémiologique des spores sexuées et asexuées serait utile. La cercosporiose jaune, causée par *M. musicola*, a été identifiée pour la première fois à Java en 1902. Elle s'est rapidement répandue tout au long de la zone intertropicale. La cercosporiose noire, causée par *M. fijiensis*, est apparue dans les îles Fiji en 1963. Dans les années 1970, elle est rapportée en Amérique centrale (Honduras) et en Afrique (Gabon) où elle se propage à une vitesse de 100 km/an environ [HCRP+10]. Depuis 2011, *M fijiensis* s'est installée dans la plupart des régions productrices de bananes (dont les Antilles Françaises) où il semble qu'elle ait remplacé *M. musicola.* Ces deux maladies sont responsables d'importantes pertes économiques.

Le cycle de vie des cercosporioses du bananier est présenté en Figure 1.1. Les spores se déposent à la surface des feuilles de bananier où elles germent et forment du mycélium. Quand un mycélium pénètre l'épiderme de la feuille, au travers les stomates, il forme une lésion et croît en consommant les cellules de la plante voisines du point d'infection. Après une phase de latence, les lésions produisent des spores asexuées (conidies). Ces spores sont dispersées par éclaboussures et infectent les feuilles voisines dans un rayon de quelques mètres seulement. Si deux mycéliums de types sexuels compatibles se rencontrent sur la même feuille, la reproduction sexuée a lieu et permet la production de spores sexuées (ascospores). Les spores sexuées sont dispersées par le vent sur une distance comprise entre quelques centaines de mètres et quelques kilomètres [RSB+14]. Dans la plupart des bananeraies, les bananiers produisent régulièrement de nouvelles feuilles saines de sorte que la densité de tissu végétal (sain et infecté) peut être considérée relativement constante pour le parasite. *M. fijiensis* produit moins de spores asexuées et plus de spores sexuées que *M. musicola*, ce qui pourrait expliquer la supériorité écologique de *M. fijiensis* [Sto80], [Fou82]. Cependant, de par un manque de modèle adéquat, notre compréhension des contributions des deux types de spores dans les dynamiques épidémiologiques de ces deux espèces reste limitée.

Fig. 1.2 – *cycle de vie de Mycosphaerella Fijiensis*



1.2 Modélisation

1.2.1 Mise en équation du modèle

Soit $i(t,x)$ la densité de feuilles infectées au temps $t > 0$ et à la position $x \in (-\infty, +\infty)$ (*i.e.* on considère un cas monodimensionnel en espace pour simplifier). Soit n la densité totale de feuilles, une constante. Pour simplifier, nous faisons l'hypothèse raisonnable (au moins dans un cadre agricole) que chaque feuille perdue est immédiatement remplacée par une feuille saine. Notons que le terme "feuille" est une abréviation de "la partie de la feuille qu'une lésion occupe" (ou site d'infection), de sorte que des infections multiples ne peuvent se produire dans le modèle. Aussi, $i(t,x)$ représente une densité de lésions.

Soit α le nombre de spores asexuées (conidies) produites par feuille infectée par unité de temps, et $0 < p < 1$ leur infectivité, c'est à dire la probabilité qu'une spore asexuée en contact avec une feuille saine parvienne à l'infecter. De même, soit σ le nombre de spores sexuées (ascospores) produites par feuille infectée par unité de temps, et $0 < q < 1$ leur infectivité. Soit M le taux de mortalité des feuilles infectées. On suppose que seules les spores sexuées diffusent et que les spores asexuées ne diffusent pas. Soit $u(t,x)$ la densité de spores sexuées, de coefficient de diffusion κ, et de taux de dépôt sur les feuilles μ.

En l'absence de reproduction sexuée (et donc de diffusion du pathogène), la dynamique épidémiologique (locale) est régie par un simple modèle SIS avec transmission fréquence-dépendante. Cette formulation est particulièrement adaptée aux bananeraies où la densité d'hôtes est relativement élevée [RLW+17]. En utilisant l'indice t pour dénoter la dérivée par rapport au temps, le modèle est :

$$i_t = p\alpha i(n-i)/n - Mi.$$

La production de spores sexuées est conditionnée par la présence locale d'un partenaire sexuel. Soient i^+ et i^- les densités de lésions de types sexuels + et − respectivement ($i = i^+ + i^-$). De même, soient u^+ et u^- les densités de spores sexuées de types sexuels + et − respectivement ($u = u^+ + u^-$). En utilisant l'indice x pour dénoter les dérivées spatiales, le modèle est :

$$
\begin{aligned}
i_t^+ &= (q\mu u^+ + p\alpha i^+)(n - i^- - i^+)/n - Mi^+,\\
i_t^- &= (q\mu u^- + p\alpha i^-)(n - i^- - i^+)/n - Mi^-,\\
u_t^+ &= \sigma i^+ \left(i^-/n\right) - \mu u^+ + \kappa u_{xx}^+,\\
u_t^- &= \sigma i^- \left(i^+/n\right) - \mu u^- + \kappa u_{xx}^-,
\end{aligned}
$$

où les fractions entre parenthèses représentent les probabilités de rencontres de partenaires sexuels compatibles.

Nous faisons ensuite l'hypothèse raisonnable d'un sexe-ratio équilibré, soit $i^+ = i^- = i/2$ et $u^+ = u^- = u/2$. Il vient alors :

$$
\begin{aligned}
i_t &= (q\mu u + p\alpha i)(n - i)/n - Mi,\\
u_t &= \sigma i \left(\frac{i}{2n}\right) - \mu u + \kappa u_{xx}.
\end{aligned}
\tag{1.1}
$$

1.2.2 Paramétrisation

Afin d'évaluer si les prédictions du modèle sont compatibles avec les données observées, nous avons paramétrisé le modèle pour la cercosporiose noire des bananiers [RLW+17], d'après [Sto80], [Fou82], [Rob12], [Lan15]. On se concentre ici uniquement sur des ordres de grandeur, car une paramétrisation plus fine demanderait des expériences dédiées.

On montre d'abord que tous les paramètres, excepté le coefficient de diffusion, peuvent être estimés à travers des mesures relativement communes en Pathologie Végétale. L'agent responsable de la cercosporiose noire (*M. Fijiensis*) produit en moyenne 200 spores asexuées par lésion. La durée moyenne d'infection est de 65 jours (incluant la période de latence laissée implicite pour simplifier). Ainsi, on a $\alpha = 200/65 \approx 3$ spores asexuées par jour. De plus, ce champignon produit environ 4000 spores sexuées par lésion, d'où $\sigma = 4000/65 \approx 60$ ascospores par jour. Les spores de *Erysiphe necator*, agent pathogène responsable l'oïdium de la vigne (un ascomycète comparable à *M. fijiensis*), soulevées dans l'atmosphère retombent dans les 30 minutes [BCL08]. Aussi, on prend

$\mu = 48$ par jour. On suppose que l'efficacité d'infection est la même pour les ascospores que pour les conidies : $p = q = 0.01$ [Lan15].

Le coefficient de diffusion peut être estimé par le flux de gènes en génétique des populations (l'écart-type de la distribution des distances parent-progéniture, [Mal01]). Plus précisément, la théorie des clines génétiques neutres permet d'estimer le flux de gènes chez *M. Fijiensis* à 1.2 km/génération$^{1/2}$ [RLC$^+$13]. La période qui sépare l'infection de la feuille de l'émission d'ascospores (environ 50 jours) représente une grande partie du temps de génération du parasite pendant lequel il ne diffuse pas, ce qui est pris en compte dans la partie immobile du modèle (variable i). Pour estimer le coefficient de diffusion des ascospores (variable u), on considère uniquement le temps réel de diffusion (30 minutes en moyenne). Cela donne $\kappa \approx 1.2^2 \times 48 \approx 70$ km^2 jour^{-1} (3 km^2 heure^{-1}).

Le tableau 1.1 résume les paramètres du modèle, leurs significations et leurs ordres de grandeurs.

TAB. 1.1 – *Dimensional variables and their estimated values for M. fijiensis.*

Notation	Définition	Unité	Valeur
t	temps		
x	position spatiale		
n	densité totale d'hôte	km^{-2}	
$i(x,t)$	densité d'hôtes infectés		
$u(x,t)$	densité de spores sexuées		
α	taux de production de spores asexuées	jour^{-1}	3
σ	taux de production de spores sexuées	jour^{-1}	60
p	infectivité des spores asexuées	aucune	.01
q	infectivité des spores sexuées	aucune	.01
κ	coefficient de diffusion des spores sexuées	km^2 jour^{-1}	70
μ	taux de dépôt des spores sexuées	jour^{-1}	48
M	taux de mortalité des infectés	jour^{-1}	
c	vitesse de propagation	km jour^{-1}	

1.2.3 Adimensionnement

Soit L l'échelle spatiale et T l'échelle temporelle qui nous intéressent dans le processus d'invasion. En re-normalisant les variables, on pose :

$$t^* = \frac{t}{T}, \;\; x^* = \frac{x}{L}, \;\; i^* = \frac{i}{n}, \;\; u^* = \frac{2\mu}{\sigma n} \times u$$

avec

$$a = \frac{2}{q\sigma T}, \;\; \varepsilon = \frac{1}{\mu T}, \;\; d = \sqrt{\frac{\kappa}{\mu L^2}}, \;\; b = \frac{2p\alpha}{q\sigma}, \;\; m^* = \frac{2M}{q\sigma}.$$

En omettant les astérisques pour alléger les notations, le modèle (1.1) devient :

$$\begin{cases} a i_t = (u + bi)(1 - i) - mi, \\ \varepsilon u_t = i^2 - u + d^2 u_{xx}. \end{cases} \tag{1.2}$$

Soit

$$\frac{\varepsilon}{a} = \frac{q\sigma}{2\mu}.$$

Pour *M. fijiensis*, $\varepsilon = 5.71\ 10^{-5}$, $a = 9.13\ 10^{-3}$, $b = 0.1$ et $d = 1.2\ 10^{-2}$ avec $L = 100$ km et $T = 365$ jours. On a $\varepsilon/a = 6.25\ 10^{-3} \ll 1$, ce qui correspond au cas $\varepsilon \ll a$. Cependant, cette relation pourrait être inversée chez des espèces où les spores diffusent bien plus longtemps dans l'environnement avant d'entrer en contact avec un hôte.

Aussi, nous considérerons par la suite a et ε comme potentiellement petits l'un par rapport à l'autre (temps rapide et temps lent, [AdLPP+08]).

1.3 Systèmes de réaction-diffusion

1.3.1 Définition

Cette introduction s'inspire de [Mur02], [LLH09].

Un système de réaction-diffusion est un modèle mathématique qui décrit l'évolution des concentrations d'une ou plusieurs substances spatiallement distribuées et soumises à deux processus : un procéssus de réactions chimiques locales, dans lequel les différentes substances se transforment, et un processus de diffusion qui provoque une répartition spatiale de ces substances. Bien que principalement appliqués à la chimie, ces systèmes de réaction-diffusion permettent aussi de décrire des modèles biologiques et écologiques, tels que la dynamique des populations, les invasions biologiques et l'écologie de la conservation. D'un point de vue écologique, un système de réaction-diffusion est perçu comme la description de la dynamique d'une population sous l'effet de deux forces : la dispersion et la croissance (naissances-décès) ([Roq13]). Grâce à deux approches différentes [Mur02], [LLH09], l'une basée sur une loi de conservation en physique mathématique, et l'autre sur une marche aléatoire en processus stochastiques, nous pouvons donner une formulation de ces modèles de réaction-diffusion. Voyons ici uniquement la première approche.

Considérons qu'une population ayant pour densité $u(t,x)$ vive et se déplace dans une région donnée. Pour décrire le mouvement de cette population au cours du temps, nous introduisons le flux de population $J(t,x) \in \mathbb{R}^n$, où n est la dimension de l'espace. A chaque temps t et à chaque position x, le flux $J(t,x)$ est un vecteur qui pointe dans la direction du mouvement à cette position. Ce flux se mesure en $m^{-2}s^{-1}$, et sa norme $|J(t,x)|$ est proportionnelle à la quantité de particules qui se déplace dans cette direction par unité de temps.

On suppose que la densité et le flux de population sont des fonctions régulières du temps et de l'espace. Considérons un volume test (arbitraire) Ω de frontière Γ et supposons que les flux intérieurs et extérieurs à Ω sur Γ sont équilibrés. La loi de conservation affirme que le taux de variation de u dans Ω est égale au taux de variation dû aux naissances, morts et intéractions plus le flux dans Ω. Mathématiquement, cela s'écrit donc :

$$\frac{\partial}{\partial t} \int_\Omega u(t,x)\ \mathrm{d}V = -\int_\Gamma J(t,x) \cdot n\ \mathrm{d}S + \int_\Omega f(u(t,x))\ \mathrm{d}V,$$

où n est le vecteur normal unitaire orienté vers l'extérieur à Γ. Le théorème de la divergence affirme que

$$\int_\Gamma J(t,x) \cdot n\ \mathrm{d}S = \int_\Omega \nabla \cdot J(t,x).n\ \mathrm{d}V,$$

ce qui nous permet d'obtenir

$$\int_{\Omega} \big(\frac{\partial u}{\partial t} - f(u) + \nabla \cdot J\big) \, \mathrm{d}V = 0.$$

Puisque cette relation est vraie pour tout volume Ω arbitrairement choisi, il s'ensuit que

$$\frac{\partial u}{\partial t} - f(u) + \nabla \cdot J = 0. \tag{1.3}$$

Par ailleurs, l'approche classique de la diffusion, à savoir la seconde loi de Fick, affirme que le flux de population J est proportionnel à l'opposé gradient de la densité de population. Ainsi, nous avons

$$J = -D\nabla u. \tag{1.4}$$

Notons que, pour que les unités coïncident dans (1.4), le coefficient de diffusion D doit s'exprimer en longueur^{2}temps^{-1}. Bien que ce coefficient dépende potentiellement de l'espace x, nous le supposerons indépendant du milieu dans toute notre étude. En outre, le signe moins dans (1.4) indique que les transports par diffusion vont nécessairement des fortes densités vers les faibles densités.

S'il y a également une advection à vitesse v, alors la loi de Fick est modifiée de la manière suivante

$$J = -D\nabla u + vu. \tag{1.5}$$

En combinant la loi de conversation (1.3) avec (1.5), nous obtenons donc le modèle de réaction-advection-diffusion

$$\frac{\partial u}{\partial t} + \nabla \cdot (vu) = \Delta u + f(u). \tag{1.6}$$

Dans toute notre étude, nous ne nous intéresserons qu'à des modèles sans advection, c'est à dire avec $v = 0$. Ainsi, en combinant (1.3) et (1.4), nous obtenons le modèle de réaction-diffusion

$$\frac{\partial u}{\partial t} = \underbrace{D\Delta u}_{\text{dispersion}} + \underbrace{f(u)}_{\text{croissance}} \,, \quad t > 0, \;\; x \in \Omega \subseteq \mathbb{R}^n, \tag{1.7}$$

où $u = (u_1,...,u_m)$, $\Delta u(t,x) = \frac{\partial^2}{\partial x_1} u(t,x) + \cdots + \frac{\partial^2}{\partial x_n} u(t,x)$ pour $x = (x_1, \cdots ,x_n) \in \mathbb{R}^n$ est le Laplacien de u, D est une matrice symétrique, f est une fonction à valeurs dans $\mathbb{R}^m$, et avec conditions initiales et conditions au bord bien choisies. Nous nous intéresserons uniquement au cas où le coefficient de diffusion est constant et indépendant de l'espace.

S'il n'y a ni advection ($v = 0$), ni croissance de population ($f = 0$), alors le modèle (1.7) est tout simplement l'équation de la chaleur.

Dans ce cas simple, si une concentration est soumise à une diffusion spatiale en une dimension d'espace initialement concentrée à l'origine, elle satisfait le problème aux données itiniales suivant

$$u_t = Du_{xx} \ , \quad u(0,x) = \delta_0(x). \tag{1.8}$$

La solution fondamentale (en dimension un), qui peut être obtenue par transformation de Fourier, est donnée par

$$u(t,x) = \frac{1}{2\sqrt{\pi D t}} e^{\frac{-x^2}{4Dt}}. \tag{1.9}$$

Avec une donnée initiale quelconque, le problème de réaction-diffusion

$$w_t = Dw_{xx} \ , \quad w(0,x) = h(x) \tag{1.10}$$

admet pour solution

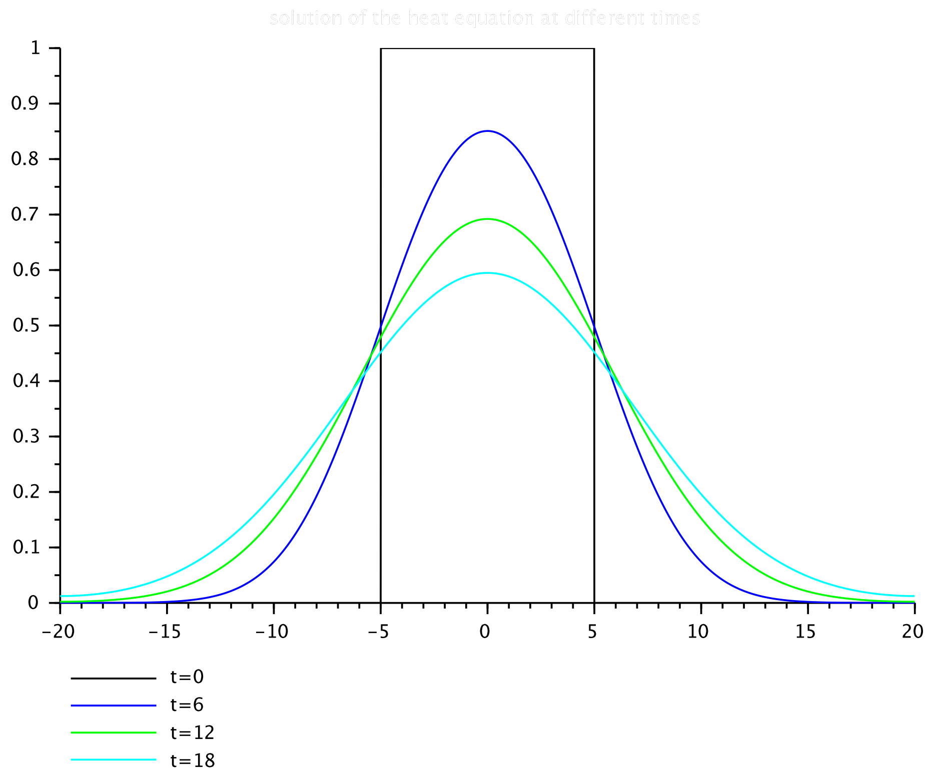
$$w(t,x) = \big(h \star u(t,.)\big)(x), \tag{1.11}$$

où la convolution est donnée par

$$\begin{aligned} \big(h \star u(t,.)\big)(x) &= \int_{-\infty}^{+\infty} h(y) w(x-y,t) \ \mathrm{d}y & (1.12) \\ &= \frac{1}{2\sqrt{\pi D t}} \int_{-\infty}^{+\infty} h(y) e^{\frac{-(x-y)^2}{4Dt}} \ \mathrm{d}y. & (1.13) \end{aligned}$$

Cette convolution de la solution fondamentale avec une donnée initiale quelconque est aussi vraie pour des opérateurs linéaires généraux, comme par exemple pour l'équation de réaction-advection-diffusion (1.6). La solution de l'équation de la chaleur (sans advection) est représentée à la figure 1.3 à plusieurs temps, pour une donnée initiale de type créneau. On remarque au passage l'effet régularisant de l'équation de la chaleur. Même en prenant une donnée initiale très peu régulière (ici, on a une fonction continue mais dérivable uniquement presque partout), la solution est continûment différentiable. On remarque également que la variance de la Gaussienne augmente en fonction du temps, et donc que la localisation des individus devient incertaine.

FIG. 1.3 – *Solution de l'équation de la chaleur à différents temps*



1.3.2 Cas particuliers

Depuis des années, une grande attention a été portée aux modèles de réaction-diffusion du type (1.7), qui décrivent par exemple la répartition d'une population dans l'espace au cours du temps. En fonction de la forme que prend le terme source f, correspondant par exemple à un processus de natalité-mortalité, plusieurs cas d'équations de réaction-diffusion peuvent se produire. Nous soulignons ici trois prototypes (parmi d'autres) pouvant décrire la dynamique d'une population. Considérons un modèle de réaction-diffusion décrivant la croissance et la dispersion d'une population $n(t,x)$ dans une échelle spatiale à une dimension. Les mouvements aléatoires, couplés à la croissance de la population, donnent lieu à l'équation de réaction-diffusion

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} + f(n).$$

Avec une croissance de population logistique

$$f(n) = rn\Big(1 - \frac{n}{K}\Big) \tag{1.14}$$

où r est le taux de croissance intrinsèque de la population et K la capacité d'accueil du milieu (exprimée en nombres d'individus), nous obtenons la célèbre équation de Fisher-KPP (Fisher-Kolmogorov, Petrovsky,Piskunov, [KPP37]) qui est le cas le plus simple de nonlinéarité pour les équations de réaction-diffusion.

Cependant, certaines populations peuvent avoir un taux de croissance *per capita* moindre aux faibles densités, telles qu'en moyenne, elles ne peuvent pas s'autoremplacer quand leurs densités sont faibles. Lorsque ce taux de croissance *per capita* $\frac{f(n)}{n}$ n'atteint plus son maximum en $n = 0$, on parle alors d'effet Allee, en hommage au biologiste Warder Clyde Allee qui introduisit cette notion en 1938. Dans ce cas, la fonction de croissance de population est

$$f(n) = rn\Big(1 - \frac{n}{K}\Big)\Big(\frac{n - C}{K}\Big), \tag{1.15}$$

où C est la densité critique en dessous de laquelle le taux de croissance de la population devient négatif.

Cet effet peut être dû à la difficulté de rencontrer un partenaire à faible densité ou à une mauvaise résistance aux phénomènes climatiques extrêmes [Roq13], et traduit la nécessité d'avoir assez d'individus autour de soi pour favoriser la reproduction.

Il convient cependant de distinguer deux formes d'effet Allee : l'effet Allee faible et l'effet Allee fort. L'effet Allee faible est caractérisé par le fait que la croissance de la population est positive, c'est à dire quand la fonction de croissance f est positive. On dira alors que f est de type monostable. L'effet Allee fort est caractérisé par le fait que la croissance est négative pour les faibles valeurs de n, c'est à dire quand la croissance est négative aux faibles densités. La fonction de croissance f est alors négative proche de 0 et positive proche de 1, et on dira que f est de type bistable ou multistable.

Effectuons un changement de variables, tel que la densité de population soit divisée par sa capacité d'accueil et que le temps et l'espace deviennent des échelles de temps et de longueur caractéristiques, à savoir

$$u = \frac{n}{K}, \quad t^* = rt, \quad x^* = \sqrt{\frac{r}{D}}x.$$

Les nouveaux paramètres engagés deviennent ainsi sans dimension. En ométtant les astérisques pour simplifier les notations, on obtient les modèles adimensionnés suivants

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u), \tag{1.16}$$

et

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u)(1-a). \tag{1.17}$$

Pour résumer, nous étudierons donc les trois cas de figures suivants, en fonction de la forme que prend le taux de croissance f :

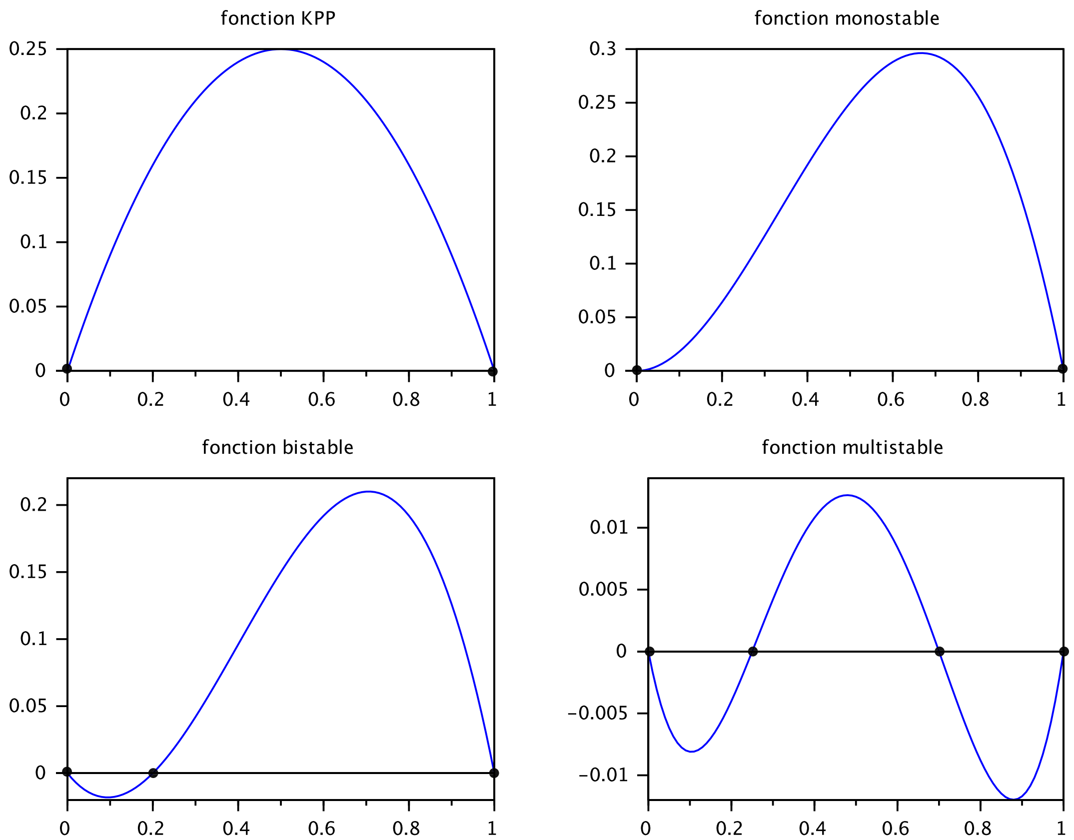
- f est de type KPP (modèle sans effet Allee) si $f(0) = f(1) = 0$, $f > 0$ sur (0,1) et $f(u) \leq f^{'}(0)u$ sur [0,1]. Le prototype est alors l'équation (1.16).

- f est de type monostable (modèle avec effet Allee faible) si $f(0) = f(1) = 0$ et $f > 0$ sur (0,1).

- f est de type bistable ou multistable (modèle avec effet Allee fort) s'il existe $0 < x_1 \leq \cdots \leq x_n < 1$ tels que $f(0) = f(x_i) = f(1) = 0$ pour tout $i \in \{1, \cdots, n\}$, $f < 0$ sur $(0,x_1)$ et $f > 0$ sur $(x_n,1)$. Le prototype est alors l'équation (1.17).

Ces différentes fonctions sont représentées à la figure 1.4 ci-dessous

FIG. 1.4 – *Graphiques des différents cas de figure du taux de croissance f*



1.3.3 Ondes progressives

Lorsque l'on cherche les solutions d'une équation de réaction-diffusion, que ce soit dans sa forme la plus générale possible (1.7) ou dans des cas particuliers comme (1.16) ou (1.17), il est fréquent de chercher ces solutions sous la forme d'ondes progressives. On appelle onde progressive une onde qui se déplace dans l'espace sans changement de forme. De ce fait, si une solution $u(t,x)$ d'une équation de réaction-diffusion représente une onde progressive, la forme de la solution est la même au cours du temps et la vitesse de propagation du front d'onde, que l'on note communément c, est constante. Mathématiquement, ces solutions s'expriment par la relation

$$u(t,x) = U(x - ct) = U(z), \quad z = x - ct, \tag{1.18}$$

où z est parfois appelée la variable d'onde et $U(z)$ le profil d'onde. On note généralement (U,c) une telle onde progressive. Au cours du temps, une onde progressive se déplace à vitesse constante c dans la direction des x positifs. Une onde se déplaçant dans la direction des x négatifs est de la forme $u(x + ct)$. Une onde progressive a pour caractéristique de joindre deux états d'équilibre, notés $U(+\infty) = u_+$ et $U(-\infty) = u_-$ et tels que $u_+ \neq u_-$. Ces solutions, dont le profil U reste constant et se déplace à vitesse $|c|$, décrivent par exemple l'invasion d'une population de l'état u_- vers l'état u_+ lorsque $c > 0$, et de l'état u_+ vers l'état u_- lorsque $c < 0$. Afin que $U(z)$ ait un sens physique réaliste, puisqu'elle représente par exemple des densités de population, le profil d'onde doit être positif et borné pour tout z. Notons enfin que l'on peut étendre la notion d'onde progressive aux dimensions supérieures par la relation

$$u(t,x) = U(x \cdot \xi - ct), \quad \xi \in \mathbb{S}^{n-1}, \tag{1.19}$$

où $\mathbb{S}^{n-1}$ désigne la sphère unité de $\mathbb{R}^n$ et ξ la direction de propagation du front. Enfin, ces notions s'étendent également à des systèmes de réaction-diffusion, c'est à dire quand les inconnues $\mathbf{u}$ et $\mathbf{U}$ sont des fonctions à valeurs vectorielles.

De nos jours, de nombreux articles traitent l'existence et la non-existence de telles ondes [VVV94]. De nombreuses méthodes d'analyse ont été étudiées afin de répondre à cette question. Parmi les plus connues, citons les quatre suivantes :

1. Les méthodes topologiques, avec en particulier la méthode de Leray-Schauder basée sur la théorie du degré topologique vérifiant le principe de rotation non nulle et l'invariance par homothopie.
2. Les méthodes issues de la théorie des bifurcations.
3. Les méthodes de réduction d'un système d'équation du second ordre à un système d'équations différentielles ordinaires du premier ordre et de nombreuses méthodes d'analyse des trajectoires du système (dans le cas d'ondes monodimensionnelles).
4. Les méthodes basées sur des propriétés de monotonie.

Si les méthodes 1 et 2 mentionnées précédemment ne seront pas développées dans la suite, prenons quelques instants pour parler de la méthode 3, sans doute la plus couramment utilisée.

Une solution $u(t,x)$ d'une équation de réaction-diffusion à une dimension, décrite par son profil d'onde $U(z)$ vérifiant (1.18) et les conditions limites $U(-\infty) = u_-$, $U(+\infty) = u_+$, satisfait nécessairement l'équation différentielle

$$DU^{''}(z) + cU^{'}(z) + f(U(z)) = 0. \tag{1.20}$$

En posant $V = U^{'}$, l'équation (1.20) peut être réduite au système d'équations différentielles du premier ordre

$$\begin{cases} U^{'} &= V \\ V^{'} &= -cV - f(U). \end{cases} \tag{1.21}$$

Par conséquent, la recherche d'ondes progressives pour un système de réaction-diffusion de type (1.7) se réduit à l'étude des trajectoires du système (1.21).

Résultats classiques pour l'équation de Fisher-KPP

Considérons que le terme source f est du type KPP (1.14). En modèle adimensionné, l'équation de réaction-diffusion étudiée est donc (1.16). Fisher [Fis37] a prouvé que sous certaines conditions sur la vitesse de propagation, il existe ou non une onde progressive connectant deux états d'équilibre du système.

En effet, les états d'équilibre du système différentiel (1.21) relatif à un taux de croissance logistique f sont $P_1 = (0,0)$ et $P_2 = (1,0)$. En linéarisant le système, on remarque que $P_1 = (0,0)$ est un équilibre stable pour $c > 0$. C'est une spirale stable pour $c > 2$, et un noeud stable pour $c \geq 2$. Le point $P_2 = (1,0)$ est quant à lui toujours un point selle. L'existence d'ondes progressives revient donc à trouver une orbite hétérocline joignant les points d'équilibres (1,0) et (0,0). En étudiant le portrait de phase, on voit que la seule orbite hétérocline possible est lorsque l'on a une connexion (noeud stable-point selle), à savoir dès lors que $c \geq 2$. Pour $c < 2$, le profil d'onde U change de signe, ce qui n'a aucun sens physique dès lors qu'il est négatif, puisqu'il représente une densité de population. Par conséquent, de telles ondes progressives ne peuvent exister que si $c \geq 2$, et n'existent pas si $c < 2$. La vitesse d'onde minimale telle qu'il y ait existence d'une onde progressive est donc $c = 2$. Cette condition nécessaire est également suffisante (voir exercice "*trapping region*" dans [LLH09]). En termes dimensionnés, la vitesse d'onde minimale est $c^* = 2\sqrt{f'(0)} = 2\sqrt{rD}$. Ainsi, dès lors que $c \geq c^*$, on a donc existence d'une infitinité (un continuum) d'ondes progressives, c'est à dire une infinité de solutions (U,c) de (1.20). Ce résultat se généralise au cas d'une fonction f monostable, même si l'hypothèse $f(u) \leq f'(0)u$ n'est plus satisfaite. La vitesse minimale s'exprime alors également par la relation $c^* = 2\sqrt{f'(0)}$.

De plus, Aronson et Weinberger [AW78] montrent qu'il existe une relation entre la vitesse minimale d'onde et le taux de propagation (*spread rate* défini ci-après). Ici, le taux de propagation se réfère au taux auquel une population localement introduite (*i.e.* de densité nulle en dehors d'un compact) se propage vers l'extérieur. Mathématiquement, c^* représente le taux de propagation si, en considérant qu'une population est initialement située dans une région suffisamment grande, une source en mouvement de cette population se développant à une vitesse inférieure à c^* rencontre l'état d'équilibre relatif à la capacité d'accueil $u = 1$, et une source en mouvement se développant à une vitesse supérieure à c^* rencontre l'état d'équilibre non envahi $u = 0$. Ces affirmations se traduisent mathématiquement comme suit : pour tout $0 < \epsilon \ll c^*$, on a

$$\lim_{t \to +\infty} \sup_{|x|>(c^*+\epsilon)t} u(t,x) = 0 \tag{1.22}$$

et

$$\lim_{t \to +\infty} \sup_{|x|<(c^*-\epsilon)t} |u(t,x) - 1| = 0. \tag{1.23}$$

Ce résultat traduit le fait que pour l'équation de Fisher KPP, le taux de propagation est exactement la vitesse minimale d'onde $c = 2\sqrt{rD}$.

Résultats classiques pour l'équation bistable

Considérons que le terme source f est de type bistable (1.15). En modèle adimensionné, l'équation de réaction-diffusion étudiée est donc (1.17). Fife et McLeod [FM77] ont prouvé qu'il existe une unique (contrairement aux cas monostable et KPP) onde progressive (U,c) où l'unique vitesse de propagation dépend du signe de $\int_0^1 f(s)\, \mathrm{d}s$, positivement ou négativement selon les conditions aux limites sur U. En effet, en considérant une fonction $f \in C^1([0,1])$ de type bistable, ils prouvent que chaque solution $u = U(x-ct)$ du système de réaction-diffusion de type (1.17) avec $U \in [0,1]$, $U(-\infty) = 0$ et $U(+\infty) = 1$ satisfait nécessairement que $U'(z) > 0$ pour $z = x - ct$ fini. Or, à tout profil d'onde U satisfaisant une équation différentielle du second ordre en z, est associé un système différentiel du premier ordre dans le plan de phase. Cette correspondance permet d'établir l'existence et l'unicité d'une onde progressive. De plus, en multipliant par $U^{'}(z) > 0$ l'équation différentielle

$$U^{''} + cU^{'} + f(U) = 0$$

et en intégrant par rapport à z, il vient

$$\underbrace{c\int_{-\infty}^{+\infty} (U^{'})^2(z)\ \mathrm{d}z}_{>0} = -\int_0^1 f(s)\ \mathrm{d}s.$$

Ceci prouve en effet que $c \geq 0$ (resp. ≤ 0) dès lors que $\int_0^1 f(s)\ \mathrm{d}s \leq 0$ (resp. ≥ 0). Avec conditions aux limites $U(-\infty) = 1$ et $U(+\infty) = 0$, alors c est du même signe que $\int_0^1 f(s)\ \mathrm{d}s$.

Une fois l'existence et l'unicité d'une unique onde progressive établies, ils se sont intéressés au comportement asymptotique des solutions quand $t \to +\infty$, et ont établi les trois résultats majeurs suivants.

Le premier résultat affirme que si une solution a initialement la même allure qu'un front d'onde, alors elle va se propager uniformément comme un tel front d'onde en temps long. Le "a initialement la même allure" signifie simplement que la solution est plus petite qu'une certaine valeur α_0 loin vers la gauche, et plus grande qu'une certaine valeur α_1 loin vers la droite. Mathématiquement, le résultat s'énonce :

Théorème. *Soit $f \in C^1[0,1]$ satisfaisant*

$$\begin{aligned} &f(0) = f(1), \quad f^{'}(0) < 0, \quad f^{'}(1) < 0, \\ &f(u) < 0 \quad \textit{pour} \quad 0 < u < \alpha_0, \\ &f(u) > 0 \quad \textit{pour} \quad \alpha_1 < u < 1, \end{aligned}$$

où $0 < \alpha_0 \leqq \alpha_1 < 1$.

Supposons qu'il existe une solution de type onde progressive (U,c) *au système de réaction-diffusion bistable associé. Soit* φ *la donnée initiale à ce problème satisfaisant* $0 \leqq \varphi \leqq 1$*, et supposons*

$$\limsup_{x \to -\infty} \varphi(x) < \alpha_0, \qquad \liminf_{x \to +\infty} \varphi(x) > \alpha_1.$$

Alors, pour des constantes z_0*,* K *et* ω *avec* K *et* ω *strictement positives, la solution* $u(t,x)$ *du système de réaction-diffusion satisfait*

$$|u(t,x) - U(x - ct - z_0)| < Ke^{-\omega t}.$$

Autrement dit, cette solution approche une onde progressive uniformément en x et exponentiellement en t quand $t \to +\infty$.

Il y a aussi des situations où la solution se propage comme une paire d'ondes progressives se déplaçant dans des directions opposées. Ceci est énoncé dans le résultat suivant.

Théorème. *Soit* f *satisfaisant les hypothèses du théorème précédent, en supposant de plus que*

$$\int_0^1 f(u)\ du > 0.$$

Supposons la donnée initiale φ *vérifiant* $0 \leqq \varphi \leqq 1$*, et*

$$\limsup_{|x| \to \infty} \varphi(x) < \alpha_0, \;\; \varphi(x) > \alpha_1 + \eta \quad \text{ pour } |x| < L,$$

où η *et* L *sont des réels strictement positifs. Alors, si* L *(dépendant de* η *et* f*) est suffisamment grand, on a pour des constantes* x_0*,* x_1*,* K *et* ω *avec* K *et* ω *strictement positives, les deux inégalités*

$$|u(t,x) - U(x - ct - x_0)| < Ke^{-\omega t}, \;\; x < 0,$$
$$|u(t,x) - U(x - ct - x_1)| < Ke^{-\omega t}, \;\; x > 0.$$

Enfin, ils considèrent le cas où la solution se propage comme une combinaison de fronts d'onde d'intervalles différents mais adjacents. Pour simplifier, le résultat suivant est énoncé pour seulement deux fronts d'onde.

Théorème. *Soit* $f(u_i) = 0$ *et* $f^{'}(u_i) < 0$, $i = 1{,}2{,}3$, *où* $u_1 < u_2 < u_3$. *Supposons qu'il existe deux fronts d'onde* $U_1(x - c_1 t)$ *et* $U_2(x - c_2 t)$ *d'intervalles respectifs* (u_1,u_2) *et* (u_2,u_3). *Supposons* $c_1 < c_2$. *Soit* α_1 *le plus petit zéro de* f *plus grand que* u_1, *et* α_2 *le plus grand zéro de* f *plus petit que* α_3. *Supposons que* $u_1 \leqq \varphi(x) \leqq u_3$, *et*

$$\limsup_{x\to-\infty} \varphi(x) < \alpha_1, \qquad \liminf_{x\to+\infty} \varphi(x) > \alpha_2.$$

Alors, il existe des constantes x_1, x_2, K *et* ω, *avec* K *et* ω *strictement positives, telles que*

$$|u(t,x) - U_1(x - c_1 t - x_1) - U_2(x - c_2 t - x_2) + u_2| < K e^{-\omega t}.$$

En particulier, notons que cette dernière inégalité entraîne que

$$\lim_{t\to\infty} u(\beta t,t) = \begin{cases} u_1 & \textit{pour} \ \ \beta < c_1, \\ u_2 & \textit{pour} \ \ c_1 < \beta < c_2, \\ u_3 & \textit{pour} \ \ c_2 < \beta. \end{cases}$$

Autrement dit, cette solution approche une combinaison d'ondes progressives uniformément en x et exponentiellement en t quand $t \to +\infty$.

1.4 Organisation du manuscrit

Dans un second chapitre, nous commençons par une étude mathématique de notre système de réaction-diffusion. De prime abord, nous effectuons une étude qualitative très informelle du système dynamique en étudiant les *null clines* associées à notre système et en exhibant une région invariante. Ces deux études nous permettent de poser les jalons et de faire les premières hypothèses nécessaires pour la suite. En effet, l'existence d'une région invariante nous donne une borne pour un couple de solutions de notre système. Cette borne nous sert à démontrer que toute solution locale à notre système est en réalité globale. De plus, l'existence d'une région invariante dite "contractante" nous permet d'obtenir des informations sur la stabilité de certains équilibres de notre système. Dans un second temps, nous prouvons que notre système de réaction-diffusion admet des solutions dans un cadre fonctionnel abstrait. Une fois cette existence justifiée, nous prouvons que la solution précédemment trouvée existe pour tout temps. Enfin, nous étudions le comportement asymptotique des solutions lorsque les petits paramètres ε et a, considérés comme des temps rapides, tendent vers 0. Nous précisons de quelle manière une solution à notre système de réaction-diffusion converge vers une solution d'un modèle approché, avec des simulations numériques pour illustrer cette convergence.

Dans un troisième chapitre, nous nous intéressons à la recherche d'ondes progressives pour notre modèle de réaction-diffusion dans le cas monostable en remarquant que notre système est coopératif. Nous définissons ces notions et montrons en quoi elles favorisent l'existence d'ondes progressives dans notre modèle de réaction-diffusion issu de l'exemple des cercosporioses du bananier. Nous vérifions enfin que cette théorie s'applique à notre système d'étude vu comme un système monostable et coopératif, et qu'il est ainsi possible de conclure à l'existence et à la non existence de solutions de type ondes progressives.

Bibliographie

[AdLPP+08] Pierre Auger, R Bravo de La Parra, Jean-Christophe Poggiale, E Sánchez, and L Sanz. Aggregation methods in dynamical systems and applications in population and community dynamics. *Physics of Life Reviews*, 5(2):79–105, 2008.

[APE+49] Warder Clyde Allee, Orlando Park, Alfred Edwards Emerson, Thomas Park, Karl Patterson Schmidt, et al. *Principles of animal ecology.* Number Edn 1. WB Saundere Co. Ltd., 1949.

[AW78] Donald G Aronson and Hans F Weinberger. Multidimensional nonlinear diffusion arising in population genetics. *Advances in Mathematics*, 30(1):33–76, 1978.

[BCL08] Jean-Baptiste Burie, Agnes Calonnec, and Michel Langlais. Modeling of the invasion of a fungal disease over a vineyard. In *Mathematical Modeling of Biological Systems, Volume II*, pages 11–21. Springer, 2008.

[BLVD+11] Sylvain Billiard, Manuela López-Villavicencio, Benjamin Devier, Michael E Hood, Cécile Fairhead, and Tatiana Giraud. Having sex, yes, but with whom? inferences from fungi on the evolution of anisogamy and mating types. *Biological reviews*, 86(2):421–442, 2011.

[Bon58] John Tyler Bonner. The relation of spore formation to recombination. *The American Naturalist*, 92(865):193–200, 1958.

[CMA+14] Magda Castel, Ludovic Mailleret, Didier Andrivon, Virginie Ravigné, and Frédéric M Hamelin. Allee effects and the evolution of polymorphism in cyclic parthenogens. *The American Naturalist*, 183(3):E75–E88, 2014.

[EB14] Iuliana V Ene and Richard J Bennett. The cryptic sexual strategies of human fungal pathogens. *Nature Reviews Microbiology*, 12(4):239–251, 2014.

[FHB+12] Matthew C Fisher, Daniel A Henk, Cheryl J Briggs, John S Brownstein, Lawrence C Madoff, Sarah L McCraw, and Sarah J Gurr. Emerging fungal threats to animal, plant and ecosystem health. *Nature*, 484(7393), 2012.

[Fis37] Ronald Aylmer Fisher. The wave of advance of advantageous genes. *Annals of Human Genetics*, 7(4):355–369, 1937.

[FM77] Paul C Fife and J Bryce McLeod. The approach of solutions of nonlinear diffusion equations to travelling front solutions. *Archive for Rational*

Mechanics and Analysis, 65(4):335–361, 1977.

[Fou82] E Fouré. Les cercosporioses du bananier et leurs traitements. comportement des variétés. 1: Incubation et évolution de la maladie. *Fruits*, 37(12):749–766, 1982.

[GBGC09] Joanna Gascoigne, Ludek Berec, Stephen Gregory, and Franck Courchamp. Dangerously few liaisons: a review of mate-finding allee effects. *Population Ecology*, 51(3):355–372, 2009.

[GHP+14] Andrin Gross, Ottmar Holdenrieder, Marco Pautasso, Valentin Queloz, and Thomas Niklaus Sieber. *Hymenoscyphus pseudoalbidus*, the causal agent of european ash dieback. *Molecular Plant Pathology*, 15(1):5–21, 2014.

[HCD+16] Frédéric M Hamelin, François Castella, Valentin Doli, Benoît Marçais, Virginie Ravigné, and Mark A Lewis. Mate finding, sexual spore production, and the spread of fungal plant parasites. *Bulletin of mathematical biology*, 78(4):695–712, 2016.

[HCRP+10] Fabien Halkett, David Coste, Gonzalo Galileo Rivas Platero, Marie Françoise Zapater, Catherine Abadie, and Jean Carlier. Genetic discontinuities and disequilibria in recently established populations of the plant pathogenic fungus mycosphaerella fijiensis. *Molecular ecology*, 19(18):3909–3923, 2010.

[KPP37] Andrei N Kolmogorov, IG Petrovsky, and NS Piskunov. Etude de l'équation de la diffusion avec croissance de la quantité de matiere et son applicationa un probleme biologique. *Moscow Univ. Math. Bull*, 1(1-25):129, 1937.

[Lan15] Clara Landry. *Modélisation des dynamiques de maladies foliaires de cultures pérennes tropicales à différentes échelles spatiales: cas de la cercosporiose noire du bananier*. PhD thesis, Université des Antilles et de la Guyane, 2015.

[LK93] MA Lewis and P Kareiva. Allee dynamics and the spread of invading organisms. *Theoretical Population Biology*, 43(2):141–158, 1993.

[LLH09] MA Lewis, F Lutscher, and T Hillen. Spatial dynamics in ecology. *Park City Mathematics Institute volume in Mathematical Biology, Institute for Advanced Study, Princeton*, 2009.

[Mal01] J Mallet. Gene flow. In I.P. Woiwod, D.R. Reynolds, and C.D. Thomas, editors, *Insect movement: mechanisms and consequences*, pages 337–360. CABI, 2001.

[Mur02] James D Murray. Mathematical biology. i, volume 17 of interdisciplinary applied mathematics, 2002.

[P+10] E Pennisi et al. Armed and dangerous (vol 327, pg 804, 2010). *Science*, 327(5970):1200–1200, 2010.

[RGHK12] Lionel Roques, Jimmy Garnier, François Hamel, and Etienne K Klein. Allee effect promotes diversity in traveling waves of colonization. *Proceedings of the National Academy of Sciences*, 109(23):8828–8833, 2012.

[RLC+13] Adrien Rieux, T Lenormand, Jean Carlier, L Lapeyre de Bellaire, and Virginie Ravigné. Using neutral cline decay to estimate contemporary dispersal: a generic tool and its application to a major crop pathogen. *Ecology letters*, 16(6):721–730, 2013.

[RLW+17] Virginie Ravigné, Valérie Lemesle, Alicia Walter, Ludovic Mailleret, and Frédéric M Hamelin. Mate limitation in fungal plant parasites can lead to cyclic epidemics in perennial host populations. *Bulletin of mathematical biology*, 79(3):430–447, 2017.

[Rob12] Stéphanie Robert. Emergence mondiale de la maladie des raies noires du bananier: histoire de l'invasion et stratégie de vie du champignon phytopathogène *Mycosphaerella fijiensis*. 2012.

[Roq13] Lionel Roques. *Modèles de réaction-diffusion pour l'écologie spatiale: Avec exercices dirigés*. Éditions Quae, 2013.

[RP16] Jean Beagle Ristaino and Donald H Pfister. "what a painfully interesting subject": Charles darwin's studies of potato late blight. *BioScience*, 66(12):1035–1045, 2016.

[RSB+14] Adrien Rieux, Samuel Soubeyrand, François Bonnot, Etienne K Klein, Josue E Ngando, Andreas Mehl, Virginie Ravigne, Jean Carlier, and Luc de Lapeyre de Bellaire. Long-distance wind-dispersal of spores in a fungal plant pathogen: estimation of anisotropic dispersal kernels from an extensive field experiment. *PLoS One*, 9(8):e103225, 2014.

[Sto80] RH Stover. Sigatoka leaf spots of. *Plant disease*, 64(8):751, 1980.

[TH05] Caz M Taylor and Alan Hastings. Allee effects in biological invasions. *Ecology Letters*, 8(8):895–908, 2005.

[VVV94] Aĭzik Isaakovich Volpert, Vitaly A Volpert, and Vladimir A Volpert. *Traveling wave solutions of parabolic systems*, volume 140. American Mathematical Soc., 1994.

[WFA+02] Roy Watling, Juliet C Frankland, AM Ainsworth, Susan Isaac, and Clare H Robinson. *Tropical mycology*, volume 2. CABI, 2002.

[Wil75] George Christopher Williams. *Sex and evolution.* Number 8. Princeton University Press, 1975.

Chapitre 2

Mathematical study of the reaction-diffusion system

Contenu du chapitre

2.1 Introduction

We are interested in modeling the spread of a fungal plant pathogen subject to mate limitation [HCD+16]. Specifically, we consider (after ecological considerations) the following system of equations:

$$\begin{cases} ai_t = (u+bi)(1-i) - mi \\ \varepsilon u_t = i^2 - u + d^2 u_{xx} \end{cases} \tag{2.1}$$

In Section 2.2, the methods of [Smo12] are used to explore the dynamical behavior of (2.1) in the parameter space. We first study the spatially independent version of (2.1), hereafter the *dynamical system*. Finding the equilibrium points of the dynamical system and characterizing their stability allow us to delimit three regions in the parameter space: extinction of the pathogen population, invasion by the pathogen (monostable case), and extinction or invasion depending on initial conditions (bistable case). In the monostable case, locating the equilibria of the dynamical system allows us to construct an invariant region in the reaction diffusion system, specifically a contracting rectangle in the phase plane. From [Smo12], an orbit that enters a contracting rectangle must enter a smaller rectangle in finite time. Providing this smaller rectangle is also contracting, the procedure can be repeated and may converge to an equilibrium point.

The existence and uniqueness of solutions to (2.1) will be thoroughly addressed in Section 2.3.

2.2 Qualitative study

In this section, we work on the space BC of continuous and bounded functions[1], following the results of [Smo12] and [LSKT96]. The dynamical system associated with the reaction diffusion system (2.1) is:

$$\begin{cases} i_t &= [(u+bi)(1-i) - mi]/a =: f(i,u), \\ u_t &= (i^2 - u)/\varepsilon =: g(i,u). \end{cases} \tag{2.2}$$

1. we prove similar results with an analysis on a different functionnal space in section 2.3

We also note $F = \begin{pmatrix} f \\ g \end{pmatrix}$ the vector field of system (2.2).

2.2.1 Study of the null clines and equilibria of the dynamical system

In this subsection, we concentrate our attention on the mere dynamical system (2.2). The goal is to identify the stable and unstable equilibria in (2.2), so as to eventually characterize the natural equilibria in the original model (2.1).

The null clines are defined as the curves corresponding to $f(i,u) = 0$ and $g(i,u) = 0$. The equilibria of system (2.2) correspond to intersections of the null clines, that is any pair (i,u) such that

$$\begin{cases} (u + bi)(1 - i) - mi = 0 \\ i^2 - u = 0. \end{cases}$$

This system reduces to $i[(i + b)(1 - i) - mi] = 0$, that is $i[i^2 + (b - 1)i + (m - b)] = 0$. Thus, the (real valued) equilibria are

$$(0,0), \ \ \big(i^-, u^- = (i^-)^2\big), \ \ \big(i^+, u^+ = (i^+)^2\big).$$

with

$$i^\pm = \frac{1 - b \pm \sqrt{(1 - b)^2 - 4(m - b)}}{2} = \frac{1 - b \pm \sqrt{(b + 1)^2 - 4m}}{2},$$

whenever $m \leq \frac{(b+1)^2}{4}$. If $m > \frac{(b+1)^2}{4}$, then only one (real valued) equilibrium subsists, namely (0,0).

Remark 1 *The distinction whether*

$$m \leq \frac{(b + 1)^2}{4} \quad or \quad m > \frac{(b + 1)^2}{4}$$

means that there is a threshold value $\frac{(b+1)^2}{4}$ *for the mortality rate* m *below (resp. above) for which births through sexual and asexual reproduction (i.e. through linear and non-linear reproduction) can (resp. cannot) compensate mortality. Note that the relevant value* $\frac{(b+1)^2}{4}$ *comes out as the cumulated effect of a nonlinear dynamics.*

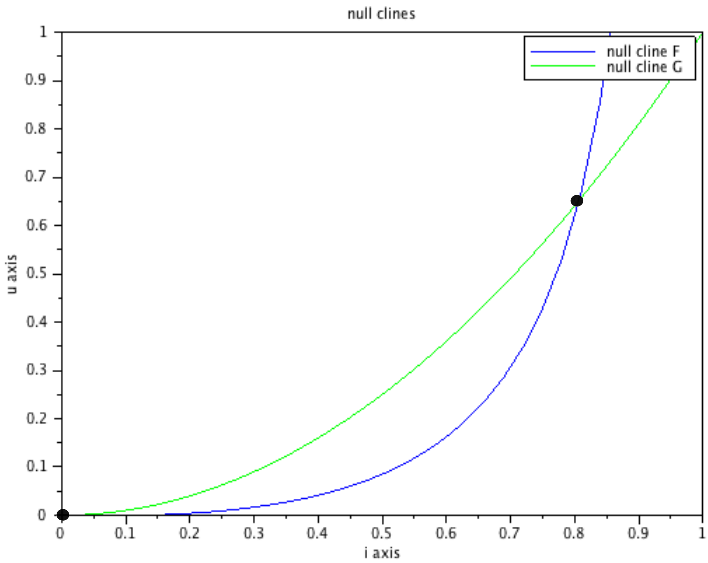
Hence, several cases can be distinguished:

• Case $b \geq m$:

Subcase $b < 1$:

In this case, we automatically have $m < \frac{(b+1)^2}{4}$. Besides, we then have $1 - b < \sqrt{(1-b)^2 - 4(m-b)}$. Hence, it follows $i^- < 0 < i^+$. Even if i^- is an equilibrium mathematically, it is not biologically meaningful, since we only consider positive population densities. Therefore, we filter out this equilibrium in this case. The two relevant equilibria here are (0,0) and $(i^+,(i^+)^2)$.

FIG. 2.1 – *Null clines for the monostable case*

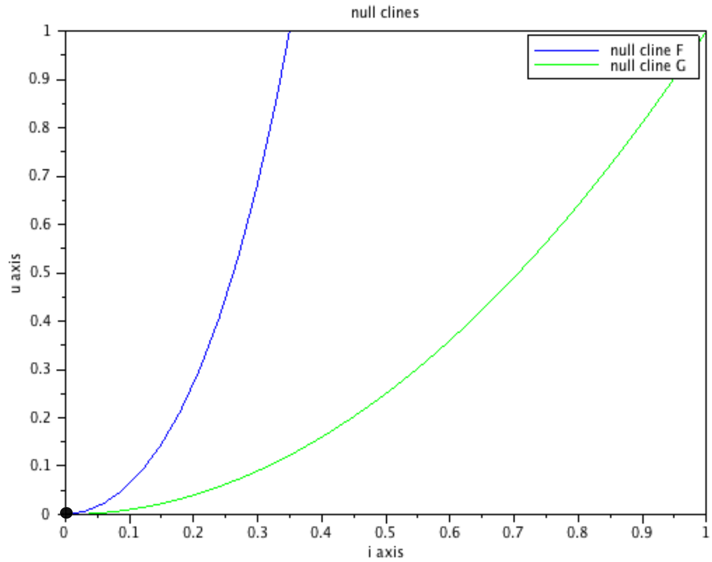


Subcase $b \geq 1$:

Subsubcase $m = b$:

In this subsubcase, we have either $i^+ = i^- = 0$ for $b = m = 1$, or $i^+ = 0$ and $i^- = 1 - b < 0$ for $b > 1$. In any case, the only relevant equilibrium is (0,0), which eventually means that populations collapse.

FIG. 2.2 – *Null clines for the extinction case*



Subsubcase $m < b$:

We are in the same case as for $m \leq b < 1$, namely with two relevant equilibria (0,0) and $(i^+,(i^+)^2)$. Thus, the null clines have the same shape.

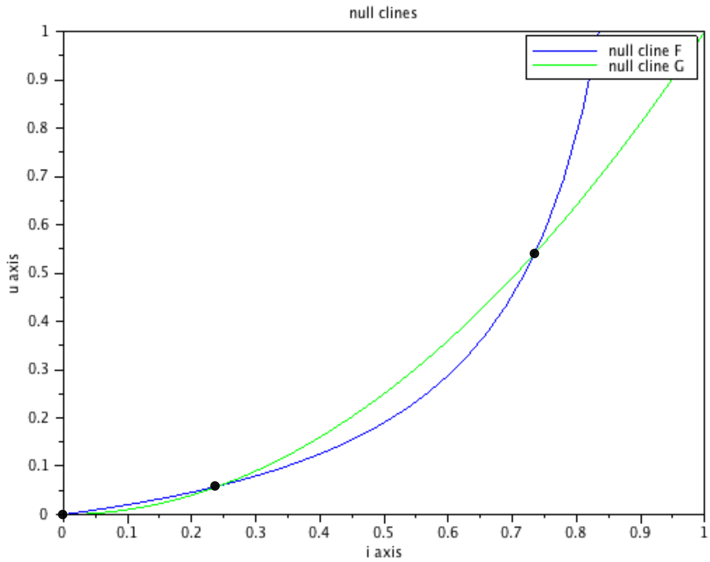
• Case $b < m$:

Subcase $b < 1$:

Subsubcase $m < \frac{(b+1)^2}{4} < 1$:

Since $1 - b > 0$ and $1 - b > \sqrt{(1-b)^2 - 4(m-b)} > 0$, we have $0 < i^- < i^+$. Here, the three equilibria are biologically meaningful.

FIG. 2.3 – *Null clines for the bistable case*



<u>*Subsubcase* $m \geq \frac{(b+1)^2}{4}$*:*</u>

Since $1-b<0$ and $1-b>\sqrt{(1-b)^2-4(m-b)}$, we have $i^- < i^+ < 0$. Still for the sake of biological meaning, we do not consider the equilibria i^- and i^+. In this case, the only relevant equilibrium is (0,0). The population density collapses. The null clines have the same shape as for $m = b \geq 1$.

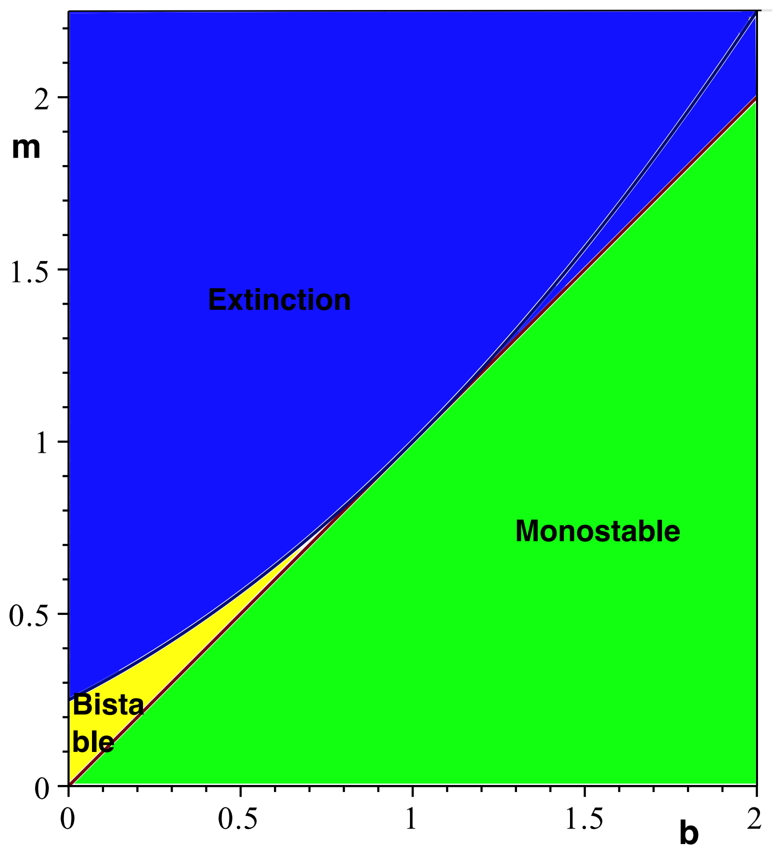
<u>Subcase $b \geq 1$:</u>

Only the trivial equilibrium (0,0) is relevant, either in the case $m < \frac{(b+1)^2}{4}$ or $m \geq \frac{(b+1)^2}{4}$.

2.2.2 Stability of the dynamical system equilibria

We follow the previous classification to explore the stability of equilibria. The remarkable regions mentionned below, namely the bistable, monostable and extinction regions, are representend on 2.4 below

Fig. 2.4 – *Graph of the remarkable regions in the parameter space*



• **Case** $b \geq m$ **:**

• *Subcase* $b < 1$*:*

In this case, we noticed that we have two equilibria (0,0) and (i^+,u^+). A simple analysis proves that (0,0) is unstable while (i^+,u^+) is stable[2]. Indeed, the Jacobian matrix $JF(i,u)$ of the system is

$$JF(i,u) = \begin{pmatrix} \frac{-2bi+b-m-u}{a} & 1-i \\ \frac{2i}{\varepsilon} & -\frac{1}{\varepsilon} \end{pmatrix}$$

Thus, we have

$$JF(0,0) = \begin{pmatrix} \frac{b-m}{a} & 1 \\ 0 & -\frac{1}{\varepsilon} \end{pmatrix}, \quad JF(i^+,u^+) = \begin{pmatrix} \frac{-2bi^+ +b-m-u^+}{a} & 1-i^+ \\ \frac{2i^+}{\varepsilon} & -\frac{1}{\varepsilon} \end{pmatrix}.$$

Hence, the equilibrium (0,0) is unstable (saddle point) because $JF(0,0)$ has one positive (and one negative) eigenvalue whenever $b > m$ and has zero as an eigenvalue whenever $b = m$.

Besides, the equilibrium (i^+,u^+) is stable since $JF(i^+,u^+)$ has two positive eigenvalues since

$$\mathrm{Tr}\big(JF(i^+,u^+)\big) = \frac{(b+1)\big(b-1-\sqrt{(1-b)^2-4(m-b)}\big)}{2a} < 0$$

and

$$\Delta\big(JF(i^+,u^+)\big) = \frac{1-b^2+(2b^2+2b-4m)a+(b+1-2ab)\sqrt{(1-b)^2-4(m-b)}}{2a} > 0.$$

This case is refered to as the **monostable case**.

• *Subcase* $b \geq 1$*:*

• Subsubcase $m = b$:

2. We prove the stabilities in this subcase. We do not write the Jacobian matrices in the subsequent cases for the reader's convenience.

Only (0,0) is an equilibrium. This equilibrium is stable (attracting node) and leads to the **extinction** of the population.

• Subsubcase $m < b$:

This subsubcase is similar to the case $1 > b > m$, namely the **monostable case**.

• Case $b < m$:

• *Subcase $b < 1$:*

• Subsubcase $m < \frac{(b+1)^2}{4} < 1$:

In this case, we have the three equilibria (0,0), (i^-,u^-) and (i^+,u^+), where (0,0) and (i^+,u^+) are stable and (i^-,u^-) is unstable. This case is referred to as the **bistable case**.

• Subsubcase $m \geq \frac{(b+1)^2}{4}$:

This case is similar to the same subsubcase for $b < 1$ and leads to the **extinction** of the population.

• *Subcase $b \geq 1$:*

Regardless of the comparison between m and $\frac{(b+1)^2}{4}$, the two equilibria (i^+,u^+) and (i^-,u^-) are negative (or equal to (0,0)) and thus not biologically meaningful. Since (0,0) is the only nonnegative equilibrium and is stable, an **extinction** of the population occurs.

As a conclusion, and since the case where populations go extinct is biologically trivial, the only two remaining nontrivial cases require in any circumstance the constraint $m < \frac{(b+1)^2}{4}$, while with this restriction in mind, the monostable case corresponds to the situation where $b > m$ whenever $b \geq 1$ or $1 > b \geq m$, and the bistable case is reached when $b < m$ (the constraint $b < 1$ being automatically satisfied in this latter case). All other situations converge to the trivial equilibrium (0,0) in equation (2.2).

The remainder part of this text is devoted to the study of the reaction diffusion system (2.1), *i.e.* of the dynamical system (2.2) where diffusion in the i-variable has been added. Here and below we shall keep the same distinction, and keep on refering to the cases $b > m$ or $1 > b \geq m$ (and, of course, $m < \frac{(b+1)^2}{4}$, which is necessarily satisfied) as the **monostable case**, and to the case $b < m$ (and $m < \frac{(b+1)^2}{4}$, the condition $b < 1$ being then automatically satisfied) as the **bistable case**.

From now on, we always refer to one of the above cases as a region of the following graph in Figure 2.4. Thus, the yellow region corresponds to the bistable case, the green region corresponds to the monostable case and the blue region corresponds to the extinction case.

2.2.3 Invariant region for the reaction-diffusion system in the monostable case

In this subsection, we aim at proving that there exists a bounded invariant region for the dynamical system (2.2). Using a result by [Smo12], this allows us to deduce that the original reaction diffusion system (2.1) possesses the same invariant region, a result that is crucial in our subsequent analysis. Note that we only treat here the monostable case (green region in Figure 2.4), namely when the birth rate is greater than the mortality so that a single nontrivial equilibrium arises. Hence, we assume that

$$b \geq m \quad \text{whenever } b < 1, \text{ and } \quad b > m \quad \text{whenever } b \geq 1.$$

There are only two equilibria, which are (0,0) and (i^+,u^+). The bistable case will not be addressed in this section. We refer to section 2.4.4 for an analysis of the bistable case, based on results by [FM77] concerning reaction diffusion systems with bistable equilibria.

Proposition 1 *The first quadrant $\{i \geq 0,\ u \geq 0\}$ is an invariant region for the pure dynamical system (2.2).*

Proof : We define $F = \begin{pmatrix} f \\ g \end{pmatrix}$ the vector field associated with system (2.2).

On the edge $i = 0$ where the outward unit normal vector is $n := \begin{pmatrix} -1 \\ 0 \end{pmatrix}$, we have

$$\begin{cases} f(0,u) = \frac{u}{a}, \\ g(0,u) = -\frac{u}{\varepsilon}. \end{cases}$$

Thus, $F.n = -f(0,u) = -\frac{u}{a} < 0$ if $u > 0$.

On the edge $u = 0$ where the outward unit normal vector is $n := \begin{pmatrix} 0 \\ -1 \end{pmatrix}$, we have

$$\begin{cases} f(i,0) = \frac{b}{a}i(1-i) - mi, \\ g(i,0) = -\frac{u}{\varepsilon}. \end{cases}$$

Thus, $F.n = -g(i,0) = -\frac{i^2}{\varepsilon} < 0$ if $i > 0$.

When $i = u = 0$, $F = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$ and there is no flow.

Therefore, the positive quadrant is positively invariant, which means that if $u(0) \geq 0$ and $i(0) \geq 0$, then $u(t) \geq 0$ and $i(t) \geq 0$ for all $t \geq 0$.

□

Now, we aim at finding a bounded positively invariant region Σ for the reaction diffusion system (2.1), that is a domain Σ such that if $u(0) \in \Sigma$ and $i(0) \in \Sigma$, then $u(t) \in \Sigma$ and $i(t) \in \Sigma$ for all $t > 0$. In fact, we will construct an invariant rectangle as such a bounded positively invariant region.

For convenience, let us rewrite system (2.1) as:

$$v_t = Dv_{xx} + F(t,v), \tag{2.3}$$

where

$$D = \begin{pmatrix} 0 & 0 \\ 0 & d^2/\varepsilon \end{pmatrix} \tag{2.4}$$

and

$$F(t,v) = \begin{pmatrix} (u+bi)(1-i) - mi \\ \dfrac{\dfrac{a}{i^2} - u}{\varepsilon} \end{pmatrix}, \tag{2.5}$$

with initial condition

$$v(0,x) = \begin{pmatrix} i \\ u \end{pmatrix}(0,x) = \begin{pmatrix} i_0 \\ u_0 \end{pmatrix}(x). \tag{2.6}$$

From now on and until the end of this subsection, we assume that the reaction-diffusion problem (2.3)-(2.6) admits a local (in time) solution that is continuous (say) in the space variable x. We refer to the subsequent sections for the proof of this local existence result.

Definition 1 *A closed subset $\Sigma \subset \mathbb{R}^2$ is called a (positively) invariant region for the local solution of (2.3), (2.6), if any solution $v(t,x)$ satisfying $v^0(x) \in \Sigma$ for all x, satisfies $v(t,x) \in \Sigma$ for all $x \in \mathbb{R}$ and for all time t for which $v(t,x)$ is defined.*

We base our analysis on Corollary 14.8 from [Smo12] to construct such an invariant region Σ.

Lemma 1 *Consider system (2.3) with initial condition (2.6). Any region of the form*

$$\Sigma = \bigcap_{k=1}^{4} \{v : \Phi_k(v) < 0\} \tag{2.7}$$

is invariant for (2.3), provided the vector field F points strictly into Σ on $\partial\Sigma$, i.e. *for all $v \in \partial\Sigma$,*

$$\nabla\Phi_k(v) \cdot F(v) < 0$$

where $\Phi_k = 0$ defines a hyperplane in $\mathbb{R}^2$, $\nabla\Phi_k$ is the outward oriented normal vector on $\partial\Sigma$ and the region $[a_k,b_k]$ is a subset of $\Phi_k = 0$.

Remark 2 *We will refer to such an invariant region (2.7) as an invariant rectangle.*

Construction of the invariant region.

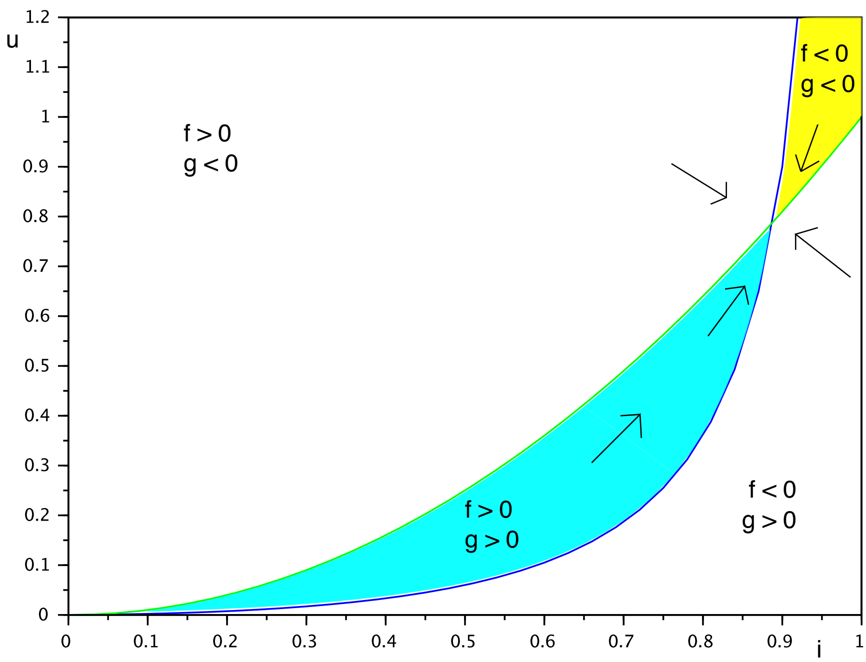
Recall that only two equilibria are biologically meaningful, namely (0,0) and (i^+,u^+). We restrict our attention to the monostable case (green region in Figure 2.4), namely $\{1 > b \geq m\} \cup \{b > m,\, b > 1\}$. We are interested in defining a rectangle in $\mathbb{R}^2_+$ that does not include the equilibrium (0,0). We define $\Phi_k = \Phi_k(v) = \Phi_k(i,u)$ so that for each $k = 1,...,4$, $\Phi_k = 0$ defines a hyperplane in $\mathbb{R}^2$, the intersection of the Φ_k's forms the boundary of Σ and $\nabla\Phi_k$'s give the outward oriented normal vectors to $\partial\Sigma$, as follows:

$$\begin{aligned}
\Phi_1 &= i - k_1\\
\Phi_2 &= u - k_2\\
\Phi_3 &= -i + \delta_1\\
\Phi_4 &= -u + \delta_2
\end{aligned}$$

where k_1, k_2, δ_1, δ_2 are constants that we choose such that $1 \geq k_1 > i^+$, $1 \geq k_2 > u^+$, $0 < \delta_1 < i^+$ and $0 < \delta_2 < u^+$. Besides, we also impose the following constraints on the parameters, namely $(k_2 + bk_1)(1 - k_1) - mk_1 < 0$ and $(k_1)^2 < k_2$, as well as $(\delta_1)^2 > \delta_2$

and $(\delta_2 + b\delta_1)(1-\delta_1) - m\delta_1 > 0$. Those choices are possible by taking $(k_1,k_2) = (i,u)$ in the (non empty) region $\{f < 0\} \cap \{g < 0\}$ of the plane, and $(\delta_1,\delta_2) = (i,u)$ in the (non empty) region $\{f > 0\} \cap \{g > 0\}$ of the plane, delimited by the null clines of (2.1). Those regions are represented in yellow and blue in Figure 2.5.

FIG. 2.5 – *Regions of the phase plane where the constraints on the k_i's (in yellow) and the δ_i's (in blue) are satisfied*



For $\Phi_1 = 0 \iff i = k_1$ and with the condition $u < k_2$ due to $\Phi_2 < 0$, since $\nabla\Phi_1 = (1,0)$, we have:

$$\begin{aligned}\big(\nabla\Phi_1 \cdot F\big)(k_1,u) = f(k_1,u) &= \frac{1}{a}\big[(u + bk_1)(1-k_1) - mk_1\big] \\ &\leq \frac{1}{a}\big[(k_2 + bk_1)(1-k_1) - mk_1\big] < 0.\end{aligned}$$

For $\Phi_2 = 0 \iff u = k_2$, and with the condition $i < k_1$ due to $\Phi_1 < 0$, since $\nabla\Phi_2 = (0,1)$, we have:

$$\begin{aligned}\big(\nabla\Phi_2 \cdot F\big)(i,k_2) &= g(i,k_2) = \frac{1}{\varepsilon}\big[i^2 - k_2\big] \\ &\leq \frac{1}{\varepsilon}\big[(k_1)^2 - k_2\big] < 0.\end{aligned}$$

For $\Phi_3 = 0 \iff i = \delta_1$ and with the condition $u > \delta_2$ due to $\Phi_4 < 0$, since $\nabla\Phi_3 = (-1,0)$, we have:

$$\begin{aligned}\big(\nabla\Phi_3 \cdot F\big)(\delta_1,u) &= -f(\delta_1,u) = -\frac{1}{a}\big[(u + b\delta_1)(1-\delta_1) - m\delta_1\big] \\ &\leq \frac{1}{a}\big[(\delta_2 + b\delta_1)(1-\delta_1) - m\delta_1\big] < 0.\end{aligned}$$

For $\Phi_4 = 0 \iff u = \delta_2$, and with $i > \delta_1$ due to $\Phi_3 < 0$, since $\nabla\Phi_4 = (0,-1)$, we have:

$$\begin{aligned}\big(\nabla\Phi_4 \cdot F\big)(i,\delta_2) &= -g(i,u) = -\frac{1}{\varepsilon}\big[i^2 - \delta_2\big] \\ &\leq -\frac{1}{\varepsilon}\big[(\delta_2)^2 - \delta_2\big] < 0.\end{aligned}$$

Therefore, defining the rectangle

$$\Sigma := \bigcap_{k=1}^{4} \Phi_k^{-1}\Big(\big] -\infty,0\big[\Big),$$

Lemma 1 asserts that Σ is a positively invariant region. In particular, choosing $(\delta_1,\delta_2) = (0,0)$ and $(k_1,k_2) = (1,1)$, the biologically relevant rectangle $[0,1] \times [0,1]$ is invariant.

Remark 3 *In fact, the previous analysis shows that the family of rectangles $[\delta_1,k_1] \times [\delta_2,k_2]$ is not only invariant but also contracting. Using this contraction property, and following [Smo12], we may prove that any solution starting in a rectangle $[\delta_1,k_1] \times [\delta_2,k_2]$ enters some smaller rectangle in finite time. Iterating the procedure, it is intuitively expected that any solution (i,u) goes to (i^+,u^+) as time goes to infinity.*

2.3 Mathematical study of the model

In this section, since the parameter values of m, b (and d) do not change the structure of the system, they do not play any role in this mathematical study. Hence, the results about local in time existence and uniqueness of solutions, and global existence of solutions, are both proved for all values of parameters m, b (and d) at once.

2.3.1 Local existence and uniqueness of solutions

We aim at proving that system (2.1) admits local (in time) solutions $\big(i(t,.),u(t,.)\big)$ defined for any $t \in [0,T]$ where T is the maximum time of existence. We define the function $\tilde{1}$ as

$$\tilde{1}(x) = \begin{cases} 1 & \text{if } x \in]-\infty,-1] \\ \varphi & \text{if } x \in]-1,1[\\ 0 & \text{if } x \in [1,+\infty[\end{cases} \tag{2.8}$$

where φ is a smooth function joining the constant states 0 and 1. Our main result of this section is the following.

Theorem 1 *There exists a unique solution* (i,u) *of system* (2.1) *where* i *and* u *belong to* $C^1\left([0,T],\alpha + H^{-1}(\mathbb{R})\right) \cap C^0\left([0,T],\alpha + H^1(\mathbb{R})\right)$ [3] *with* $\alpha = i^+\tilde{1}$ *for* i *and* $\alpha = (i^+)^2\tilde{1}$ *for* u.

Proof : Fix $T > 0$. We work on the functional space $C^1\left([0,T],i^+\tilde{1} + H^{-1}(\mathbb{R})\right) \cap C^0\left([0,T],i^+\tilde{1} + H^1(\mathbb{R})\right)$.

Consider two functions $i,u \in C^1\left([0,T],i^+\tilde{1} + H^{-1}(\mathbb{R})\right) \cap C^0\left([0,T],i^+\tilde{1} + H^1(\mathbb{R})\right)$.

For all $t \in [0,T]$, the functions $i(t,)$ and $u(t,.)$ belong to $\left(i^+\tilde{1} + H^1(\mathbb{R})\right)$.

Define the change of variables $i = i^+\tilde{1} + j$ and $u = i^+\tilde{1} + v$ [4], with $j,v \in C^0\left([0,T],H^1(\mathbb{R})\right)$.

3. This shorthand notation means that $(i,u) \in C^0\big((i^+\tilde{1} + H^1)^2\big)$ and that $(\partial_t i,\partial_t u) \in C^0\big((H^{-1})^2\big)$. Besides, $\tilde{1} + H^1$ denotes functions of the form $\tilde{1} + v$ with $v \in H^1$.

4. The reader should keep in mind that the letter v now is related to u through the relation $u = (i^+\tilde{1})^2 + v$. This is in contrast with the previous paragraphs, where v stands for the pair (i,u).

The initial system

$$\begin{cases} a\partial_t i &= (u+bi)(1-i)-mi \\ \varepsilon\partial_t u &= i^2-u+d^2\partial_{xx}u \end{cases}$$

can be written as

$$\begin{cases} a\partial_t j = \alpha_0+\beta_1 j+\beta_2(bj+v)-j(bj+v) \\ \varepsilon\partial_t v = -(1-d^2\partial_{xx})v+\gamma_0+\gamma_1 j+j^2 \end{cases} \tag{2.9}$$

with

$$\begin{aligned} \alpha_0 &= \big((i^+\tilde{1})^2+bi^+\tilde{1}\big)\big(1-i^+\tilde{1}\big)-mi^+\tilde{1} \\ \beta_1 &= -\big(m+(b+i^+\tilde{1})i^+\tilde{1}\big) \\ \beta_2 &= 1-i^+\tilde{1} \\ \gamma_0 &= d^2\partial_{xx}\big[(i^+\tilde{1})^2\big] \\ \gamma_1 &= 2i^+\tilde{1}. \end{aligned}$$

It is easily observed that

$$\alpha_0,\ \alpha_1,\ \alpha_2,\ \gamma_0,\ \gamma_1 \in W^{1,\infty}.$$

The key point to our analysis now lies in the fact, by definition of i^+ as an equilibrium point of the vector field F, we also have

$$\alpha_0 \in H^1, \quad \gamma_0 \in H^1.$$

We may therefore write

$$\partial_t \begin{pmatrix} j \\ v \end{pmatrix} = \begin{pmatrix} 0 \\ -\frac{1}{\varepsilon}(1-d^2\partial_{xx})v \end{pmatrix} + \begin{pmatrix} f(j,v)/a \\ g(j,v)/\varepsilon \end{pmatrix},$$

with[5] f, g defined as

$$\begin{aligned} f(j,v) &= \alpha_0+\beta_1 j+\beta_2(bj+v)-j(bj+v); \\ g(j,v) &= \gamma_0+\gamma_1 j+j^2. \end{aligned}$$

5. Again, the reader should keep in mind that the letters f and g now stand for functions depending on (j,v), in contrast with the previous paragraphs where they stand for functions depending on (i,u).

The point now lies in observing, as we do in the next few lines, that f, g map $H^1 \times H^1$ to itself, in a locally Lipschitz fashion.

Lemma 2 *If u, $v \in H^1(\mathbb{R})$, then $uv \in H^1(\mathbb{R})$.*

Proof : Since u, $v \in H^1(\mathbb{R})$, then u, $v \in L^\infty(\mathbb{R})$ by Sobolev embedding.
Thus, we have $||uv||_{L^2} \leq ||u||_{L^\infty}||v||_{L^2} < +\infty$, and $uv \in L^2(\mathbb{R})$.

Besides, we have $\nabla(uv) = (\nabla u)v + u(\nabla v)$ and

$$\begin{aligned}|\nabla(uv)|^2 &\leq |u|^2|\nabla v|^2 + 2|u||v||\nabla u||\nabla v| + |v|^2|\nabla u|^2 \\ &\leq |u|^2|\nabla v|^2 + |u||v|(|\nabla u|^2 + |\nabla v|^2) + |v|^2|\nabla u|^2.\end{aligned}$$

Since u, $v \in L^\infty(\mathbb{R})$ and ∇u, $\nabla v \in L^2(\mathbb{R})$, we deduce that $||\nabla(uv)||_{L^2} < +\infty$ and that $\nabla(uv) \in L^2(\mathbb{R})$.

As a conclusion, we have $uv \in H^1(\mathbb{R})$.

□

Remark 4 *We can even prove the inequality $||uv||_{H^1(\mathbb{R})} \leq 2||u||_{H^1(\mathbb{R})}||v||_{H^1(\mathbb{R})}$.*

This, together with the fact that α_0 and γ_0 belong to H^1, proves that f and g are well defined with values in H^1.

For notational convenience, we write without ambiguity respectively j and v instead of $j(t,.)$ and $v(t,.)$.

For any initial datum $\begin{pmatrix} j_0 \\ v_0 \end{pmatrix}$, we define $\Phi : H^1 \times H^1 \to H^1 \times H^1$ through

$$\Phi \begin{pmatrix} j \\ v \end{pmatrix} = \begin{pmatrix} j_0 \\ e^{-\frac{t}{\varepsilon}(1-d^2\partial_{xx})}v_0 \end{pmatrix} + \int_0^t \begin{pmatrix} f(j,v) \\ e^{-\frac{t-s}{\varepsilon}(1-d^2\partial_{xx})}g(j,v) \end{pmatrix} (s,.)\, \mathrm{d}s.$$

where j_0 and v_0 are given initial data, fixed throughout this paragraph. More precisely, the map Φ satisfies:

$$\begin{array}{ccccc} \Phi & : & \left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2 & \longrightarrow & \left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2 \\ & & \left[t \mapsto \begin{pmatrix} j(t,.) \\ v(t,.) \end{pmatrix}\right] & \longmapsto & \Phi\begin{pmatrix} j \\ v \end{pmatrix} \end{array}$$

where

$$\Phi\begin{pmatrix} j \\ v \end{pmatrix} = \left[t \mapsto \begin{pmatrix} j_0 \\ e^{-\frac{t}{\varepsilon}(1-d^2\partial_{xx})}v_0 \end{pmatrix} + \int_0^t \begin{pmatrix} f(j,v) \\ e^{-\frac{t-s}{\varepsilon}(1-d^2\partial_{xx})}g(j,v) \end{pmatrix}(s,.)\,\mathrm{d}s\right].$$

We seek a fixed point of this map Φ.

Remark 5 *We define Φ on $\left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$ rather than on $\left(C^1\left([0,T],H^{-1}(\mathbb{R})\right)\cap C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$. Indeed, the C^1 nature comes from the fact that if our solution belongs to $\left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$ and is also C^1 in time, then the solution belongs to $\left(C^1\left([0,T],H^{-1}(\mathbb{R})\right)\cap C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$. This justifies that we do our fixed point procedure only on $\left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$. This functional space is equipped with the norm*

$$\left\|\begin{pmatrix} j \\ v \end{pmatrix}\right\|_{(C^0([0,T],H^1(\mathbb{R})))^2} = \sup_{t\in[0,T]}\left(\left\|\begin{pmatrix} j \\ v \end{pmatrix}(t,.)\right\|_{H^1(\mathbb{R})\times H^1(\mathbb{R})}\right).$$

Remark 6 *We also consider the following norm on $H^1 \times H^1$:*

$$||(j_1,v_1) - (j_2,v_2)||^2_{H^1\times H^1} = ||j_1 - j_2||^2_{H^1} + ||v_1 - v_2||^2_{H^1}.$$

In what follows, we sometimes denote $A := -\frac{1}{\varepsilon}(1 - d^2\partial_{xx})$.

i) We first prove that Φ maps $\left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$ to $\left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$.

Lemma 3 *e^{tA} maps H^1 to H^1 with an operator norm less than 1.*

Proof : We recall that:

$$u \in H^1 \Longleftrightarrow \widehat{u} \in L^2_{1+|\xi|^2} \Longleftrightarrow (1+|\xi|^2)^{\frac{1}{2}}\widehat{u} \in L^2.$$

Besides, $e^{-t|\xi|^2} \in L^2$ and even L^∞.

Since $|e^{-t|\xi|^2}\widehat{u}|^2 \leq |\widehat{u}|^2$, then $|(1+|\xi|^2)^{\frac{1}{2}}e^{-t|\xi|^2}\widehat{u}|^2 \leq (1+|\xi|^2)^{\frac{1}{2}}|\widehat{u}|^2$.

Hence, $e^{-t|\xi|^2}\widehat{u} \in H^1$ and $e^{t\partial_{xx}}u := \mathcal{F}^{-1}(e^{-t|\xi|^2}\widehat{u}) \in H^1$.

Define

$$\widehat{e^{tA}u} := e^{-\frac{t}{\varepsilon}(I+d^2\xi^2)}\widehat{u}.$$

Thus, we have

$$||\widehat{e^{tA}u}||_{H^1} = ||e^{-\frac{t}{\varepsilon}(I+d^2\xi^2)}\widehat{u}||_{H^1} \leq ||\widehat{u}||_{H^1}.$$

Moreover, for all $u \in H^1$, we have

$$||\widehat{u}||_{H^1} = ||(1+\xi^2)^{\frac{1}{2}}\widehat{\widehat{u}}||_{L^2} = ||(1+\xi^2)^{\frac{1}{2}}u(-\xi)||_{L^2} = ||(1+\xi^2)^{\frac{1}{2}}u(\xi)||_{L^2} = ||u||_{H^1}.$$

As a conclusion, we deduce the following inequality

$$||e^{tA}u||_{H^1} = ||\widehat{e^{tA}u}||_{H^1} \leq ||\widehat{u}||_{H^1} = ||u||_{H^1}.$$

□

This allows to say that Φ maps $\left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$ into itself.

ii) Let us show that Φ is a local contraction on $\left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$ for T small enough.

We work on $\left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$ which is a Banach space. Let $B = \overline{B(0,R)} \subset H^1(\mathbb{R})$ be a closed ball where R is chosen so that $(j_0,v_0) \in B(0,R/2)$.

Consider $\begin{pmatrix} j_1 \\ v_1 \end{pmatrix}, \begin{pmatrix} j_2 \\ v_2 \end{pmatrix}$ with j_1, j_2, v_1, $v_2 \in B$, $\big(i.e\ ||j_i||_{H^1(\mathbb{R})}, ||v_i||_{H^1(\mathbb{R})} \leq R, \forall i = 1,2\big)$.

We first show that f, g are locally Lipschitz functions. First of all, we have

$$
\begin{aligned}
& f(j_1,v_1) - f(j_2,v_2) \\
& = \beta_1(j_1 - j_2) + b\beta_2(j_1 - j_2) + \beta_2(v_1 - v_2) \\
& - b(j_1 + j_2)(j_1 - j_2) - j_1 v_1 + j_2 v_2 \\
& = \beta_1(j_1 - j_2) + b\beta_2(j_1 - j_2) + \beta_2(v_1 - v_2) \\
& - b(j_1 + j_2)(j_1 - j_2) + (j_2 - j_1)v_1 + j_2(v_2 - v_1) \\
& = \big[\beta_1 + b\beta_2 - v_1 - b(j_1 + j_2)\big](j_1 - j_2) + \big[\beta_2 - j_2\big](v_1 - v_2).
\end{aligned}
$$

Thus, we have

$$
\begin{aligned}
||f(j_1,v_1) - f(j_2,v_2)||_{L^2} &\leq c_1||j_1 - j_2||_{L^2} + c_2||v_1 - v_2||_{L^2} \\
&\leq c_1||j_1 - j_2||_{H^1} + c_2||v_1 - v_2||_{H^1}
\end{aligned}
$$

with

$$
c_1 = c_1(R,b,m) := \|\beta_1 + b\beta_2 - v_1 - b(j_1 + j_2)\|_{L^\infty} < +\infty
$$

and

$$
c_2 = c_2(R,b,m) := \|\beta_2 - j_2\|_{L^\infty} < +\infty,
$$

since $\|v\|_{L^\infty} \leq C_0\|v\|_{H^1} \leq C_0 R$ and $\|j_1+j_2\|_{L^\infty} \leq 2C_0 R$, where C_0 is a Sobolev constant.

Hence, we obtain the following inequality

$$
||f(j_1,v_1) - f(j_2,v_2)||_{L^2}^2 \leq C_1 \left(||j_1 - j_2||_{H^1}^2 + ||v_1 - v_2||_{H^1}^2\right). \tag{2.10}
$$

with $C_1 = C_1(R,b,m) := 2\max(c_1^2,c_2^2) < +\infty$.

Besides, we have

$$
\begin{aligned}
& \nabla[f(j_1,v_1) - f(j_2,v_2)] \\
& = \big[\beta_1 + b\beta_2 - v_1 - b(j_1 + j_2)\big]\nabla(j_1 - j_2) + \big[\beta_2 - j_2\big]\nabla(v_1 - v_2) \\
& + \big[\nabla\beta_1 + b\nabla\beta_2 - \nabla v_1 + b\nabla(j_1 + j_2)\big](j_1 - j_2) - \big[\nabla\beta_2 + \nabla j_2\big](v_1 - v_2).
\end{aligned}
$$

Hence, it follows

$$\begin{aligned}
&||\nabla\big(f(j_1,v_1) - f(j_2,v_2)\big)||_{L^2} \\
&\leq c_1||\nabla(j_1 - j_2)||_{L^2} + c_2||\nabla(v_1 - v_2)||_{L^2} + c_3\|j_1 - j_2\|_{L^\infty} + c_4\|v_1 - v_2\|_{L^\infty} \\
&\leq (c_1 + c_3)||j_1 - j_2||_{H^1} + (c_2 + c_4)||v_1 - v_2||_{H^1}
\end{aligned}$$

with

$$c_3 = c_3(R,b,m) := ||\nabla\beta_1 + b\nabla\beta_2 - \nabla v_1 + b\nabla(j_1 + j_2)||_{L^2}$$

and

$$c_4 = c_4(R,b,m) := ||\nabla\beta_2 + \nabla j_2||_{L^2}$$

Thus, we obtain the inequality

$$\nabla[f(j_1,v_1) - f(j_2,v_2)]||_{L^2}^2 \leq C_2\left(||j_1 - j_2||_{H^1}^2 + ||v_1 - v_2||_{H^1}^2\right), \tag{2.11}$$

with

$$C_2 = C_2(R,b,m) := 2\big(\max(c_1 + c_3,c_2 + c_4)\big)^2$$

To conclude, (2.10) and (2.11) provide

$$||f(j_1,v_1) - f(j_2,v_2)||_{H^1}^2 \leq C_3\left(||j_1 - j_2||_{H^1}^2 + ||v_1 - v_2||_{H^1}^2\right).$$

with

$$C_3 = C_3(R,b,m) := C_1 + C_2,$$

Namely

$$||f(j_1,v_1) - f(j_2,v_2)||_{H^1} \leq C_3||(j_1,v_1) - (j_2,v_2)||_{H^1\times H^1}. \tag{2.12}$$

On the other hand, we have

$$g(j_1,v_1) - g(j_2,v_2) = \frac{1}{\varepsilon}\big(\gamma_1(j_1 - j_2) + j_1^2 - j_2^2\big)$$
$$= \frac{1}{\varepsilon}\big(\gamma_1 + j_1 + j_2\big)(j_1 - j_2).$$

Thus, by similar methods as above, we establish the inequality

$$||g(j_1,v_1) - g(j_2,v_2)||_{L^2}^2 \leq d_1\big(||j_1 - j_2||_{H^1}^2 + ||v_1 - v_2||_{H^1}^2\big)$$

with

$$d_1 := d_1(R,b,m,d,\varepsilon) = \frac{1}{\varepsilon^2}(\|\gamma_1\|_{L^\infty} + 2R)^2 < +\infty$$

and the inequality on the gradient

$$||\nabla[g(j_1,v_1) - g(j_2,v_2)]||_{H^1}^2 \leq d_2\big(||j_1 - j_2||_{H^1}^2 + ||v_1 - v_2||_{H^1}^2\big)$$

with

$$d_2 := d_2(R,b,m,\varepsilon) = \frac{2}{\varepsilon^2}\big(\|\gamma_1 + j_1 + j_2\|_{L^\infty} + \|\nabla\gamma_1 + \nabla j_1 + \nabla j_2\|_{L^2}\big)^2 < +\infty.$$

As a conclusion, we obtain

$$||g(j_1,v_1) - g(j_2,v_2)||_{H^1} \leq D_3||(j_1,v_1) - (j_2,v_2)||_{H^1\times H^1}.$$

with

$$D_3 = D_3(R,b,m,\varepsilon) := d_1 + d_2.$$

Therefore, f and g are locally Lipschitz functions from $H^1 \times H^1$ to H^1.

Eventually, we have

$$\Phi(j_1,v_1) - \Phi(j_2,v_2) = \int_0^t \begin{pmatrix} f(j_1,v_1) - f(j_2,v_2) \\ e^{-\frac{t-s}{\varepsilon}(1-d^2\partial_{xx})}(g(j_1,v_1) - g(j_2,v_2)) \end{pmatrix} (s)\ \mathrm{d}s.$$

Thus :

$$
\begin{aligned}
&\left\| \Phi \begin{pmatrix} j_1 \\ v_1 \end{pmatrix} - \Phi \begin{pmatrix} j_2 \\ v_2 \end{pmatrix} \right\|_{H^1 \times H^1} (s) \\
&\leq \int_0^t \left\| \begin{pmatrix} f(j_1,v_1) - f(j_2,v_2) \\ e^{-\frac{t-s}{\varepsilon}(1-d^2\partial_{xx})}\big(g(j_1,v_1) - g(j_2,v_2)\big) \end{pmatrix} \right\|_{H^1 \times H^1} (s)\ \mathrm{d}s \\
&= \int_0^t \sqrt{\|f(j_1,v_1) - f(j_2,v_2)\|_{H^1}^2 + e^{-2\frac{t-s}{\varepsilon}} \|g(j_1,v_1) - g(j_2,v_2)\|_{H^1}^2} (s)\ \mathrm{d}s \\
&\leq \int_0^t \left(\|f(j_1,v_1) - f(j_2,v_2)\|_{H^1} + e^{-\frac{t-s}{\varepsilon}} \|g(j_1,v_1) - g(j_2,v_2)\|_{H^1} \right) (s)\ \mathrm{d}s \\
&\leq \int_0^t C_3 \left\| \begin{pmatrix} j_1 \\ v_1 \end{pmatrix} - \begin{pmatrix} j_2 \\ v_2 \end{pmatrix} \right\|_{H^1 \times H^1} (s)\ \mathrm{d}s + \int_0^t D_3 \left\| \begin{pmatrix} j_1 \\ v_1 \end{pmatrix} - \begin{pmatrix} j_2 \\ v_2 \end{pmatrix} \right\|_{H^1 \times H^1} (s)\ \mathrm{d}s \\
&\leq C_3 T \left\| \begin{pmatrix} j_1 \\ v_1 \end{pmatrix} - \begin{pmatrix} j_2 \\ v_2 \end{pmatrix} \right\|_{C^0(H^1) \times C^0(H^1)} + D_3 T \left\| \begin{pmatrix} j_1 \\ v_1 \end{pmatrix} - \begin{pmatrix} j_2 \\ v_2 \end{pmatrix} \right\|_{C^0(H^1) \times C^0(H^1)} \\
&\leq (C_3 + D_3)\, T \left\| \begin{pmatrix} j_1 \\ v_1 \end{pmatrix} - \begin{pmatrix} j_2 \\ v_2 \end{pmatrix} \right\|_{C^0(H^1) \times C^0(H^1)} .
\end{aligned}
$$

Thus, we deduce

$$
\left\| \Phi \begin{pmatrix} j_1 \\ v_1 \end{pmatrix} - \Phi \begin{pmatrix} j_2 \\ v_2 \end{pmatrix} \right\|_{C^0(H^1) \times C^0(H^1)} (s) \leq C(R)\ T\ \left\| \begin{pmatrix} j_1 \\ v_1 \end{pmatrix} - \begin{pmatrix} j_2 \\ v_2 \end{pmatrix} \right\|_{C^0(H^1) \times C^0(H^1)} .
$$

with

$$
C(R) = C(R,b,m,\varepsilon) := C_3 + D_3.
$$

As a consequence, for $T < \frac{1}{C(R)}$, Φ is a contraction on $\left(C^0\left([0,T],\overline{B(0,R)}\right)\right)^2$.

Naturally, similar estimates show that Φ maps $\left(C^0\left([0,T],\overline{B(0,R)}\right)\right)^2$ into itself provided $T < \frac{R}{2C(R)}$. Therefore, we deduce that Φ admits a unique fixed point $\begin{pmatrix} j \\ v \end{pmatrix}$ such that $\Phi \begin{pmatrix} j \\ v \end{pmatrix} = \begin{pmatrix} j \\ v \end{pmatrix}$, *i.e.* for any initial datum $\begin{pmatrix} j_0 \\ v_0 \end{pmatrix}$, there exists a unique solution $\begin{pmatrix} j \\ v \end{pmatrix}$ to system (2.9). As a consequence, there exists a unique local in time solution

$(i,u) \in \left(C^0\left([0,T],H^1(\mathbb{R})\right)\right)^2$ to the original system (2.1).

$\square$

In section 2.2.3, we proved that there exists a bounded invariant region for any pair of solution (i,u) choosing $k_1 > i^+$ and $k_2 > u^+$ arbitrarily large. Thus, since $i^+ < 1$ and $u^+ < 1$, we can choose $k_1 = k_2 = 1$ which provides us the following property.

Proposition 2 *Any (i,u) solution of (2.1) satisfies $\|i\|_{L^\infty} \leq 1$ and $\|u\|_{L^\infty} \leq 1$.*

Remark 7 *Since i and u lie in $[0,1]$, we deduce that $j = i - i^+\tilde{1}$ and $v = u - (i^+\tilde{1})^2$ also satisfy $\|j\|_{L^\infty} \leq 1$ and $\|v\|_{L^\infty} \leq 1$.*

2.3.2 Global existence of solutions

In this section, we prove that the unique solution constructed in the last section is actually global in time. In other words, this solution is defined for any time $t \geq 0$. We remind the reader that the results presented in this paragraph hold true for any value of the parameters m, b (and d).

Theorem 2 *The solution of system (2.1) is global in time, that is we can choose $T = +\infty$, for any $\varepsilon > 0$.*

Proof : We prove this result by contradiction. Let us assume that $T < +\infty$, where T is the maximum time of existence.

As previously, we work on the system

$$\begin{cases} a\partial_t j = \alpha_0 + \beta_1 j + \beta_2(bj + v) - j(bj + v) \\ \varepsilon \partial_t v = -(1 - d^2\partial_{xx})v + \gamma_0 + \gamma_1 j + j^2 \end{cases}$$

We define

$$U^0 = (1 - d^2\partial_{xx})^{-1}(i^2) = (1 - d^2\partial_{xx})^{-1}((i^+\tilde{1})^2 + 2i^+\tilde{1}j + j^2).$$

Moreover, define

$$v = V^0 + w,$$

with $w \in H^1(\mathbb{R})$ and

$$V^0 = (1 - d^2\partial_{xx})^{-1}(d^2\partial_{xx}[(i^+\tilde{1})^2] + 2i^+\tilde{1}j + j^2) = (1 - d^2\partial_{xx})^{-1}(\gamma_0 + \gamma_1 j + j^2).$$

Thus: $V^0 = U^0 - (i^+\tilde{1})^2$.

Lemma 4 *The operator $(1 - d^2\partial_{xx})^{-1}$ maps H^1 into H^1.*

Proof : Let $\phi \in H^1(\mathbb{R})$, and recall that $H(x) = \frac{1}{2d}e^{\frac{-|x|}{d}}$. Then:

$$\begin{aligned}
\left\|(1 - d^2\partial_{xx})^{-1}\phi\right\|_{L^2} &= \|H \star \phi\|_{L^2} \\
&\le \|H\|_{L^1} \|\phi\|_{L^2} \\
&\le \|\phi\|_{L^2} \\
&< +\infty.
\end{aligned}$$

Besides,

$$\begin{aligned}
\left\|\nabla(1 - d^2\partial_{xx})^{-1}\phi\right\|_{L^2} &= \left\|(1 - d^2\partial_{xx})^{-1}\nabla\phi\right\|_{L^2} \\
&= \|H \star \nabla\phi\|_{L^2} \\
&\le \|H\|_{L^1} \|\nabla\phi\|_{L^2} \\
&\le \|\nabla\phi\|_{L^2} \\
&< +\infty.
\end{aligned}$$

□

Lemma 5 *There exists a constant $C > 0$ independent of t and ε such that $\|w\|_{L^\infty} \le C$.*

Proof : We have $w = v - V^0 = v - (1 - d^2\partial_{xx})^{-1}(\gamma_0 + \gamma_1 j + j^2)$.

Thus, the triangle inequality gives

$$||w||_{L^\infty} \leq ||v||_{L^\infty} + \left\|(1 - d^2\partial_{xx})^{-1}\left(\gamma_0 + \gamma_1 j + j^2\right)\right\|_{L^\infty}.$$

Furthermore, we have

$$\begin{aligned}&(1 - d^2\partial_{xx})^{-1}\left(\gamma_0 + \gamma_1 j + j^2\right)(x)\\ &= \int_{\mathbb{R}} H(x-y)\left(\gamma_0 + \gamma_1 j + j^2\right)(y)\,\mathrm{d}y\end{aligned}$$

with $H(x) = \frac{1}{2d} e^{\frac{-|x|}{d}}$.

Thus, since $||j||_{L^\infty} \leq 1$ according to Remark 7, we have

$$\begin{aligned}&\left|(1 - d^2\partial_{xx})^{-1}\left(\gamma_0 + \gamma_1 j + j^2\right)(x)\right|\\ &\leq \int_{\mathbb{R}} H(x-y)\left|\gamma_0 + \gamma_1 j + j^2\right|(y)\mathrm{d}y\\ &\leq \left(||\gamma_0 + \gamma_1 j + j^2||_{L^\infty}\right)\int_{\mathbb{R}} H(x-y)\mathrm{d}y\\ &\leq 1 + ||\gamma_0||_{L^\infty} + ||\gamma_1||_{L^\infty}.\end{aligned}$$

Moreover, $||v||_{L^\infty}$ is bounded by a constant independent of t and ε.

Therefore, $||w||_{L^\infty} \leq C$ with C independent of t and ε.

$\square$

This also proves that V^0 is well defined on H^1 and $||V^0||_{L^2} \leq C < +\infty$ with a constant C that does not depend on T. Let us now establish some bounds that are useful in the sequel.

Bounds on $||(j,w)||_{L^2}$ **:**

$$\begin{aligned}\partial_t j &= \frac{1}{a}\big(\alpha_0 + \beta_1 j + \beta_2(bj + V^0 + w) - j(bj + V^0 + w)\big)\\ &= \frac{1}{a}\big(\alpha_0 + \beta_1 j + (\beta_2 - j)V^0 + (\beta_2 - j)(bj + w)\big).\end{aligned}$$

Thus, we have

$$j(t) = \frac{1}{a}\big(j_0 + \int_0^t \big[\alpha_0 + \beta_2 V^0 + [\beta_1 - V^0 + b\beta_2 - w]j + \beta_2 w - bj^2\big](s)\ \mathrm{d}s.\big)$$

Hence, we deduce

$$||j(t)||_{L^2} \leq \kappa_1 + \kappa_2 T + \kappa_3 \int_0^t (||j(s)||_{L^2} + ||w(s)||_{L^2})\ \mathrm{d}s$$

with

$$\begin{aligned}
\kappa_1 &:= \frac{1}{a}||j_0||_{L^2} \\
\kappa_2 &:= \frac{1}{a}||\alpha_0 + \beta_2 V^0||_{L^2} \\
\kappa_3 &:= \frac{1}{a}\max\big(\|\beta_1 - V^0 + b\beta_2\|_{L^\infty} + \|w\|_{L^\infty} + b\|j\|_{L^\infty}, \|\beta_2\|_{L^\infty}\big).
\end{aligned}$$

Furthermore, we have

$$\begin{aligned}
\varepsilon\partial_t w &= \varepsilon\partial_t v - \varepsilon\partial_t V^0 \\
&= -(1 - d^2\partial_{xx})v + \gamma_0 + \gamma_1 j + j^2 - \varepsilon\partial_t(1 - d^2\partial_{xx})^{-1}\left(\gamma_0 + \gamma_1 j + j^2\right) \\
&= -(1 - d^2\partial_{xx})(v - V^0) - \varepsilon(1 - d^2\partial_{xx})^{-1}\left(\gamma_1\partial_t j + 2j\partial_t j\right) \\
&= -(1 - d^2\partial_{xx})w - 2\varepsilon(1 - d^2\partial_{xx})^{-1}\left((i^+\tilde{1} + j)\partial_t j\right).
\end{aligned}$$

Therefore, Duhamel's formula yields :

$$w(t) = e^{-\frac{t}{\varepsilon}(1-d^2\partial_{xx})}w_0 - 2\int_0^t e^{-\frac{t-s}{\varepsilon}(1-d^2\partial_{xx})}(1 - d^2\partial_{xx})^{-1}\left((i^+\tilde{1} + j)\partial_t j\right)(s)\ \mathrm{d}s.$$

Thus, we have the following inequality

$$\begin{aligned}
||w(t)||_{L^2} &\leq ||w_0||_{L^2} + 2\int_0^t ||i^+\tilde{1} + j||_{L^\infty}||\partial_t j||_{L^2}(s)\ \mathrm{d}s \\
&\leq \kappa_4 + \kappa_5 T + \kappa_6 \int_0^t (||j(s)||_{L^2} + ||w(s)||_{L^2})\ \mathrm{d}s.
\end{aligned}$$

with

$$\begin{aligned}
\kappa_4 &:= ||w_0||_{L^2} \\
\kappa_5 &:= 2\|i^+\tilde{1} + j\|_{L^\infty}\kappa_2 \\
\kappa_6 &:= 2\|i^+\tilde{1} + j\|_{L^\infty}\kappa_3.
\end{aligned}$$

Here, we used the estimates established above on $\|\partial_t j\|_{L^2}$.

Hence, we obtain

$$||j(t)||_{L^2} + ||w(t)||_{L^2} \leq K_1 \left(1 + \int_0^t (||j(s)||_{L^2} + ||w(s)||_{L^2}) \ \mathrm{d}s\right).$$

with

$$K_1 = K_1(T) := \max\big(\kappa_1 + \kappa_4 + (\kappa_2 + \kappa_5)T, \kappa_3 + \kappa_6\big)$$

By Gronwall's Lemma, we deduce

$$||(j,w)||_{L^2} \leq K_1 e^{K_1 T} < +\infty.$$

Remark 8 *We proved in passing that* $\|\partial_t j\|_{L^2} \leq C(T)$. *A similar proof provides a similar inequality for* $\|\nabla(\partial_t j)\|_{L^2}$ *as we see below.*

Bounds on $||(\nabla j, \nabla w)||_{L^2}$ ***:***

$$\begin{aligned}
a\partial_t(\nabla j) &= \nabla\alpha_0 + j\nabla\beta_1 + v\nabla\beta_2 + \beta_2 v + (b\beta_2 - v - 2bj)\nabla j + (\beta_2 - j)\nabla v \\
&= \nabla\alpha_0 + j\nabla\beta_1 + (V^0 + w)\nabla\beta_2 + \beta_2(V^0 + w) + (b\beta_2 - V^0 - w - 2bj)\nabla j \\
&+ (\beta_2 - j)\nabla V^0 + \nabla w.
\end{aligned}$$

Besides, we have

$$\nabla j(t) = \nabla j_0 + \int_0^t \partial_t \nabla j(s) \ \mathrm{d}s.$$

By the same method as for $||j||_{L^2}$, we can similarly prove that

$$\|\partial_t(\nabla j)\|_{L^2} \leq \lambda_2 + \lambda_3\big(\|\nabla j\|_{L^2} + \|\nabla w\|_{L^2}\big)$$

and thus

$$||\nabla j(t)||_{L^2} \leq \lambda_1 + \lambda_2 T + \lambda_3 \int_0^t \big(||\nabla j(s)||_{L^2} + ||\nabla w(s)||_{L^2}\big)\ \mathrm{d}s.$$

where the constants λ_1,λ_2,λ_3 are defined as

$$\begin{aligned}
\lambda_1 &:= \frac{1}{a}\|\nabla j_0\|_{L^2} \\
\lambda_2 &:= \frac{1}{a}\big(\|\nabla\alpha_0 + V^0\nabla\beta_2 + \beta_2 V^0 + \beta_2\nabla V^0\|_{L^2} + \|\nabla\beta_1 - \nabla V^0\|_{L^\infty}\|j\|_{L^2} \\
&\quad + \|\beta_2 + \nabla\beta_2\|_{L^\infty}\|w\|_{L^2}\big) \\
\lambda_3 &:= \frac{1}{a}\big(\max(\|b\beta_2 - v\|_{L^\infty} + 2b\|j\|_{L^\infty} + \|w\|_{L^\infty},1)\big).
\end{aligned}$$

Besides,

$$\varepsilon\partial_t(\nabla w) = -\big(1 - d^2\partial_{xx}\big)(\nabla w) - 2\varepsilon\big(1 - d^2\partial_{xx}\big)^{-1}\left(\nabla\{(i^+\tilde{1} + j)\partial_t j\}\right).$$

On the other hand,

$$\nabla\{(i^+\tilde{1} + j)\partial_t j\} = \big(\nabla(i^+\tilde{1}) + \nabla j\big)\partial_t j + \big(i^+\tilde{1} + j\big)\nabla(\partial_t j).$$

Since $\nabla(i^+\tilde{1})$ and ∇j belongs to L^2 and $\partial_t j$ belongs to L^∞ (by Lemma 5 in particular), then $\big(\nabla(i^+\tilde{1}) + \nabla j\big)\partial_t j \in L^2$.

Moreover, $i^+\tilde{1} + j \in L^\infty$ and $\nabla(\partial_t j) \in L^2$ since it contains the term $\partial_t j$ which belongs to L^2 according to Remark 8. For the other terms, since we have $v^0 \in H^1(\mathbb{R})$ according to Lemma 4 (and even in L^∞ according to Lemma 5), we have $(i^+\tilde{1}+j)\nabla(\partial_t j) \in L^2$.

From the above bounds, we also have the following inequality

$$||\nabla\{(i^+\tilde{1} + j)\partial_t j\}||_{L^2} \leq \mu_2 + \mu_3\big(||\nabla j||_{L^2} + ||\nabla w||_{L^2}\big).$$

with

$$\begin{aligned}
\mu_2 &:= \|\nabla(i^+\tilde{1}) + \nabla j\|_{L^2}\|\partial_t j\|_{L^\infty} + \lambda_2\|i^+\tilde{1} + j\|_{L^\infty} \\
\mu_3 &:= \max\left(\|\partial_t j\|_{L^\infty},\lambda_3\|i^+\tilde{1} + j\|_{L^\infty}\right).
\end{aligned}$$

In addition, we have

$$\nabla w(t) = e^{-\frac{t}{\varepsilon}(1-d^2\partial_{xx})}\nabla w_0 - 2\int_0^t e^{-\frac{t-s}{\varepsilon}(1-d^2\partial_{xx})}(1-d^2\partial_{xx})^{-1}\left(\nabla\{(i^+\tilde{1}+j)\partial_t j\}\right)(s)\ \mathrm{d}s.$$

Hence, we obtain

$$||\nabla w(t)||_{L^2} \leq \lambda_4 + \lambda_5 T + \lambda_6 \int_0^t (||\nabla j(s)||_{L^2} + ||\nabla w(s)||_{L^2})\ \mathrm{d}s.$$

where

$$\lambda_4 := \|\nabla w_0\|_{L^2}$$
$$\lambda_5 := 2\mu_2$$
$$\lambda_6 := 2\mu_3.$$

Eventually, we recover

$$||\nabla j(t)||_{L^2} + ||\nabla w(t)||_{L^2} \leq K_2\left(1 + \int_0^t (||\nabla j(s)||_{L^2} + ||\nabla w(s)||_{L^2})\ \mathrm{d}s\right).$$

with

$$K_2 = K_2(T) := \max\big(\lambda_1 + \lambda_4 + (\lambda_2+\lambda_5)T, \lambda_3 + \lambda_6\big).$$

By Gronwall's Lemma, we deduce

$$||(\nabla j, \nabla w)||_{L^2} \leq K_2 e^{K_2 T} < +\infty.$$

Conclusion : Taking $K = K(T) := \max(K_1, K_2)$, we proved that $||(j,w)||_{H^1} \leq Ke^{KT} < +\infty$, which is a contradiction with the assumption $T < +\infty$, due to the uniform boundedness principle.

Therefore, $T = +\infty$. This proves the global existence of the pair (j,w), namely the global existence of a pair (j,v) on $\left(C^0\left([0,+\infty], H^1(\mathbb{R})\right)\right)^2$. By bijectivity, we eventually obtain the global existence of a pair (i,u) on $\left(C^0\left([0,+\infty], i^+\tilde{1} + H^1(\mathbb{R})\right)\right)^2$.

□

2.4 Approximated systems

2.4.1 Convergence rate when $\varepsilon \to 0$

In this subsection, we aim at proving that any solution (i,u) of system (2.1) with $\varepsilon \neq 0$ converges to a solution (I^0,U^0) of system (2.1) with $\varepsilon = 0$. Note that the equation on u does not involve the birth and mortality rates: the subsequent analysis holds true for any value of the parameter m, b (and d). To prove this convergence, we work on the modified system (2.9) in (j,w), and prove the subsequent result.

Theorem 3 *The solution (j,w) of system (2.9) with $\varepsilon \neq 0$ converges to the solution (J^0,W^0) of system (2.9) with $\varepsilon = 0$ with a convergence rate $O\left(e^{-\frac{t}{\varepsilon}} + \varepsilon\right)$. In other words, for all $T > 0$, there exists a positive constant C_T (depending on T) such that for any $t \in [0,T]$, we have*

$$\|(j,w) - (J^0,W^0)\|_{H^1} \leq C_T \left(e^{-\frac{t}{\varepsilon}} + \varepsilon\right).$$

Remark 9 *The previous theorem provides that any solution (i,u) of (2.1) converges to (I^0,U^0) solution of the reduced system*

$$\begin{cases} a(I^0)_t = (U^0 + bI^0)(1 - I^0) - mI^0 \\ U^0 = \left(1 - d^2\partial_{xx}\right)^{-1}((I^0)^2). \end{cases}$$

Proof : By the previous section, we have

$$\partial_t w = -\frac{(1 - d^2\partial_{xx})}{\varepsilon} w - 2(1 - d^2\partial_{xx})^{-1}\left\{(i^+\tilde{1} + j)\partial_t j\right\}.$$

By Duhamel's formula, it follows that:

$$w(t) = e^{-\frac{t}{\varepsilon}(1-d^2\partial_{xx})} w_0 - 2\int_0^t e^{-\frac{t-s}{\varepsilon}(1-d^2\partial_{xx})}(1 - d^2\partial_{xx})^{-1}\left((i^+\tilde{1} + j)\partial_t j\right)(s)\ \mathrm{d}s.$$

According to Lemma 4, we know that $(1 - d^2\partial_{xx})^{-1}$ maps H^1 into H^1 with a norm less than 1. The same result can be proved if we replace H^1 by L^∞ using the same scheme of proof as Lemma 4. Furthermore, since $(i^+\tilde{1}+j)$ is bounded in L^∞ and $\partial_t j$ is bounded in L^2, then $(i^+\tilde{1}+j)\partial_t j$ has a norm less than a constant c_T depending on T. Thus, we have

$$\begin{aligned} ||w(t)||_{H^1} &\leq e^{-\frac{t}{\varepsilon}}||w_0||_{H^1} + \int_0^t c_T e^{-\frac{t-s}{\varepsilon}} \mathrm{d}s \\ &\leq C_T \left(e^{-\frac{t}{\varepsilon}} + \varepsilon\right) \underset{\varepsilon\to 0}{\longrightarrow} 0. \end{aligned}$$

with $C_T = \max\big(||w_0||_{H^1}, c_T\big)$.

Let (j,w) be a solution of system (2.9) for $\varepsilon \neq 0$ and (J^0,W^0) be a solution of system (2.9) for $\varepsilon = 0$. We can actually consider $W^0 = 0$ according to the inequality above.

For all $t \in [0, +\infty)$, we have

$$\partial_t(j - J^0) = f(j,w) - f(J^0,0)$$

with f a locally Lipschitz function with a Lipschitz constant k.

Thus:

$$\begin{aligned} ||\partial_t(j - J^0)||_{H^1} &\leq k\big(||j - J^0||_{H^1} + ||w||_{H^1}\big) \\ &\leq k||j - J^0||_{H^1} + kC_T\left(e^{-\frac{t}{\varepsilon}} + \varepsilon\right). \end{aligned}$$

Considering the same initial datum for j and J^0, namely $j(0,x) = J^0(0,x)$, we have:

$$\begin{aligned} ||j - J^0||_{H^1}(t) &\leq \int_0^t k||j - J^0||_{H^1}(s)\ \mathrm{d}s + kC_T \int_0^t \left(e^{-\frac{s}{\varepsilon}} + \varepsilon\right)\ \mathrm{d}s \\ &= k\int_0^t ||j - J^0||_{H^1}(s)\ \mathrm{d}s + kC_T\left(\varepsilon t + \varepsilon - \varepsilon e^{-\frac{t}{\varepsilon}}\right) \\ &\leq k\int_0^t ||j - J^0||_{H^1}(s)\ \mathrm{d}s + \underbrace{kC_T\varepsilon\,(t+1)}_{\underset{\varepsilon\to 0}{\longrightarrow} 0}. \end{aligned}$$

Hence, Gronwall's Lemma implies

$$\begin{aligned}||j - J^0||_{H^1}(t) &\leq kC_T\varepsilon\,(t+1) + \int_0^t C_T k^2 \varepsilon\,(s+1)\,e^{\int_s^t k\;\mathrm{d}\sigma}\;\mathrm{d}s \\ &= kC_T\varepsilon\Big(t+1+ke^{kt}\int_0^t (s+1)\,e^{-ks}\;\mathrm{d}s\Big) \\ &\leq kC_T\varepsilon\Big(t+1+ke^{kt}(t+1)\int_0^t e^{-ks}\;\mathrm{d}s\Big) \\ &= kC_T\varepsilon(t+1)\Big(1+ke^{kt}(\frac{1-e^{-kt}}{k})\Big) \\ &= kC_T(t+1)e^{kt}\varepsilon \underset{\varepsilon\to 0}{\longrightarrow} 0.\end{aligned}$$

Therefore, a solution (j,w) of system (2.9) with $\varepsilon \neq 0$ converges when $\varepsilon \to 0$ to a solution of the approximated system for $\varepsilon = 0$ with a convergence rate $O\left(e^{-\frac{t}{\varepsilon}} + \varepsilon\right)$.

As a conclusion, by virtue of the correspondance (i,u) with (j,w), the result is proved.

□

2.4.2 Application of the Centre Manifold Theorem

In this subsection, we aim at deriving a reduced quasy steady state dynamics, namely an approximated system whose correctors can be computed at any order. To do so, we need to check that our system satisfies the assumptions of the Centre Manifold Theorem in a partial differential equation framework. Even if the book of [Car12] is one of the pioneering works about applications to the Centre Manifold Theorem, we follow the PDE extension of [CHL09] and see how this can be applied to our case.

Recall that our initial system is :

$$\begin{cases} a\partial_t i &= (u+bi)(1-i) - mi \\ \varepsilon\partial_t u &= i^2 - u + d^2\partial_{xx}u. \end{cases}$$

Define the change of variables

$$i = i^+\tilde{1} + j,\;\; u = (i^+\tilde{1})^2 + v,\;\; v = V^0 + w,$$

with j, v, $w \in H^1(\mathbb{R})$ and

$$V^0 = (1 - d^2\partial_{xx})^{-1}(d^2\partial_{xx}[(i^+\tilde{1})^2] + 2i^+\tilde{1}j + j^2) = (1 - d^2\partial_{xx})^{-1}(\gamma_0 + \gamma_1 j + j^2).$$

Hence, we have

$$\begin{cases} \partial_t j & = \frac{1}{a}\big(\alpha_0 + \beta_1 j + \beta_2(bj + V^0 + w) - j(bj + V^0 + w)\big) \\ \partial_t w & = -\frac{(1-d^2\partial_{xx})}{\varepsilon} w - 2\,(1 - d^2\partial_{xx})^{-1}\left\{(i^+\tilde{1} + j)\partial_t j\right\} \end{cases}$$

which can be written

$$(S_\varepsilon) \qquad \begin{cases} \partial_t j & = f_0(j,w,\varepsilon) \\ \partial_t w & = \frac{K}{\varepsilon} w + g_1(j,w,\varepsilon) \end{cases}$$

with

$$\begin{cases} K & = -\,(1 - d^2\partial_{xx}) \\ f_0(j,w) & = \frac{1}{a}\big(\alpha_0 + \beta_1 j + \beta_2(bj + V^0 + w) - j(bj + V^0 + w)\big) \\ g_1(j,w) & = -2K^{-1}\left\{(i^+\tilde{1} + j)f_0(j,w)\right\} \end{cases}$$

Let us show that system (S_ε) satisfies the assumptions of the following Centre Manifold Theorem in an infinite dimensional case, stated in [CHL09].

Theorem 4 (Centre Manifold Theorem) *Let E and F be two Banach spaces and take an integer $r \geq 1$. Let $f_0(x,y,\varepsilon) \in C^r(E \times F \times [0,1]; E)$ and $g_1(x,y,\varepsilon) \in C^r(E \times F \times [0,1]; F)$. Take a bounded linear operator $K \in \mathcal{L}(F)$, which is invertible. We assume the following:*
(I) the functions f_0, g_1 as well as their derivatives up to order r are bounded;
(II) there are a number $\mu > 0$ and a constant $C > 0$ such that for any $y \in F$, we have

$$\forall t \geq 0, \;\; \forall \varepsilon \in]0,1], \quad \left\|\exp\left(\frac{t}{\varepsilon}K\right) y\right\|_F \leq C \left\|y\right\|_F \exp\left(-\mu\frac{t}{\varepsilon}\right).$$

Under the above assumptions, for any $x_0 \in E$, $y_0 \in F$, $\varepsilon \in]0,1]$, we define $X^\varepsilon(t,x_0,y_0) \equiv X^\varepsilon(t)$ and $Y^\varepsilon(t,x_0,y_0) \equiv Y^\varepsilon(t)$ as the solution for $t \geq 0$ of the differential system

$$(S_\varepsilon) \qquad \begin{cases} \dfrac{d}{dt}X^\varepsilon(t) = f_0(X^\varepsilon(t),Y^\varepsilon(t),\varepsilon), \qquad X^\varepsilon(0) = x_0, \\ \\ \dfrac{d}{dt}Y^\varepsilon(t) = \dfrac{K}{\varepsilon}Y^\varepsilon(t) + g_1(X^\varepsilon(t),Y^\varepsilon(t),\varepsilon), \qquad Y^\varepsilon(0) = y_0, \end{cases}$$

Then, there is an $\varepsilon_0 > 0$ such that for any $\varepsilon < \varepsilon_0$, the differential system (S_ε) possesses a centre manifold in the following sense:

i) there exists a function $h(x,\varepsilon) \in C^r(E \times [0,\varepsilon_0]; F)$ such that for any $\varepsilon \in]0,\varepsilon_0]$, the set $\mathbf{C}_\varepsilon := \{(x,h(x,\varepsilon)); x \in E\}$ is invariant under the flow generated by (S_ε) for $t \geq 0$. Besides, we have $\|h(x,\varepsilon)\|_{L^\infty(E;F)} = O(\varepsilon)$ as $\varepsilon \to 0$.

ii) the function $h(x,\varepsilon)$ satisfies the partial differential equation

$$D_x h(x,\varepsilon) f_0(x,h(x,\varepsilon),\varepsilon) = \frac{K}{\varepsilon} h(x,\varepsilon) + g_1(x,h(x,\varepsilon),\varepsilon),$$

where $D_x h$ stands for $(Dh)/(Dx)$. On top of that, any bounded function $\tilde{h}$ such that $\|\tilde{h}\|_{L^\infty} \leq 1$, $\|D_x \tilde{h}\|_{L^\infty} \leq 1$, and such that we have

$$D_x \tilde{h}(x,\varepsilon) f_0(x,\tilde{h}(x,\varepsilon),\varepsilon) = \frac{K}{\varepsilon} \tilde{h}(x,\varepsilon) + g_1(x,\tilde{h}(x,\varepsilon),\varepsilon) + O(\varepsilon^\ell)$$

in L^∞, for some integer $\ell \geq 0$, also necessarily satisfies

$$\|h - \tilde{h}\|_{L^\infty} = O(\varepsilon^{\ell+1}).$$

iii) the invariant manifold $\mathbf{C}_\varepsilon$ may be approximated in the following sense. There are functions h_j $(0 \leq j < r)$, which may be computed recursively, such that for any integer $\ell < r$, we have

$$\left\|h(x,\varepsilon) - h^{[\ell]}(x,\varepsilon)\right\|_{L^\infty(E;F)} = O(\varepsilon^{\ell+1}), \text{ where } h^{[\ell]}(x,\varepsilon) = \sum_{j=1}^{\ell} \varepsilon^\ell h_j(x).$$

Note that i, $u \in C^1\left([0,T], i^+\tilde{1} + H^{-1}(\mathbb{R})\right) \cap C^0\left([0,T], i^+\tilde{1} + H^1(\mathbb{R})\right)$, and hence j, v, $w \in C^1([0,T], H^{-1}(\mathbb{R})) \cap C^0([0,T], H^1(\mathbb{R}))$.

Let us take $E = F = H^1(\mathbb{R})$ and $r = 1$ so that :

$$f_0(j,w,\varepsilon),\ g_1(j,w,\varepsilon) \ \in C^1\left(H^1(\mathbb{R}) \times H^1(\mathbb{R}) \times [0,1]\ ;\ H^1(\mathbb{R})\right).$$

Note that, since (j,w) belong to a fixed ball of $H^1 \times H^1$ whenever T is fixed, the locally

Lipschitz functions f_0 and g_1 may be considered as globally Lipschitz functions in the subsequent analysis, with a Lipschitz constant that depends on the (fixed) parameter T.

(I) We previously proved that f_0, g_1 are locally Lipschitz functions. Since i and u are bounded functions, so are j and w and so are f_0 and g_1 which are polynomial functions in j and w. Furthermore, the derivatives of f_0 and g_1 involve the bounded functions j, w, $\partial_t j$, $\partial_t w$. Hence, the derivates of f_0 and g_1 are also bounded. *(I)* is satisfied.

(II) We use the proof of Lemma 3 where we stated that e^{tA} sends $H^1(\mathbb{R})$ into itself with a norm less than 1.

For any $w \in H^1(\mathbb{R})$, we define

$$\mathcal{F}\left(\exp\big(\frac{t}{\varepsilon}(d^2\partial_{xx}-1)\big)w\right) := \exp\big(-\frac{t}{\varepsilon}(d^2\xi^2+1)\big)\hat{w}.$$

Thus, we have by Lemma 3

$$\left\|\exp\big(\frac{t}{\varepsilon}(d^2\partial_{xx}-1)\big)w\right\|_{H^1} \leq \exp(-\frac{t}{\varepsilon})\|w\|_{H^1}.$$

Hence, (II) is satisfied for $\mu = C = 1 > 0$.

Eventually, by the Centre Manifold Theorem, we have

$$\exists \varepsilon_0 > 0,\, \forall \varepsilon < \varepsilon_0,\, \exists h(j,\varepsilon) \in C^1\left(H^1(\mathbb{R}) \times [0,\varepsilon_0]\ ;\ H^1(\mathbb{R})\right),\ \ w = h(j,\varepsilon).$$

We can thus approximate system (S_ε) by the system:

$$(S_\varepsilon^\infty) \qquad \begin{cases} \partial_t j^\infty = f_0\left(j^\infty, h(j^\infty,\varepsilon),\varepsilon\right) \\ w^{\varepsilon,\infty} = h(j^\infty,\varepsilon) \end{cases}$$

with

$$h(j^\infty,\varepsilon) = \varepsilon h_1(j^\infty) + \varepsilon^2 h_2(j^\infty) + O(\varepsilon^3).$$

System (S_ε^∞), supplemented with the appropriate initial datum, approximates the real system (S_ε) with a convergence rate $O(e^{-t/\varepsilon})$ (see [CHL09], theorem 2).

Furthermore, we can compute recursively functions $h_1,h_2,\ldots$ to obtain the expansion of h in powers of ε which describes the centre manifold, with

$$\begin{aligned} h_1(j) &= -K^{-1}\big\{g_1(j,0)\big\} \\ h_2(j) &= K^{-1}\big\{\partial_j h_1(j) f_0(j,0) - \partial_w g_1(j,0) h_1(j)\big\}. \end{aligned}$$

2.4.3 Convergence rate when $a \to 0$ in the bistable case

In this section, we suppose that a is the fast time. We now denote our system as (S_a) to underline the dependence in the parameter a. Here, $\varepsilon > 0$ can have any fixed value and does not play any role in this analysis. We also suppose that we are in the bistable case (yellow region in Figure 2.4), namely that even if the mortality is greater than the birth rate, then the sexual reproduction characterized by the nonlinearity on i compensates the lack of births and allows the population to survive. Hence, we assume the comparisons

$$b < m < \frac{(b+1)^2}{4} < 1$$

on parameters m and b. We now consider

$$(S_a) \qquad \begin{cases} a\partial_t i = (u+bi)(1-i) - mi \\ \varepsilon \partial_t u = i^2 - u + d^2 \partial_{xx} u. \end{cases}$$

Define[6] $i = \tilde{I}^0 + v$ where $\tilde{I}^0 = \tilde{I}^0(u)$ is the positive solution of $(u+bi)(1-i) - mi = 0$, namely the solution of our original system with $a = 0$. We also note $\tilde{I}^1 = \tilde{I}^1(u)$ the negative solution of $(u+bi)(1-i) - mi = 0$.

6. In this paragraph, we consider that i and u belong to $C^1\left([0,T],i^+\tilde{1} + H^1(\mathbb{R})\right) \cap C^0\left([0,T],i^+\tilde{1} + H^3(\mathbb{R})\right)$ in order to bound $\partial_{xx}u$. In other words, we assume that the initial data i^0 and u^0 belong to H^3.

We have

$$\tilde{I}^0 = \frac{b-u-m+\sqrt{(b-u-m)^2+4bu}}{2b}, \ \ \tilde{I}^1 = \frac{b-u-m-\sqrt{(b-u-m)^2+4bu}}{2b}.$$

The bistable assumption allows to assert that the functions under the square root of $\tilde{I}^0$ and $\tilde{I}^1$ are positive.

We aim at proving that there exists a positive number $\alpha > 0$ and a positive constant C_T such that

$$\|i-\tilde{I}^0\|_{H^1} \leq C_T\big(a+e^{-\alpha\frac{t}{a}}\big).$$

First of all, we remark that

$$\frac{d\tilde{I}^1}{du} = -\frac{1}{2b}\big(1+\frac{b+m+u}{\sqrt{(b-m-u)^2+4bu}}\big).$$

This derivative is negative. Thus, $\tilde{I}^1$ is a decreasing function, and this function is less than $2(b-m)$. Hence, $-\tilde{I}^1$ is greater than $\alpha := 2(m-b) > 0$.

We have

$$a\partial_t(i-\tilde{I}^0) = -b(i-\tilde{I}^0)(i-\tilde{I}^1) - a\partial_t\big(\tilde{I}^0\big).$$

Define $y = i-\tilde{I}^0$. By Duhamel's formula, we have

$$y(t) = y_0 \exp\big(-\frac{1}{a}\int_0^t (i-\tilde{I}^1)(s)\ \mathrm{d}s\big) - \int_0^t \exp\big(-\frac{1}{a}\int_0^{t-s}(i-\tilde{I}^1)(\sigma)\ \mathrm{d}\sigma\big)\partial_s\big(\tilde{I}^0\big)\ \mathrm{d}s.$$

Furthermore, we have

$$\partial_t\big(\tilde{I}^0\big) = \partial_t u\frac{d\tilde{I}^0}{du} = \big(i^2-u+d^2\partial_{xx}u\big)\frac{d\tilde{I}^0}{du}.$$

Since $\frac{d\tilde{I}^0}{du}$ is bounded in L^∞, then if $\partial_t u(t,.)$ is bounded in L^∞, so is $\partial_t(\tilde{I}^0)(t,.)$. On top of that, since $H^1(\mathbb{R}) \subset L^\infty(\mathbb{R})$ by virtue of Sobolev's embedding, it is sufficient to prove that $\partial_t u(t,.) \in H^1(\mathbb{R})$.

Recall that $\partial_t u = i^2 - u + d^2\partial_{xx}u$. Since i and u belongs to $C^1\big(\mathbb{R}^+, i^+\tilde{1} + H^3(\mathbb{R})\big)$, then $\partial_{xx}u(t,.) \in H^1(\mathbb{R})$. Hence, $\partial_t u(t,.) \in H^1(\mathbb{R}) \subset L^\infty(\mathbb{R})$. Eventually, $\partial_t(\tilde{I}^0)(s,.)$ is bounded in H^1 by a constant ν_T depending on T.

Therefore, we recover

$$\begin{aligned}\|y\|_{H^1} &\leq \|y_0\|_{H^1} \exp\big(-\alpha\frac{t}{a}\big) + \int_0^t \nu_T \exp\big(-\alpha\frac{t-s}{a}\big)\ \mathrm{d}s\\ &\leq C_T\big(a + e^{-\alpha\frac{t}{a}}\big) \underset{a\to 0}{\longrightarrow} 0\end{aligned}$$

with $C_T := \max\big(\|y_0\|_{H^1}, \frac{\nu_T}{\alpha}\big)$.

On the other hand, for u solution of (S_a) with $a \neq 0$ and $\tilde{U}^0$ solution[7] of (S_0), we have

$$\partial_t(u - \tilde{U}^0) = (i)^2 - (\tilde{I}^0)^2 - (1 - d^2\partial_{xx})(u - \tilde{U}^0).$$

Thus, considering that u and $\tilde{U}^0$ have the same initial datum, namely $u(0,.) = \tilde{U}^0(0,.)$, Duhamel's formula gives

$$(u - \tilde{U}^0)(t,.) = \int_0^t e^{-(t-s)(1-d^2\partial_{xx})}\big((i)^2 - (\tilde{I}^0)^2\big)(s)\ \mathrm{d}s.$$

Hence, we have

$$\begin{aligned}\|u - \tilde{U}^0\|_{H^1}(t) &\leq \int_0^t \|e^{-(t-s)(1-d^2\partial_{xx})}\big((i)^2 - (\tilde{I}^0)^2\big)\|_{H^1}(s)\ \mathrm{d}s\\ &\leq \int_0^t \|i + \tilde{I}^0\|_{H^1}\|i - \tilde{I}^0\|_{H^1}(s)\ \mathrm{d}s\\ &\leq \mu C_T \int_0^t \big(a + e^{-\frac{\alpha}{a}s}\big)\ \mathrm{d}s\\ &\leq a\mu C_T\big(T + \frac{1}{\alpha}\big) \underset{a\to 0}{\longrightarrow} 0.\end{aligned}$$

with $\mu := \|i + \tilde{I}^0\|_{C^0(H^1)}$.

7. Obviously, this function $\tilde{U}^0$ is not the same as the function U^0 define previously.

As a conclusion, we proved that $(i,u) \underset{a\to 0}{\longrightarrow} (\tilde{I}^0,\tilde{U}^0)$. More precisely, we proved that

$$\|(i,u) - (\tilde{I}^0,\tilde{U}^0)\|_{H^1} \leq C_T\big(a + e^{-\alpha\frac{t}{a}}\big).$$

Remark 10 *The above analysis allows to assert that any solution (i,u) of (2.1) converges as $a \to 0$ to $(\tilde{I}^0,\tilde{U}^0)$ solution of*

$$\begin{cases} (\tilde{U}^0 + b\tilde{I}^0)(1-\tilde{I}^0) - m\tilde{I}^0 = 0 \\ \varepsilon\tilde{U}^0_t = (\tilde{I}^0)^2 - \tilde{U}^0 + d^2\tilde{U}^0_{xx}. \end{cases}$$

2.4.4 Approximated system when $a = 0$

In this section, we still study the system

$$(S_a) \qquad \begin{cases} ai_t &= (u+bi)(1-i) - mi \\ \varepsilon u_t &= i^2 - u + d^2u_{xx} \end{cases}$$

in the limiting case when $a = 0$. As in the previous subsection, we still make the assumption that

$$b < m < \frac{(b+1)^2}{4} < 1$$

so that we are in the bistable case (yellow region in Figure 2.4).

Existence of traveling waves in the bistable case

In the previous subsection, we proved that system (S_a) converges as $a \to 0$ to the approximated system

$$(S_0) \qquad \begin{cases} (\tilde{U}^0 + b\tilde{I}^0)(1-\tilde{I}^0) - m\tilde{I}^0 = 0 \\ \varepsilon\tilde{U}^0_t = (\tilde{I}^0)^2 - \tilde{U}^0 + d^2\tilde{U}^0_{xx}. \end{cases}$$

This approximation is called the quasi steady state approximation. Recall that $\tilde{I}^0 =$

$\tilde{I}^0(\tilde{U}^0)$ is defined as the positive solution of $(\tilde{U}^0 + bi)(1-i) - mi = 0$ seen as a second order polynomial in the variable i. The other solution of this polynomial equation is filtered out because it is negative and thus does not have any biological meaning.

Let us now rewrite system (S_0) as

$$\begin{cases} \tilde{I}^0 = \dfrac{b-u-m+\sqrt{(b-u-m)^2+4bu}}{2b}, \\ \varepsilon u_t = (\tilde{I}^0)^2 - u + d^2 u_{xx}. \end{cases}$$

where for the sake of simplicity, the unknown $\tilde{U^0}$ has been renamed u.

Eventually, this yields the approximated reaction-diffusion equation

$$u_t = d^2 u_{xx} + F(u)$$

where the function F is defined as

$$F(u) = (\tilde{I}^0)^2 - u = \Big(\frac{b-u-m+\sqrt{(b-u-m)^2+4bu}}{2b}\Big)^2 - u.$$

We aim at studying the properties F.

This function has three zeros, which are 0, U^- and U^+ where $U^\pm$ are defined as

$$U^\pm = \frac{1}{2}(b^2+1) - m \pm \frac{1}{2}\sqrt{(b-1)^2\big((b+1)^2-4m\big)}.$$

All these zeros are positive whenever $b < m < \frac{(b+1)^2}{4}$. Furthermore, as a function from $\mathbb{R}^+ \to \mathbb{R}$, the function F is differentiable and we have

$$F^{'}(u) = \Big[\frac{\big(b-u-m+\sqrt{(b-u-m)^2+4bu}\big)}{2b^2}\big(-1+\frac{b+u+m}{\sqrt{(b-u-m)^2+4bu}}\big)\Big] - 1.$$

Hence, we have

$$\begin{aligned} F^{'}(0) &= \Big[\frac{1}{2b^2}\big(b-m+\sqrt{(b-m)^2}\big)\big(-1+\frac{b+m}{\sqrt{(b-m)^2}}\big)\Big] - 1 \\ &= -1 \quad \text{since} \;\; m > b. \end{aligned}$$

We can also verify (using an algebraic computing program like Maple) that $F^{'}(U^{-}) > 0$ and $F^{'}(U^{+}) < 0$. Thus, whenever $b < m < \frac{(b+1)^2}{4} < 1$, the function F satisfies the following properties:

$$\begin{aligned}
&F(0) = F(U^{+}),\ \ F^{'}(0) < 0,\ \ F^{'}(U^{+}) < 0,\\
&F(u) < 0 \quad \text{for} \ \ 0 < u < U^{-},\\
&F(u) > 0 \quad \text{for} \ \ 0 < U^{-} < u < U^{+}.
\end{aligned}$$

Therefore, according to the theory of [FM77] mentionned in the introduction, we can assert the following result.

Theorem. (borrowed from [FM77]) *There exists a unique traveling wave solution (U,c) for system (2.1) when $a = 0$. The sign of the wave speed c depends on the sign of the integral $\int_0^{U^+} F(u)\ \mathrm{d}u$.*

Dependence on the wave speed

In the bistable case, the previous result is not sufficient to state whether we have invasion of a population from an initial location to another one. To decide whether we have invasion or extinction of a population, we need to have a look at the potential wave speed c, which has the same sign as $\int_0^{U^+} F(u)\ \mathrm{d}u$. Indeed, we have

$$c = 0 \Longleftrightarrow G(U^{+},m,b) := \int_0^{U^{+}(m^*,b)} F(u,m^*,b)\ \mathrm{d}u = 0.$$

Hence, we can answer the question of invasion or extinction finding a $m^* := m^*(b)$ solution of the integral equation above. Although we cannot have an explicit formula for this function $m^*(b)$, which is implicitely defined as the solution of

$$G(U^{+},m,b) := \int_0^{U^{+}(m^*,b)} F(u,m^*,b)\ \mathrm{d}u = 0,$$

we can have the graph of this function numerically by computing the integral $G(U^{+},m,b)$ and looking at its contour lines.

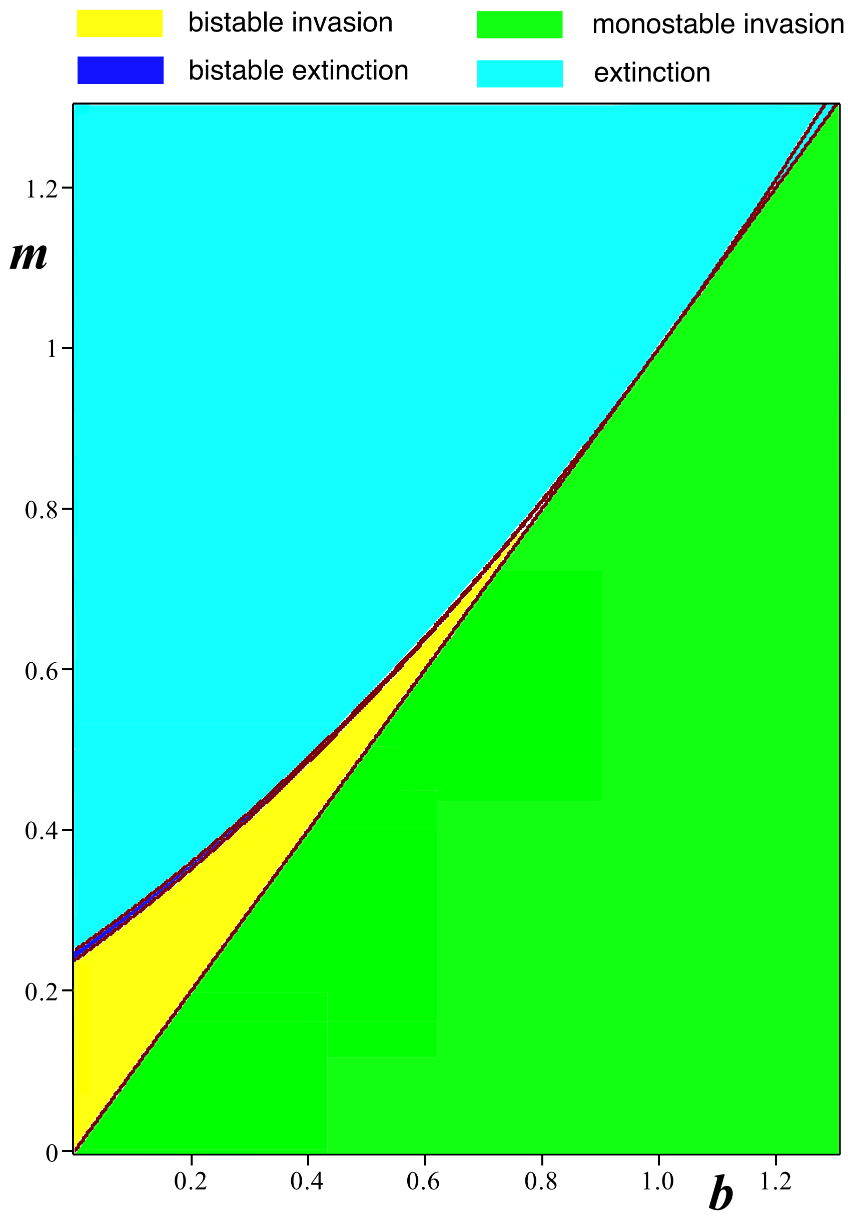
In other words, we expect a bistable invasion whenever $0 < m < m^*$[8] and a bistable extinction whenever $m^* < m < \frac{(b+1)^2}{4} < 1$.

In next chapter, we will see that in the monostable case, we can expect to have a traveling wave connecting (0,0) and (i^+,u^+). We can thus expect to have invasion of a population from an initial location to another one.

Nevertheless, whenever $1 > m > \frac{(b+1)^2}{4}$ or $1 \leq b \leq m$, the single equilibrium (0,0) is asymptotically stable. Thus, we have extinction of the population density anyhow. We summarize this discussion on potential traveling waves in Figure 2.6.

8. we will see further that we can also have extinction of the population in a case where the initial population is too weak. This phenomenon is called sharp transition.

FIG. 2.6 – *Expected dynamical behavior of the system for $a = 0$*



Dependence on the initial datum

In the bistable case, that is in the yellow region in Figure 2.6, whether invasion occurs depends on the initial datum. If initially, a population has a low density, then there are not enough individuals to favor the reproduction, and the mortality predominates births. Thus, the population density collapses. On the other hand, if initially, the population density is important enough to favor the reproduction, births predominate mortality and the population can grow. This phenomenon of critical initial datum size is called sharp transition. This phenomenon arises in our model as illustrated by the numerical simulations in Figures 2.7 and 2.8. The parameter values are $a = 0.1$, $\varepsilon = 1$, $b = 0.04$, $m = 0.2$ so that $m \gg b$ and $\varepsilon \gg a$, namely a is the fast time and the mortality rate is greater enough than the birth rate. The initial datum choosed here is a step function of half-width r.

FIG. 2.7 – *Population density for an initial datum of half-width* $r = 0.20$

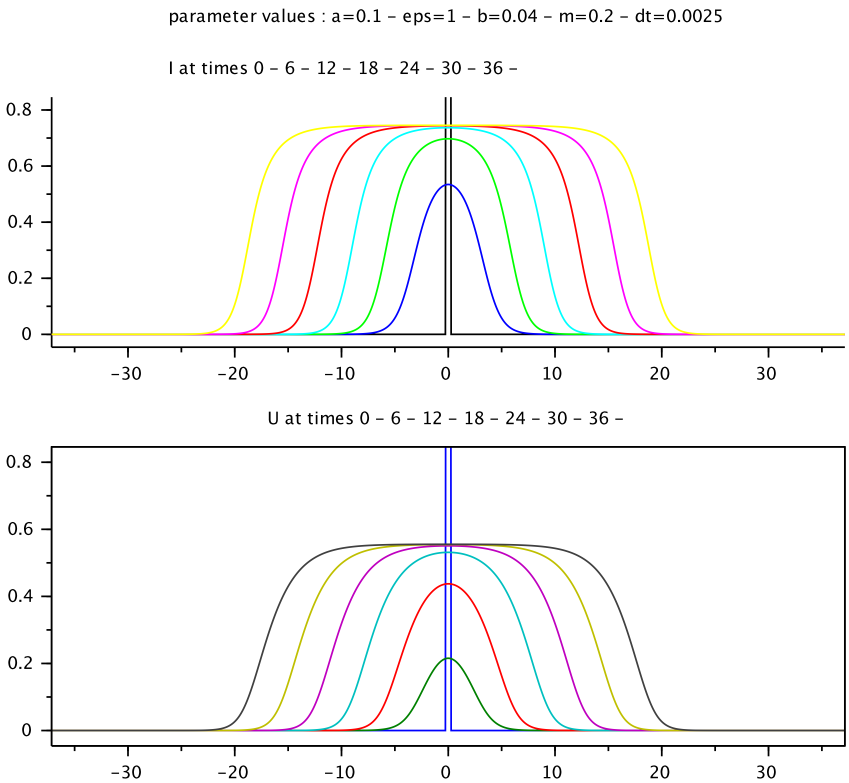
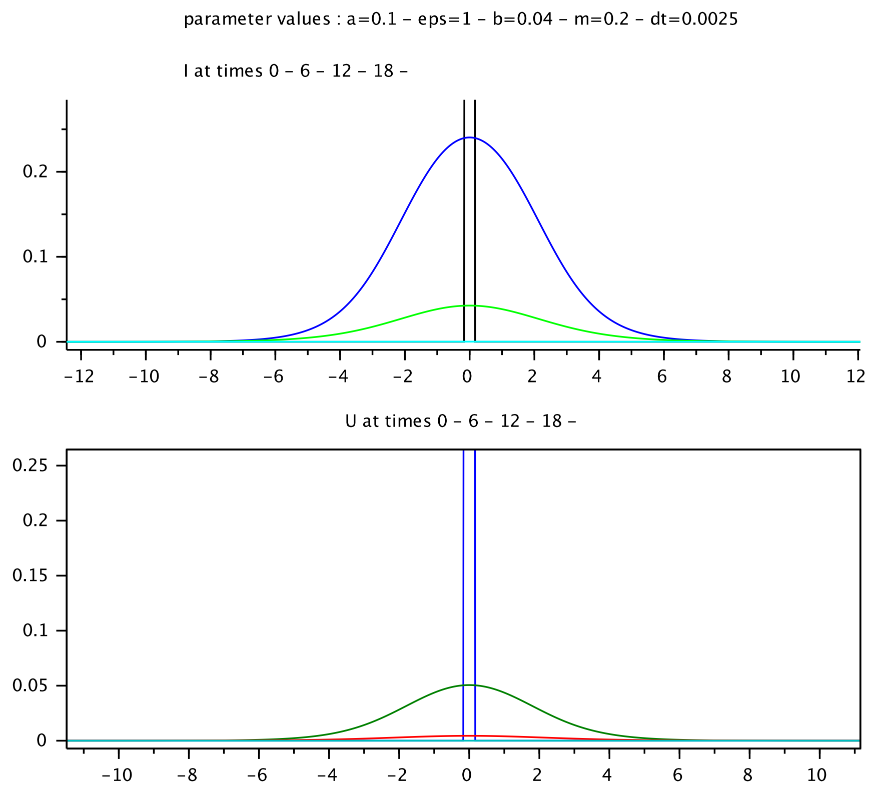


FIG. 2.8 – *Population density for an initial datum of half-width* $r = 0.15$



References

[Car12] Jack Carr. *Applications of centre manifold theory*, volume 35. Springer Science & Business Media, 2012.

[CHL09] François Castella, Jean-Philippe Hoffbeck, and Yvan Lagadeuc. A reduced model for spatially structured predator–prey systems with fast spatial migrations and slow demographic evolutions. *Asymptotic Analysis*, 61(3-4):125–175, 2009.

[FM77] Paul C Fife and J Bryce McLeod. The approach of solutions of nonlinear diffusion equations to travelling front solutions. *Archive for Rational Mechanics and Analysis*, 65(4):335–361, 1977.

[HCD+16] Frédéric M Hamelin, François Castella, Valentin Doli, Benoît Marçais, Virginie Ravigné, and Mark A Lewis. Mate finding, sexual spore production, and the spread of fungal plant parasites. *Bulletin of mathematical biology*, 78(4):695–712, 2016.

[LSKT96] MA Lewis, G Schmitz, P Kareiva, and JT Trevors. Models to examine containment and spread of genetically engineered microbes. *Molecular Ecology*, 5(2):165–175, 1996.

[Smo12] Joel Smoller. *Shock waves and reaction—diffusion equations*, volume 258. Springer Science & Business Media, 2012.

Chapitre 3

Traveling wave solutions in the monostable case

Contenu du chapitre

3.1 Introduction

We are interested in modeling the spread of a fungal plant pathogen subject to mate limitation ([HCD+16], Hamelin et al, 2016). Specifically, we consider (after ecological considerations) the following system of equations:

$$(S) \qquad \begin{cases} ai_t &= (u+bi)(1-i) - mi \\ \varepsilon u_t &= i^2 - u + d^2 u_{xx} \end{cases},$$

where $i = i(t,x) \in \mathbb{R}$ and $u = u(t,x) \in \mathbb{R}$ depend on a time variable $t \geq 0$ and on a dimensional space variable $x \in \mathbb{R}$. Here and throughout this chapter, we make the assumption

$$b > m.$$

A simple analysis of this differential system shows that whenever $b > m$, there exist two equilibria, namely (0,0) which is unstable, and $\bar{v} = (\bar{i},\bar{u})$ with $\bar{i} > 0$, $\bar{u} > 0$ (see below) which is globally attracting. Our system is thus monostable. Based on this observation, we aim at proving the existence of traveling wave solutions for this reaction-diffusion system. Recall that traveling wave solutions of this system are functions i, u which propagate in a single direction with negligible change in shape. In our case, traveling waves satisfy $i(t,x) = I(x-ct)$ and $u(t,x) = U(x-ct)$ for some given profiles (I,U), where the quantity c is the associated wave speed, and the profiles (I,U) connect $\bar{v} = (\bar{i},\bar{u})$ to (0,0). The key observation of our analysis, which provides such traveling waves, is that this system is cooperative, namely the rate of change of i increases when u increases and conversely.

For reaction-diffusion models, there exists a wide range of results concerning traveling waves. In our case, our main result is the following:

Main result. There exists a minimal wave speed $c_+^* > 0$ such that for any initial datum, the following holds:
- whenever $c \geq c_+^*$, there exists a traveling wave $W = (I,U)$ with associated wave speed c connecting $\bar{v}$ to (0,0).
- whenever $c < c_+^*$, there is no traveling wave connecting $\bar{v}$ to (0,0).

To prove the existence of traveling waves, a general method consists in seeking heteroclinic orbits connecting the two equilibria. More precisely, defining the traveling wave variable $z = x - ct$, traveling wave solutions of (S) are functions (I,U) which satisfy a 3-dimensional differential system in z. Starting from this observation, the results about traveling waves are based on geometric properties of the linearized system and on a global nonlinear analysis of the diffusion system, such as the existence of invariant regions (see for example [Dun83]).

In our case, one of the equations does not involve diffusion. Besides, the reaction-diffusion equation presents a nonlinear term i^2 whose differential vanishes at $i = 0$. For these reasons, the linearization methods quoted above do not work in our context and the linearized system around (0,0) does not provide any information about the equilibrium and the associated nearby trajectories. Therefore, we give up differential methods and focus on an "integrated version" of our system, see below. More specifically, we focus on methods based on monotonicity properties following the approach developped by Fang and Zhao [FZ14] and Weinberger, Li and Lewis [LWL05] in the special case of a reaction-diffusion system whose unknown belongs to $\mathbb{R}^2$ (reference [FZ14] takes care of reaction-diffusion systems whose unknown may belong to an infinite dimensional space).

Let us now provide a the sketch of proof of our main result.

Let us define $v = \begin{pmatrix} i \\ u \end{pmatrix}$. System (S) can be written as:

$$v_t = Dv_{xx} + f(v),$$

where

$$D = \begin{pmatrix} 0 & 0 \\ 0 & d^2/\varepsilon \end{pmatrix}, \quad f(v) = \begin{pmatrix} a^{-1}\left[(u + bi)(1 - i) - mi\right] \\ \varepsilon^{-1}\left[i^2 - u\right] \end{pmatrix}.$$

The initial condition is

$$v_0(x) = v(0,x) = \begin{pmatrix} i \\ u \end{pmatrix}(0,x) = \begin{pmatrix} i_0 \\ u_0 \end{pmatrix}(x).$$

We define the family of time-t maps $(Q_t)_{t\geq 0}$ by the relation

$$Q_t[v_0](x) := v(t,x).$$

In other words, Q_t is the propagator associated with the nonliear system $v_t = Dv_{xx} + f(v)$. It means that Q_t takes the initial values $v^0(x)$ into the values $v(t,x)$ at time t of the solution of (S). Note in passing that standard nonlinear analysis for the nonlinear heat system (S) provides existence and uniqueness of solutions of (S) whenever the initial datum is continuous and bounded, and the associated solution is continuous and bounded as well (see e.g. [Thi79]). Hence, Q_t is well defined as an operator on continuous and bounded functions[1].

With this notation, we define a nonnegative function $W = (I,U)$ to be a traveling wave of the reaction-diffusion system (S) with associated wave speed c, whenever there exists a countable subset Σ of $\mathbb{R}$ such that

$$Q_t[W](x) = W(x - ct), \ \ \forall x \in \mathbb{R}\backslash\Sigma, \, \forall t \geq 0.$$

Therefore, introducing the translation operator in space as

$$T_y[W](x) = W(x - y), \, \forall y \in \mathbb{R},$$

a traveling wave satisfies

$$W(x) = T_{-ct}Q_t[W](x), \ \ \forall x \in \mathbb{R}\backslash\Sigma, \, \forall t \geq 0.$$

Hence, W is a traveling wave whenever W is a fixed point of the operator $T_{-ct}Q_t$. To obtain such a fixed point, it is thus natural to construct a recursion iterating the operator $T_{-ct}Q_t$ so as to obtain W as the limit of $(T_{-ct}Q_t)^n$ in some sense.

On the other hand, since f is cooperative, Q_t is monotone (nondecreasing)[2]. Thus, it is natural to seek traveling waves on the functional space $\mathcal{M}$ of nonincreasing and bounded functions from $\mathbb{R}$ to $\mathbb{R}^2$. Now, monotone and bounded functions have good properties such as the existence of left and right limits at any discontinuity point, the

1. Since Q_t maps C_b^0 into itelf, by a simple extension it turns out that Q_t maps the set of monotone and bounded functions into itself as well. We shall mainly work on this space later.

2. The ordering on $\mathbb{R}^2$ which is refered to here is the componentwise ordering

countability of discontinuity points, the Lebesgue integrability and a certain type of compactness through the following result that we shall use repeatedly in the sequel:

Theorem. (Helly) *Let (v_n) be a sequence of monotone functions from $\mathbb{R}$ to $[-1,1]$. There exists a subsequence of (v_n) which converges pointwise.*

Unfortunately, it turns out that the iteration of $T_{-ct}Q_t$ may converge to the null traveling wave while we seek a traveling wave connecting the equilibria $\bar{v}$ to $(0,0)$, that is a function W satisfying $W(-\infty) = \bar{v}$ and $W(+\infty) = 0$.

To avoid the convergence of $(T_{-ct}Q_t)^n$ to zero, we introduce a function ϕ, positive at $-\infty$ and vanishing on $\mathbb{R}^+$, representing a minimal threshold, which eventually imposes the contraint that $W(-\infty) = \bar{v}$. Based on this choice of ϕ, we define the operator $R_{c,k}$, for any $k \in]0,1]$, as

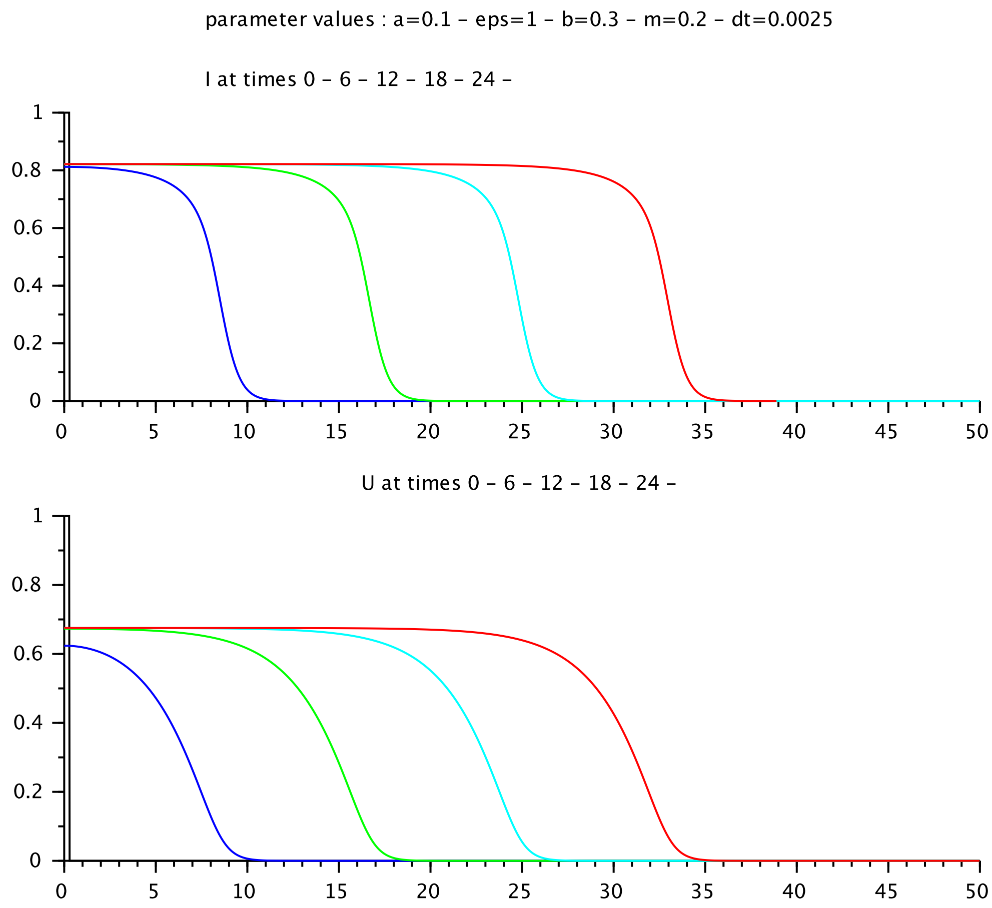
$$R_{c,k}[v](x) = \max\left\{k\phi(x), T_{-ct}Q_t[v](x)\right\}.$$

In doing so, we sort of construct an equivalent problem to the previous one, guaranteeing that the iteration does not collapse to zero. Now, we iterate the operator $R_{c,k}$ and take the limit of $(R_{c,k})^n$ as $n \to +\infty$.

Passing to the limit, we obtain a fixed point of the operator $R_{c,k}$. In a second time, decreasing the minimal threshold function ϕ to zero by letting $k \to 0$, we actually obtain a non trivial fixed point of $T_{-ct}Q_t$.

Technically, we first start proving the main result with the operator $R^n_{c,1}$ for $t = 1$ and $k = 1$. Then, splitting the interval $[0,1]$, we extend the result for $t = \frac{1}{2}$, $t = \frac{1}{4}$, and so on for any $t = 2^{-n}$, and for any fixed value of $k > 0$. Eventually, we obtain the main result for any time $t \geq 0$ by a density argument and by taking the limit $k \to 0$.

The numerical results show that we expect a traveling wave connecting $\bar{v}$ to 0 in the region $b > m$ of the (b,m) plane.



The above simulations represent the traveling waves I and U at time $t = 0$ (with the black step function near the origin as the initial datum), $t = 6$ (in blue), $t = 12$ (in green) and so on. We notice a rightward propagation whenever we choose b greater than m.

3.2 Assumptions and preliminary results

We consider here the functional spaces:

$$\mathbb{R}^2_{\bar{v}} := \{v \in \mathbb{R}^2,\, 0 \le v \le \bar{v}\}$$
$$\mathcal{M} := \{v : \mathbb{R} \to \mathbb{R}^2,\, v \text{ is nonincreasing and bounded}\}$$
$$\mathcal{M}_{\bar{v}} := \{v \in \mathcal{M},\, 0 \le v \le \bar{v}\},$$

where the ordering on $\mathbb{R}^2$ is defined by

$$(x_1,x_2) \le (y_1,y_2) \Longleftrightarrow x_1 \le y_1 \text{ and } x_2 \le y_2$$
$$(x_1,x_2) \ll (y_1,y_2) \Longleftrightarrow x_1 < y_1 \text{ and } x_2 < y_2.$$

We define for any $y \in \mathbb{R}$ the translation operator $T_y : \mathcal{M} \to \mathcal{M}$ by

$$T_y[v](x) = v(x-y), \;\; \forall x \in \mathbb{R}.$$

We introduce the following properties, which are satisfied by our operator

$$Q_1 = Q : \mathcal{M}_{\bar{v}} \to \mathcal{M}_{\bar{v}}.$$

These properties are proved true in section 4.

(A1) Q is translation invariant: $T_y \circ Q = Q \circ T_y, \;\; \forall y \in \mathbb{R}$.

(A2) Q is continuous: if $v_k \to v$ uniformly on every compact set of $\mathbb{R}$ where $v \in \mathcal{M}_{\bar{v}}$ and $v_k \in \mathcal{M}_{\bar{v}}$, then $Q[v_n](x) \to Q[v](x)$ pointwise in $\mathbb{R}^2$ at any point of continuity x of $Q[v]$.

(A3) $Q : \mathcal{M}_{\bar{v}} \to \mathcal{M}_{\bar{v}}$ is monotone: if $u, v \in \mathcal{M}_{\bar{v}}$ are such that $u \le v$, then $Q[u] \le Q[v]$.

(A4) Monostability: Q admits two fixed points 0 and $\bar{v}$ ($\gg 0$) with $0 \in \mathbb{R}^2$ and $\bar{v} \in \mathbb{R}^2$. Besides, for any $\omega \in \mathbb{R}^2$ such that $0 \ll \omega \ll \bar{v}$, we have $\lim\limits_{n\to\infty} Q^n[\omega] = \bar{v}$.

Remark 11 *For a family of continuous-time semiflows $(Q_t)_{t\geq 0}$, because of the dependence in time, we actually need an extended version of (A2), also called (A2) for convenience:*
i) If $t_n \to t$, then $Q_{t_n}[v](x) \to Q_t[v](x)$ pointwise in $\mathbb{R}^2$ at any point of continuity x of $Q_t[v]$.
ii) If $v_n \to v$ uniformly on every compact set of $\mathbb{R}$, then $Q_t[v_n](x) \to Q_t[v](x)$ pointwise in $\mathbb{R}^2$ at any point of continuity x of $Q_t[v]$.

■

We now present more specific properties of bounded and monotone functions from $\mathbb{R}$ to $\mathbb{R}^2$ that we use throughout the paper. In the Lemma below, the first statement is only a tool in order to prove the other Lemmas, while the last two statements are necessary to prove the Theorems stating the existence of traveling waves.

Lemma 6 *i) If a sequence $v_n \in \mathcal{M}$ converges to a continuous function v almost everywhere, then v_n converges to v in $\mathcal{M}$ uniformly on every compact set.*
ii) If a sequence $v_n \in \mathcal{M}$ converges to a function $v \in \mathcal{M}$ almost everywhere, then $v_n(x)$ converges pointwise to $v(x)$ at any point of continuity x of v.
iii) If a sequence $v_n \in \mathcal{M}$ converges to $v \in \mathcal{M}$ almost everywhere and $Q[v](x)$ is continuous almost everywhere, then $Q[v_n](x)$ converges pointwise to $Q[v](x)$ at any point of continuity x of $Q[v]$.

Proof : i) Let $R > 0$ and $\epsilon > 0$. Since v is continuous, there exists $\eta > 0$ such that for all $x,y \in [-R-1,R+1]$, $|x-y| < \eta$ implies $|v(x)-v(y)| < \frac{\epsilon}{4}$.

Now, v_n is monotone and has at most a countable set D of points of discontinuity. We thus construct an increasing sequence $(x_k)_{k=1,\ldots,N}$ of real numbers in $\mathbb{R}\backslash D$, with $N \in \mathbb{N}^*$ and such that $-R-1 \leq x_1 \leq -R$, $x_k < x_{k+1} < x_k + \eta$ and $R < x_N < R+1$.

Choosing $n \in \mathbb{N}$ sufficiently large, we have $\max\limits_{k=1,\ldots,N} \left\{|v_n(x_k) - v(x_k)|\right\} < \frac{\epsilon}{4}$.

For $x \in [-R,R]$, there exists $k \in \{1,2,\ldots,N\}$ such that $x_k \leq x \leq x_{k+1}$. With this construction of (x_k), we also have $|x_{k+1} - x_k| < \eta$ and $|x_k - x| < \eta$.

Thus, using the decay of v, we have

$$\begin{aligned}|v_n(x) - v(x)| &\leq |v_n(x_{k+1}) - v(x)| + |v_n(x_k) - v(x)| \\ &\leq |v_n(x_{k+1}) - v(x_{k+1})| + |v(x_{k+1}) - v(x)| \\ &+ |v_n(x_k) - v(x_k)| + |v(x_k) - v(x)| \\ &\leq \frac{\epsilon}{4} + \frac{\epsilon}{4} + \frac{\epsilon}{4} + \frac{\epsilon}{4} \\ &= \epsilon.\end{aligned}$$

ii) Since v is monotone from $\mathbb{R}$ to $\mathbb{R}^2$, v has at most a countable set D of points of discontinuity. Let $x \in \mathbb{R}\backslash D$ and $h > 0$. Consider $y^- \in]x-h,x]$ and $y^+ \in [x,x+h[$. Since v_k is nonincreasing, we have

$$v_k(y^-) \geq v_k(x) \geq v_k(y^+).$$

Furthermore, v_k converges to v almost everywhere on $\mathbb{R}^2$ and admits left and right limits. Hence, we can consider that $\lim\limits_{k\to+\infty} v_k(y^-) = v(y^-)$ and $\lim\limits_{k\to+\infty} v_k(y^+) = v(y^+)$ without loss of generality. Thus,

$$\lim_{k\to+\infty} v_k(y^-) \geq \limsup_{k\to+\infty} v_k(x) \geq \liminf_{k\to+\infty} v_k(x) \geq \lim_{k\to\infty} v_k(y^+),$$

that is

$$v(y^-) \geq \limsup_{k\to+\infty} v_k(x) \geq \liminf_{k\to+\infty} v_k(x) \geq v(y^+).$$

Moreover, since $x \notin D$, taking the limit $h \to 0$, we have $v(y^-) = v(y^+) = v(x)$. Hence, $\limsup\limits_{k\to+\infty} v_k(x) = \liminf\limits_{k\to+\infty} v_k(x) = v(x)$ for any point of continuity x of v.

iii) The proof of this point is inspired from [FZ14]. Since $v \in \mathcal{M}$, we can find two continuous functions $\overline{v}_n$ and $\underline{v}_n$ in $\mathcal{M}$ such that for any $n \in \mathbb{N}$ and any $x \in \mathbb{R}$,

$$v(x + 2^{-n}) \leq \underline{v}_n(x) \leq v(x) \leq \overline{v}_n(x) \leq v(x - 2^{-n}).$$

Furthermore, $v_k \to v$ *a.e.* provides that for any integer n, $\min\{v_k,\underline{v}_n\} \to \underline{v}_n$ *a.e.*

Hence, according to i) and using the continuity of $\underline{v}_n$, we have the convergence

$$\min\{v_k,\underline{v}_n\} \to \underline{v}_n \ , \quad \forall x \in \mathbb{R}.$$

The same argument as above implies

$$\max\{v_k,\overline{v}_n\} \to \overline{v}_n \ , \quad \forall x \in \mathbb{R}.$$

Since Q satisfies (A1)$-$(A3) where $Q[v](x)$ is continuous almost everywhere, by virtue of the first inequality and the convergences established above, we deduce the following series of equalities and inequalities below

$$\begin{aligned}
Q[v](x) &= \lim_{n\to+\infty} Q[v](x+2^{-n}) \\
&= \lim_{n\to+\infty} Q[v(.+2^{-n})](x) \\
&\leq \lim_{n\to+\infty} Q[\underline{v}_n](x) \\
&= \lim_{n\to+\infty} \lim_{k\to+\infty} Q[\min\{v_k,\underline{v}_n\}](x) \\
&\leq \lim_{k\to+\infty} Q[v_k](x) \\
&\leq \lim_{n\to+\infty} \lim_{k\to+\infty} Q[\max\{v_k,\overline{v}_n\}](x) \\
&= \lim_{n\to+\infty} Q[\overline{v}_n](x) \\
&\leq \lim_{n\to+\infty} Q[v](x-2^{-n}) \\
&= Q[v](x) \ \ a.e.\ x \in \mathbb{R}.
\end{aligned}$$

Therefore, $Q[v_k](x) \to Q[v](x)$ $a.e.$ and statement ii) of this Lemma gives the conclusion.

■

3.3 Existence and nonexistence of traveling waves

In this section, we prove the existence of traveling waves. Take $\omega \in \mathbb{R}^2$ with $0 \ll \omega \ll \bar{v}$. We pick up a continuous function $\phi : \mathbb{R} \to \mathbb{R}^2$ satisfying the following properties:

i) ϕ is a nonincreasing function;
ii) $\phi(x) = 0$ for all $x \geq 0$;
iii) $\phi(-\infty) = \omega$.

Let c and k be some real numbers with $k \in]0,1]$. We define the operator $R_{c,k}$ as follows

$$R_{c,k}[a](s) := \max\{k\phi(s), T_{-c}Q[a](s)\}.$$

We also define a recursive sequence of functions $a_n(c,k,s)$ by

$$a_0(c,k,s) = k\phi(s),\ a_{n+1}(c,k,s) = R_{c,k}[a_n(c,k,.)](s)].$$

For convenience, we denote

$$R_c = R_{c,1},\ \ a_n(c;s) = a_n(c,1;s).$$

In the Lemmas below, we give some properties about the convergence of the sequence $(a_n)_{n\geq 0}$ constructed above and about its limit a.

Lemma 7 *The following statements are satisfied:*
i) $R_c : \mathcal{M}_{\bar{v}} \to \mathcal{M}_{\bar{v}}$ is monotone: if $u,v \in \mathcal{M}_{\bar{v}}$ satisfy $u \geq v$, then $Q[u] \geq Q[v]$.
ii) $a_n(c;s)$ is nondecreasing in n, and nonincreasing in both s and c.
iii) For each n, we have $a_n(c;-\infty) \geq Q^n[\omega]$[3], and $a_n(c;+\infty) = 0$.
iv) For each $s \in \mathbb{R}$, $a_n(c;s)$ converges pointwise to $a(c;s)$ in $\mathbb{R}^2$ and the limit $a(c;s)$ is nonincreasing in both s and c.

Proof : This proof is inspired from [FZ14].
i) This statement is just a consequence of the fact that $Q : \mathcal{M}_{\bar{v}} \to \mathcal{M}_{\bar{v}}$ is order preserving.

3. here, $Q^n[\omega]$ is identified as a constant function of $\mathbb{R}^2_{\bar{v}}$.

ii) We prove the result by induction. It is clear that

$$a_1(c,s) = \max\{a_0(s),T_{-c}Q[a_0(c,.)](s)\} \geq a_0(c,s).$$

Assume that the property $a_n(c,s) \geq a_{n-1}(c,s)$ holds. Then,

$$\begin{aligned}
a_{n+1}(c,s) &= \max\left\{a_0(s),T_{-c}Q[a_n(c,.)](s)\right\} \\
&\geq T_{-c}Q[a_n(c,.)](s) \\
&= Q[a_n(c,.)](s+c) \\
&\geq Q[a_{n-1}(c,.)](s+c) \text{ by the induction assumption and (A3)} \\
&= T_{-c}Q[a_{n-1}(c,.)](s).
\end{aligned}$$

Therefore, $a_{n+1}(c,s) \geq \max\left\{a_0(s),T_{-c}Q[a_{n-1}(c,.)](s)\right\} = a_n(c,s)$. This proves that $a_n(c,s)$ is nondecreasing in n. Similarly, using $(A3)$ and the decay of ϕ provides the decay of u in both s and c.

iii) We prove this result by induction. We have $a_0(c,-\infty) = \phi(-\infty) = \omega$ and $a_0(c,+\infty) = 0$. Since Q is translation invariant, using Lemma 6 iii), we have

$$\lim_{s\to\pm\infty} Q[a_n(c,.)](s) = \lim_{s\to\pm\infty} Q[a_n(c,.+s)](0) = Q[a(c,\pm\infty)](0).$$

Thus, we have

$$\begin{aligned}
a_{n+1}(c,-\infty) &= \lim_{s\to-\infty} \max\{a_0(c,s),T_{-c}Q[a_n(c,.)](s)\} \\
&= \max\{\phi(-\infty),Q[a_n(c,-\infty)](0)\} \\
&\geq Q[a_n(c,-\infty)](0) \\
&\geq Q^{n+1}[\omega].
\end{aligned}$$

By the same argument, we also prove that $a_{n+1}(c,+\infty) = 0$.

iv) Since $(a_n(c,s))_{n\geq 0}$ is a sequence of monotone and bounded functions for each $s \in \mathbb{R}^2$, Helly's convergence theorem asserts that it admits a subsequence of functions converging pointwise on $\mathbb{R}^2$. As a limit of a sequence of nonincreasing functions, $a(c,s)$ is nonincreasing in both s and c.

■

In the subsequent Lemma, we prove that the limit $a(c,s)$ is a fixed point of R_c. Hence, the limit can also be seen as some kind of upper traveling wave.

Lemma 8 *i)* $a(c,.) \in \mathcal{M}$ *and* $R_c[a(c,.)](s) = a(c,s)$ *at any point of continuity of* $R_c[a(c,.)]$.
ii) $a(c;\pm\infty)$ *exist in* $\mathbb{R}^2$ *and* $a(c,-\infty) = \bar{v}$.
iii) $a(c,+\infty) \in \mathbb{R}^2$ *is a fixed point of* Q.
iv) $a(c,+\infty) = \bar{v} \Longleftrightarrow a_n(c,0) \gg \omega$ *for some* $n \in \mathbb{N}$.

Proof : Again, this proof is inspired from [FZ14].
i) As the limit of the sequence $(a_n(c,s))_{n\geq 0}$, the function $a(c,s)$ is also a monotone (nonincreasing) and bounded function from $\mathbb{R}$ to $\mathbb{R}^2$, hence it has at most a countable set of points of discontinuity. The function $Q[a(c,.)](s)$ is also a monotone and bounded function from $\mathbb{R}$ to $\mathbb{R}^2$, and hence has at most a countable set Σ of points of discontinuity. In Lemma 7 iv), we proved that $a_n(c,s)$ converges pointwise to $a(c,s)$ in $\mathbb{R}^2$. By Lemma 6 iii), we have $Q[a_n(c,.)](s) \to Q[a(c,.)](s)$ at any point of continuity of $Q[a(c,.)]$. Since ϕ is continuous, we have $R_c[a_n(c,.)](s) \to R_c[a(c,.)](s)$ at any point of continuity of $R_c[a(c,.)]$ [4]. Consequently, we have

$$a(c,s) = \lim_{n\to\infty} a_{n+1}(c,s) = \lim_{n\to\infty} R_c[a_n(c,.)](s) = R_c[a(c,.)](s), \ \ \forall s \in \mathbb{R}\backslash\Sigma.$$

ii) $a(c,\pm\infty)$ exist in $\mathbb{R}^2$ since $a(c,s)$ is monotone and bounded. Eventually, thanks to Lemma 7 iii) and the monotonicity in n of $a_n(c,s)$, we have

$$\bar{v} \geq a(c,-\infty) \geq \lim_{n\to\infty} a_n(c,-\infty) \geq \lim_{n\to\infty} Q^n[\omega] = \bar{v}.$$

Thus, $a(c,-\infty) = \bar{v}$.

iii) Since Q is a continuous operator in the sense of (A2), so is R_c. Besides, $\phi(+\infty) = 0$, and passing to the limit when s goes to $+\infty$ in i) gives the conclusion.

iv) ($\Longrightarrow$) The decay of a and $a(c,+\infty) = \bar{v}$ give $\lim_{n\to\infty} a_n(c,s) = \bar{v}$ for any $s \in \mathbb{R}$.

Furthermore, since $a_n(c,.)$ is a nonincreasing function, we have the inequality

4. The discontinuity points of $R_c[a(c,.)]$ are those of $Q[a(c,.)]$ according to the definition of R_c.

$a_n(c,s_2) \leq a_n(c,s_1) \leq \bar{v}$ for all $s_1 \leq s_2$. Hence, $|a_n(c,s_1) - \bar{v}| \leq |a_n(c,s_2) - \bar{v}|$.

Therefore, $a_n(c,s)$ converges to $\bar{v}$ uniformly for all s in a bounded interval, that is $a_n(c,.)$ converges to $\bar{v}$ uniformly on every compact set.

In particular, $a_{n+1}(c,0) = T_{-c}Q[a_n(c,.)](0)$ converges to $\bar{v}$ in $\mathbb{R}^2$. Since $\bar{v} \gg \omega$, we deduce that $a_n(c,0) \gg \phi(-\infty) = \omega$ for n sufficiently large.

($\Longleftarrow$) Note that for any $s \geq 0$, we have $a_n(c,s) = T_{-c}Q[a_{n-1}(c,.)](s) \in \mathbb{R}^2_{\bar{v}}$. Since ϕ is continuous and $T_{-c}Q$ is continuous from $\mathcal{M}_{\bar{v}}$ to $\mathcal{M}_{\bar{v}}$ (and in particular on $\mathbb{R}^2_{\bar{v}}$), we deduce that $a_n(c,.)$ is continuous and we recover $\lim\limits_{s\to 0} a_n(c,s) = a_n(c,0) \in \mathbb{R}^2_{\bar{v}}$. Thus, by continuity, we can find a sufficiently small $s_0 > 0$ such that $a_n(c,s_0) \gg \omega$.

Hence, we have $T_{-s_0}[a_n(c,.)] \geq \phi(.) = a_0(c,.)$. Moreover, since Q is translation invariant, we can also write

$$
\begin{aligned}
&T_{-s_0}[a_{n+1}(c,.)] \geq T_{-s_0}[a_n(c,.)] \geq a_0(c,.)\\
&T_{-s_0}[a_{n+1}(c,.)] \geq T_{-s_0-c}\big[Q[a_n(c,.)]\big] \geq T_{-c}\big[Q[a_0(c,.)]\big] = a_1(c,.).
\end{aligned}
$$

By an induction argument, we actually prove that $T_{-s_0}[a_{n+\ell}(c,.)] \geq a_\ell(c,.)$ holds for all $\ell \geq 1$. Thus, we have $a_{n+\ell}(c,s_0 + t) \geq a_\ell(c,t)$, $\forall t \in \mathbb{R}$.

Letting $\ell \to +\infty$, it follows that $a(c,s_0 + t) \geq a(c,t)$, $\forall t \in \mathbb{R}$. Furthermore, since a is a nonincreasing function, namely $a(c,s+t) \leq a(c,t)$ for any $s > 0$, this implies that $a(c,.)$ is constant and hence $a(c,+\infty) = \bar{v}$.

■

Remark 12 *We stated the last three Lemmas in the convenient case $k = 1$ but we can also state and prove them for any $k \in]0,1]$. Thus, $a(c,k,s)$ is both a fixed point of $R_{c,k}$ and also an upper traveling wave.*

■

Definition and Lemma *As in [LWL05], we define the wave speed*

$$c^*_+ = \sup\{c : a(c,+\infty) = \bar{v}\}.$$

associated with a. With this definition, the wave speed satisfies

$$c^*_+ > -\infty.$$

Proof : We follow the proof of [FZ14]. Since $0 \ll \omega \ll \bar{v}$ and $\lim_{n\to+\infty} Q^n[\omega] = \bar{v}$, there exist $p,q \in \mathbb{N}^*$ satisfying both $Q[\frac{\omega}{p}] \ll Q^p[\omega]$ and $\omega \ll Q^{q+1}[\frac{\omega}{p}]$. Lemma 7 implies that

$$Q[\frac{\omega}{p}] \ll Q^p[\omega] \ll a_p(c,-\infty), \ \ \forall c \in \mathbb{R}.$$

Besides, we have $T_{-c}Q[a_p(c,.)](s) \leq a_{p+1}(c,s), \ \ \forall c \in \mathbb{R}$.

Thus, a direct induction gives

$$(T_{-c}Q)^q[a_p(c,.)](s) \leq a_{p+q}(c,s), \ \ \forall c \in \mathbb{R}.$$

Hence, we have

$$\begin{aligned}\omega \ll Q^{q+1}[\frac{\omega}{p}] &\leq Q^q[a_p(c,-\infty)] \\ &= (T_{-c}Q)^q[a_p(c,-\infty)] \\ &= \lim_{s\to-\infty}(T_{-c}Q)^q T_{-s}[a_p(c,.)](0), \ \ \forall c \in \mathbb{R}.\end{aligned}$$

Now, using the decay in c and taking the limit as $c \to -\infty$, we recover

$$\omega \ll \lim_{c\to-\infty}(T_{-c}Q)^q[a_p(c,.)](0) \leq \lim_{c\to-\infty} a_{p+q}(c,0).$$

As a conclusion, when c is a sufficiently large negative number, we recover $\omega \ll a_{p+q}(c,0)$. Lemma 8 iv) gives the conclusion.

■

Remark 13 *In the definition of c_+^*, the symbol $+$ means that the wave propagates rightward. It is also possible to introduce a wave propagating leftward choosing the function ϕ representing the initial condition to be nondecreasing.*

■

Remark 14 *Consider c_+^* as defined above and $\mathcal{C}_{\bar{v}}$ the space of continuous functions from $\mathbb{R}$ to $\mathbb{R}^2_{\bar{v}}$ equipped with the compact open topology (the uniform convergence on every compact sets). Let $Q : \mathcal{C}_{\bar{v}} \to \mathcal{C}_{\bar{v}}$ be continuous and satisfy (A1), (A3) and (A4)* *where $\mathcal{M}_{\bar{v}}$ is replaced by $\mathcal{C}_{\bar{v}}$. According to arguments in [LZ07], the two following statements are satisfied:*

i) If $u_0 \in \mathcal{C}_{\bar{v}}$, $0 \leq u_0(x) \ll \bar{v}$ and $u_0(x) = 0$, $\forall x \geq L$ for some $L \in \mathbb{R}$, then $\lim_{n\to+\infty,\ x\geq cn} Q^n[u_0](x) = 0$ for any $c > c_+^*$.

This means that if a wave spreads at a speed c faster than the minimal wave speed c_+^*, then this wave will only "see" the steady state 0, that is the front of the wave.

ii) If $u_0 \in \mathcal{C}_{\bar{v}}$, $u_0(x) \geq m$, $\forall x \leq M$ for some $m \gg 0$ and $M \in \mathbb{R}$, then $\lim_{n\to+\infty,\ x\leq cn} Q^n[u_0](x) = \bar{v}$ for any $c < c_+^*$.

This means that if a wave spreads at a speed c less than the minimal wave speed c_+^*, then this wave will only "see" the steady state $\bar{v}$, that is only the back of the wave.

Hence, a condition for a rightward spreading is determined by whether the speed of the wave is greater or less than c_+^*, the minimal wave speed of the discrete-time system $(Q^n)_{n\geq 0}$ on $\mathcal{C}_{\bar{v}}$.

$\blacksquare$

We are now ready to state the main theorem of this part, giving the existence or the nonexistence of traveling waves to the time-one family $(Q^n)_{n\geq 0}$ representing the reaction-diffusion system seen as a discrete-time recursion.

Theorem 5 (Traveling waves for the time-one map) *Assume that Q satisfies $(A1)-(A4)$. Let c_+^* be defined as previously. The three following statements are satisfied:*
i) For any $c \geq c_+^*$, there is a left-continuous traveling wave $W(x-cn)$ connecting $\bar{v}$ to 0.
ii) For any $c < c_+^*$, there is no traveling wave connecting $\bar{v}$ to 0.
iii) Since Q maps left-continuous functions to left-continuous functions, the traveling waves connecting $\bar{v}$ to 0 satisfy the relation

$$Q^n[W](x) = W(x-cn), \quad \forall x \in \mathbb{R}, \forall n \geq 0.$$

Proof : We follow the proof of [FZ14].
i) Since $c \geq c_+^*$ implies $a(c,+\infty) < \bar{v} = a(c,-\infty)$, we deduce that $a(c,+\infty)$ is an

equilibrium of Q (Lemma 8) which is different from $\bar{v}$. On the other hand, Q has two different equilibria, which are $\bar{v}$ and 0. Therefore, setting $\delta = (\frac{\bar{i}}{2},\frac{\bar{u}}{2}) \in \mathbb{R}^2$, we have $\delta \gg 0$. We also have $\bar{v} - \delta \gg 0$ and $\bar{v}$ is the only fixed point of Q in the rectangle of $\mathbb{R}^2$ $[\bar{v} - \delta,\bar{v}]$. Since $a(c,\frac{1}{n},s)$ for all $n \geq 1$ is a decreasing and bounded function connecting $\bar{v}$ to $0 \notin [\bar{v} - \delta,\bar{v}]$, we can find a real number s_n such that

$$\lim_{s \nearrow s_n} a(c,\frac{1}{n},s) \in [\bar{v} - \delta,\bar{v}], \text{ but } \lim_{s \searrow s_n} a(c,\frac{1}{n},s) \leq \bar{v} - \delta.$$

Define the sequence of nonincreasing functions $f_n(s) := a(c,\frac{1}{n},s + s_n)$ from $\mathbb{R}$ to $\mathbb{R}^2$. Helly's theorem asserts that there exists a subsequence (still denoted $f_n(s)$) converging pointwise to a function W for $s \in \mathbb{R}$. Then, combining Lemma 8 i) and Lemma 6 iii), we have (except for the countable set Σ of points of discontinuity of W) the following equalities

$$\begin{aligned}
W(s) :&= \lim_{n\to+\infty} f_n(s) \\
&= \lim_{n\to+\infty} a\big(c,\frac{1}{n},s + s_n\big) \\
&= \lim_{n\to+\infty} R_{c,\frac{1}{n}}\big[a(c,\frac{1}{n},.)\big](s + s_n) \\
&= \lim_{n\to+\infty} R_{c,\frac{1}{n}}\big[f_n(. - s_n)\big](s + s_n) \\
&= \lim_{n\to+\infty} \max\big\{\frac{1}{n}\phi(s + s_n),T_{-c}Q[f_n](s)\big\} \\
&= \lim_{n\to+\infty} \max\big\{\frac{1}{n}\phi(s + s_n),Q[f_n](s + c)\big\} \\
&= Q[W](s + c), \ \ \forall s \in \mathbb{R}\backslash\Sigma.
\end{aligned}$$

Furthermore, we deduce that $W(\pm\infty)$ are necessarily fixed points of Q. Finally, $f_n(0^+) \not\gg \bar{v} - \delta$ implies that $W(+\infty) \not\gg \bar{v} - \delta$ and $f_n(0^-) \geq \bar{v} - \delta$ implies that $W(-\infty) \geq \bar{v} - \delta$. Thus, since $\bar{v}$ is the only fixed point in $[\bar{v} - \delta,\bar{v}]$ and $0 \notin [\bar{v} - \delta,\bar{v}]$ is the other fixed point, we have

$$W(-\infty) = \bar{v} \text{ and } W(+\infty) = 0$$

Moreover, we have proved above that the two functions $T_c[W]$ and $Q[W]$ are equal for all $x \in \mathbb{R}\backslash\Sigma$. Thus, we have the immediate recursion relation

$$Q^n[W](x) = T_c^n[W](x) = W(x - cn), \ \ \forall n \geq 0, \forall x \in \mathbb{R}\backslash\Sigma.$$

ii) Suppose that $c < c_+^*$. By contradiction, let us assume that there exists a traveling wave W connecting $\bar{v}$ to 0. Then by definition of the initial datum ϕ, we can find $s_0 \in \mathbb{R}$ such that

$$\phi(s) \leq W(s+s_0), \ \ \forall s \in \mathbb{R}.$$

According to i), since W is an upper fixed point of $T_{-c}Q$, it satisfies the inequality

$$a_1(c,s) = \max\left\{\phi(s), T_{-c}Q[\phi](s)\right\} \leq W(s+s_0), \quad \forall s \in \mathbb{R}.$$

and by an immediate induction,

$$a_n(c,s) = \max\left\{\phi(s), T_{-c}Q[a_{n-1}(c,.)](s)\right\} \leq W(s+s_0), \ \ \forall s \in \mathbb{R}, \forall n \geq 1.$$

Hence,

$$a(c,+\infty) = \lim_{s\to+\infty}\lim_{n\to+\infty} a_n(c,s) \leq \lim_{s\to+\infty}\lim_{n\to+\infty} W(s+s_0) = W(+\infty) = 0.$$

This implies that $c \geq c_+^*$, which is a contradiction with the assumption.

iii) The fact that Q maps left-continuous functions to left-continuous functions is proved in section 3.4. We refer to [FZ14] for the proof of the fact that this particular property implies that the relation $Q^n[W](x) = W(x-cn)$ is satisfied for all $x \in \mathbb{R}$.

$\blacksquare$

We are now ready to state our main result for continuous-time semiflows as mentionned in introduction.

Theorem 6 (Traveling waves for a time-t map) *Take $(Q_t)_{t\geq 0}$ a family of continuous-time semiflows satisfying $(A1)-(A4)$. Let c_+^* be defined as previously. The three following statements are satisfied:*
i) For any $c \geq c_+^*$, there is a left-continuous traveling wave $W(x-ct)$ connecting $\bar{v}$ to 0.
ii) For any $c < c_+^*$, there is no traveling wave connecting $\bar{v}$ to 0.

iii) Since Q_t maps left-continuous functions to left-continuous functions, then the traveling waves connecting $\bar{v}$ to 0 satisfy the relation

$$Q_t[W](x) = W(x - ct), \quad \forall x \in \mathbb{R}, \forall t \geq 0.$$

We only give a sketch of proof for this result. We refer to [FZ14] for an exhaustive proof. As previously, we define for any integer $p \geq 1$ a sequence

$$b_0(p,c,s) = \phi(s), \quad b_n(p,c,s) := \max\left\{\phi(s), T_{-c} Q_{\frac{1}{p}}[b_{n-1}(p,c,.)](s)\right\}.$$

where ϕ has the same properties as before.

The sequence b_n converges pointwise to a function b which has the same properties as function a (Lemma 8). Furthermore, we define the minimal wave speed

$$c^*_{+,p} = \sup\{c, \, b(p,c,+\infty) = \bar{v}\}.$$

associated with the semiflow $Q_{\frac{1}{p}}$.

Roughly speaking, we have the following comparison result for the wave speeds c^*_+ of Q_1 and $c^*_{+,p}$ of $Q_{\frac{1}{p}}$, for any integer $p \geq 1$. The proof of this Lemma can be checked in [FZ14] in a more abstract case.

Lemma 9 *For any integer $p \geq 1$, we have $c^*_{+,p} = \frac{1}{p} c^*_{+,1}$.*

Based on this key observation, to prove the existence of traveling wave solutions for continuous-time semiflows, we focus on the maps $(Q_{2^{-n}})_{n \geq 0}$ which are used as building blocks to approximate the family of semiflows $(Q_t)_{t \geq 0}$. More precisely, we use the minimal wave speeds and wave profiles associated with $Q_{2^{-n}}$. It is clear that all we proved for the semiflow $Q = Q_1$ on the time interval $[0,1]$ can be adapted to the time interval $[0,\frac{1}{2}]$ and $[\frac{1}{2},1]$ by translation in time. Hence, Lemma 9 allows to determine the wave speed of any map $Q_{2^{-n}}$ and as foreseen, the speed associated with $Q_{2^{-n}}$ is 2^{-n} times the speed of the time one map Q_1. Therefore, Theorem 5 can be adapted to the time 2^{-n} map $Q_{2^{-n}}$ in the natural way, and the same can be done with all maps $Q_{p2^{-n}}$ whenever p is an integer. As a conclusion, since any nonnegative real number $t \geq 0$ can be approximated by its binary decomposition thanks to a density argument, the result about traveling waves of the semiflows $(Q_t)_{t\geq 0}$ follows. This is where the continuity in time stated in (A2)-i) is exploited.

Let us now see a sketch of proof of Lemma 9. Recall that

$$\frac{1}{p}c^*_{+,1} = \sup\{\frac{c}{p} : b(1,c;+\infty) = \bar{v}\} = \sup\{c : b(1,pc,+\infty) = \bar{v}\}$$

and

$$c^*_{+,p} = \sup\{c : b(p,c,+\infty) = \bar{v}\}.$$

Thus, to prove the Lemma, it is sufficient to verify that $b(1,pc,+\infty) = b(p,c,+\infty)$.

To verify that $b(1,pc,+\infty) \leq b(p,c,+\infty)$, thanks to the definition of b_n and by virtue of the translation invariance of Q_t, it is possible to deduce (see [FZ14]) that

$$b_1(1,pc,s) \leq b_p(p,c,s), \ \ \forall s \in \mathbb{R}.$$

Hence, an induction allows to obtain

$$b_n(1,pc,s) \leq b_{np}(p,c,s), \ \ \forall n \geq 1,$$

which implies, taking the limit $n \to +\infty$, that

$$b(1,pc,s) \leq b(p,c,s), \ \ \forall s \in \mathbb{R}.$$

Therefore, the first inequality follows letting $s \to +\infty$.

Conversely, since $b(1,pc,.)$ is a fixed point almost everywhere of R_{pc}, we deduce that the quantity defined as

$$\bar{b}(1,pc,s) = \lim_{\substack{x \nearrow s \\ x\in\Sigma}} b(1,pc,x),$$

where Σ denotes the points of continuity of $b(1,pc,s)$, is an upper fixed point of R_{pc}. Thanks to this upper fixed point, we define a new threshold function ψ and a new sequence of functions, whose initial datum is a translation in space of ψ and satisfies

$\psi \geq \phi$. This sequence of functions, which is less than a leftward translation of $\bar{b}(1,pc,.)$ allows to obtain, for a positive real number s_1, the inequality

$$b(1,pc,s - s_1) \geq b(p,c,s).$$

Hence, we deduce $b(1,pc,+\infty) \geq b(p,c,+\infty)$.

3.4 Application to reaction-diffusion systems

Let us get back to our system (S) defined at the beginning of this paper. Recall that in our case

$$f(v) = \begin{pmatrix} \frac{(u+bi)(1-i)-mi}{a} \\ \frac{i^2-u}{\varepsilon} \end{pmatrix}.$$

The associated system is cooperative in the sense that the first component f_1 of f is nondecreasing with respect to u and f_2 in nondecreasing with respect to i.

When $b > m$, the function f has two equilibria: (0,0) and $\bar{v} = (\bar{i},\bar{u})$ where

$$\bar{i} = \frac{1-b+\sqrt{(1-b)^2+4(b-m)}}{2}, \quad \bar{u} = \bar{i}^2.$$

In the sequel, we identify 0 with the zero vector of $\mathbb{R}^2$ and we note $\bar{v} = (\bar{i},\bar{u})$ the vector of $\mathbb{R}^2$ whose values are defined above.

We have $\bar{v} \gg 0$ and $\bar{v}$ satisfies the condition called (A5). Namely, $\bar{v}$ attracts all the solutions of the dynamical system

$$\begin{cases} y' = f(y) \\ y(0) = \omega \end{cases},$$

with

$$\omega \in \mathbb{R}^2 \text{ and } 0 \ll \omega \ll \bar{v}.$$

Furthermore, f is continuous and locally Lipschitz.

Define $P(t) = \begin{pmatrix} P_1(t) \\ P_2(t) \end{pmatrix}$ the semigroup of the linear heat system $v_t = Dv_{xx}$, *i.e.*

$$P_\ell(t)[\phi](x) = \begin{cases} \frac{1}{\sqrt{4\pi d_\ell t}} \displaystyle\int_{\mathbb{R}} e^{-\frac{(x-y)^2}{4d_\ell t}} \phi_\ell(y)\, dy & \text{if } d_\ell \neq 0 \\ \phi_\ell(x) \;\; \text{if } d_\ell = 0 \end{cases}$$

where $D = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}$ and $\phi = (\phi_1,\phi_2)$.

In our case, we have

$$P(t)[v_0](x) = \begin{pmatrix} i_0(x) \\ \frac{\sqrt{\varepsilon}}{2d\sqrt{\pi t}} \int_{\mathbb{R}} e^{-\varepsilon \frac{(x-y)^2}{4d^2 t}} u_0(y) \, \mathrm{d}y \end{pmatrix} = \begin{pmatrix} i_0(x) \\ H \star u_0(x) \end{pmatrix},$$

with the Green function $H(x) = \frac{\sqrt{\varepsilon}}{2d\sqrt{\pi t}} e^{-\varepsilon \frac{x^2}{4d^2 t}}$.

By Duhamel's formula, the solution of our system (S) can be written:

$$v(t,x) = P(t)[v(0,.)](x) + \int_0^t P(t-s)[f(v(s,.))](x) \, \mathrm{d}s, \;\; \forall \, t \geq 0, \, \forall x \in \mathbb{R}.$$

It can be proved (see for example [Thi79]) that this integral equation posseses a unique solution for any initial datum $v_0 \in \mathcal{M}_{\bar{v}}$. We note $v(t,.,\phi)$ a solution of system (S), such that $v(0,.,\phi) = \phi$ for any function $\phi \in \mathcal{M}_{\bar{v}}$. We also note Q_t the semiflow of our system (S), namely $Q_t(\phi) = v(t,.,\phi)$ for any $\phi \in \mathcal{M}_{\bar{v}}$ as before.

We have in our case

$$\begin{aligned} Q_t[v_0](x) &= v(t,x,v_0) \\ &= P(t)[v_0](x) + \int_0^t P(t-s)[f(v(s,.,v_0))](x) \, \mathrm{d}s, \;\; \forall t \geq 0, \, \forall x \in \mathbb{R}. \end{aligned}$$

To apply the construction of the previous section, we need to prove that the semiflow Q_t satisfies the conditions (A1) $-$ (A4).

Proof of (A1) : Since the nonlinear heat equation is translation invariant, for each solution $v(t,x)$ of system (S), the translated function $v(t,x-y)$ is also solution of system (S). Then, $T_y \circ Q_t[v](x) = Q_t \circ T_y[v](x)$ for all x, $y \in \mathbb{R}$ and $u \in \mathcal{M}_{\bar{v}}$. Thus, Q_t is translation invariant.

Proof of (A2) and (A3) - Preliminary : We pick up an $\alpha > 0$ and define the change of variable $w(t,x) = e^{\alpha t} v(t,x)$. Then, w satisfies the partial differential equation

$$w_t = D w_{xx} + f_\alpha(t,w),$$

where

$$f_\alpha(t,w) = e^{\alpha t} f(e^{-\alpha t} w) + \alpha w.$$

The function $f : \mathbb{R}^2_{\bar{v}} \to \mathbb{R}^2$ representing the nonlinearity is locally Lipschitz, continuous and cooperative. We note $k \in \mathbb{R}^2_{\bar{v}}$ (depending on $\bar{v}$) its Lipschitz constant on the compact set $\mathbb{R}^2_{\bar{v}}$. Since f is cooperative, the first coordinate of f with respect to its second variable and the second coordinate of f with respect to its first coordinate are nondecreasing. Therefore, choosing $\alpha > 0$ arbitrarily large, namely $\alpha > k$, it appears that $f_\alpha(t,.)$ is a nondecreasing function on $\mathbb{R}^2_{\bar{v}}$.

Furthermore, if $v \in \mathcal{M}_{\bar{v}}$, then $w = e^{\alpha t} v \in \mathcal{M}_{e^{\alpha t}\bar{v}}$, and for all w_1, $w_2 \in \mathcal{M}_{e^{\alpha t}\bar{v}}$, we have

$$\begin{aligned}
\|f_\alpha(t,w_1) - f_\alpha(t,w_2)\|_{\mathbb{R}^2_{\bar{v}e^{\alpha t}}} &\le \alpha \|w_1 - w_2\| + e^{\alpha t} \|f(e^{-\alpha t} w_1) - f(e^{-\alpha t} w_2)\| \\
&\le \alpha \|w_1 - w_2\| + e^{\alpha t} k \|e^{-\alpha t} w_1 - e^{-\alpha t} w_2\| \\
&= (\alpha + k) \|w_1 - w_2\|_{\mathbb{R}^2_{\bar{v}e^{\alpha t}}}.
\end{aligned}$$

Thus $f_\alpha(t,.) : \mathbb{R}^2_{\bar{v}e^{\alpha t}} \to \mathbb{R}^2_{\bar{v}e^{\alpha t}}$ is globally Lipschitz with a Lispchitz constant equal to $\alpha + k$.

Therefore, writing Duhamel's formula for the new reaction diffusion system $\partial_t w = D w_{xx} + f_\alpha(t,w)$ with initial datum $w(0,x) = v(0,x) = v_0(x)$, we have for all $t \ge 0$ and $x \in \mathbb{R}$

$$\begin{aligned}
e^{\alpha t} Q_t[v_0](x) &= w(t,x,v_0) \\
&= P(t)[v_0](x) + \int_0^t P(t-s)\big[f_\alpha\big(s, w(s,.,v_0)\big)\big](x) \, \mathrm{d}s.
\end{aligned}$$

Proof of (A2) : Recall that we need to prove the version of (A2) stated in Remark 11 for a general time-t map.

i) Assume that a sequence $t_n \to t$. For any $v_0 \in \mathcal{M}_{\bar{v}}$, we have

$$e^{\alpha t} Q_{t_n}[v_0](x) = P(t_n)[v_0](x) + \int_0^{t_n} P(t_n - s)\big[f_\alpha\big(s,w(s,.,v_0)\big)\big](x)\ \mathrm{d}s$$

where

$$P(t_n)[v_0](x) = \begin{pmatrix} i_0(x) \\ \frac{\sqrt{\varepsilon}}{2d\sqrt{\pi t_n}} \displaystyle\int_{\mathbb{R}} e^{-\varepsilon \frac{(x-y)^2}{4d^2 t_n}} u_0(y)\ \mathrm{d}y \end{pmatrix} = \begin{pmatrix} i_0(x) \\ H \star u_0(x) \end{pmatrix}.$$

Define the sequence of functions $g_n(t) = \frac{\sqrt{\varepsilon}}{2d\sqrt{\pi t_n}} e^{-\varepsilon \frac{(x-y)^2}{4d^2 t_n}} u_0(y)$. For any $t > 0$, this sequence converges pointwise to $\frac{\sqrt{\varepsilon}}{2d\sqrt{\pi t}} e^{-\varepsilon \frac{(x-y)^2}{4d^2 t}} u_0(y) \in L^1(\mathbb{R})$.

The dominated convergence theorem asserts that

$$P(t_n)[v_0](x) \underset{n\to+\infty}{\longrightarrow} \begin{pmatrix} i_0(x) \\ \frac{\sqrt{\varepsilon}}{2d\sqrt{\pi t}} \displaystyle\int_{\mathbb{R}} e^{-\varepsilon \frac{(x-y)^2}{4d^2 t}} u_0(y)\ \mathrm{d}y \end{pmatrix} := P(t)[v_0](x) \quad a.e.\ \ x \in \mathbb{R}.$$

Then, $P(t_n)[v_0] \underset{n\to+\infty}{\longrightarrow} P(t)[v_0]$ almost everywhere.

By the continuity of the integral and the boundedness of f_α, we deduce by a similar argument that the integral term converges almost everywhere as well.

Therefore, we have $e^{\alpha t_n} Q_{t_n}[v_0] \underset{n\to+\infty}{\longrightarrow} e^{\alpha t} Q_t[v_0]$ almost everywhere, that is $Q_{t_n}[v_0] \underset{n\to+\infty}{\longrightarrow} Q_t[v_0]$ almost everywhere. Eventually, due to the monotonicity of v_0, Lemma 6 iii) implies $Q_{t_n}[v_0] \underset{n\to+\infty}{\longrightarrow} Q_t[v_0]$ at any point of continuity of $Q_t[v_0]$.

ii) Let $(v_0^n) \in \mathcal{M}_{\bar{v}}^{\mathbb{N}}$ such that $v_0^n \underset{n\to+\infty}{\longrightarrow} v_0 \in \mathcal{M}_{\bar{v}}$ uniformly on every compact set of $\mathbb{R}$.

Consider $w^n = e^{\alpha t} v^n$ and $w = e^{\alpha t} v$ the respective solutions of the Cauchy problem

$$\begin{cases} z_t = D z_{xx} + f_\alpha(t,z) \\ z(t=0) = z_0 \end{cases},$$

with $w^n(0,.) = w_0^n = v_0^n$ and $w(0,.) = w_0 = v_0$.

A function z is said to be a sub (*resp* super) solution of this Cauchy problem whenever z satisfies $z_t - Dz_{xx} \leq$ (*resp* $\geq$) $f_\alpha(t,z)$ with $z(t=0) = z_0$.

Let us define $r_n = w^n - w$. Since f_α is globally Lipschitz, we have

$$\begin{aligned}(r_n)_t = (w^n - w)_t &= D(w^n - w)_{xx} + f_\alpha(t,w^n) - f_\alpha(t,w)\\ &\leq D(w^n - w)_{xx} + (\alpha + k)(w^n - w)\\ &= D(r_n)_{xx} + (\alpha + k)r_n.\end{aligned}$$

This means that r_n is a subsolution of

$$\begin{cases} z_t = Dz_{xx} + (\alpha + k)z \\ z(t=0) = v_0^n - v_0. \end{cases}$$

We also notice that r_n is a supersolution of

$$\begin{cases} z_t = Dz_{xx} + (\alpha - k)z \\ z(t=0) = v_0^n - v_0. \end{cases}$$

Therefore, the maximum principle, which is independent of the diffusion, asserts that for all $t \geq 0$, we have

$$e^{(\alpha-k)t}P(t)\big(v_0^n - v_0\big)(x) \leq r_n(t,x) \leq e^{(\alpha+k)t}P(t)\big(v_0^n - v_0\big)(x).$$

By virtue of the dominated convergence theorem, the functions $e^{(\alpha\pm k)t}P(t)\big(v_0^n - v_0\big)(x) \underset{n\to+\infty}{\longrightarrow} 0$ almost everywhere since $v_0^n \to v_0$ uniformly on every compact set of $\mathbb{R}$.

Hence, we have $r_n = w^n - w \underset{n\to+\infty}{\longrightarrow} 0$ almost everywhere, that is $v^n - v \underset{n\to+\infty}{\longrightarrow} 0$ almost everywhere. By application of Lemma 6 iii), we deduce that $v^n - v \underset{n\to+\infty}{\longrightarrow} 0$ at any point of continuity of v.

To conclude, since $Q_t[v_0^n] = v^n$ and $Q_t[v_0] = v$, the convergence $v_0^n \underset{n\to+\infty}{\longrightarrow} v_0$ uniformly on every compact set implies $Q_t[v_0^n] \underset{n\to+\infty}{\longrightarrow} Q_t[v_0]$ at any point of continuity of $Q_t[v_0]$.

Proof of (A3): Let $\phi_1,\phi_2 \in \mathcal{M}_{\bar{v}}$ such that $\phi_1 \leq \phi_2$. Take w_1,w_2 two solutions of

$$z_t = Dz_{xx} + f_\alpha(t,z),$$

with $w_1(0,.) = \phi_1$ and $w_2(0,.) = \phi_2$.

We have:

$$\begin{aligned} &e^{\alpha t}\big(Q_t[\phi_1] - Q_t[\phi_2]\big)(x) \\ &\quad = P(t)\big[\phi_1 - \phi_2\big](x) + \int_0^t P(t-s)\big[f_\alpha\big(s,w_1(s,.)\big) - f_\alpha\big(s,w_2(s,.)\big)\big](x)\ \mathrm{d}s. \end{aligned}$$

Obviously, $P(t)\big[\phi_1 - \phi_2\big](x)$ is nonpositive.

Besides, $w_1(0,.,\phi_1) = \phi_1 \leq w_2(0,.,\phi_2) = \phi_2$ with w_1,w_2 solutions of the above non-linear heat system in z. The maximum principle gives $w_1(s,.,\phi_1) \leq w_2(s,.,\phi_2)$ for all $s \geq 0$.

Furthermore, since f_α is nondecreasing, the integral term is nonpositive as well. Hence, $e^{\alpha t}Q_t[\phi_1] \leq e^{\alpha t}Q_t[\phi_2]$ and eventually $Q_t[\phi_1] \leq Q_t[\phi_2]$.

As a conclusion, $Q_t : \mathcal{M}_{\bar{v}} \to \mathcal{M}_{\bar{v}}$ is monotone (nondecreasing) for all $t > 0$.

Proof of (A4): Assume that (A5) holds. Let $\omega \in \mathbb{R}^2$ such that $0 \ll \omega \ll \bar{v}$. Clearly, we have $Q[0] = 0$ and $Q[\bar{v}] = \bar{v}$.

Furthermore, since Q_t is nondecreasing (monotone), an immediate recursion provides $0 \ll Q_t^n[\omega] \ll \bar{v}$.

By definition of Q_t, $Q_t^n[\omega]$ is the solution of the nonlinear heat system at time nt starting from ω, namely $v(nt,.,\omega)$, and hence

$$\lim_{n\to\infty} Q_t^n[\omega] = \lim_{n\to\infty} v(nt,.,\omega).$$

On the other hand, $Q_t^n[\omega] = v(nt,.,\omega)$ is independent of x (we start from the constant initial condition $\omega \in \mathbb{R}^2$ identified to a constant function of $\mathcal{M}_{\bar{v}}$). Thus, $v(nt,.,\omega)$ is also solution of the pure reaction system $y^{'} = f(y)$. Since $\bar{v}$ attracts any solution of this reaction system, we have $\lim_{n\to\infty} v(nt,.,\omega) = \bar{v}$ and

$$\lim_{n\to\infty} Q_t^n[\omega] = \lim_{n\to\infty} v(nt,.,\omega) = \bar{v}.$$

Eventually, let us verify that Q_t maps left-continuous functions to left-continuous functions. Let v^0 be a nonincreasing function which is left continuous with a right-handed limit. We have

$$\begin{aligned} v^0(x^-) &:= \lim_{h\to 0^+} v^0(x-h) = v^0(x), \\ v^0(x^+) &:= \lim_{h\to 0^+} v^0(x+h) \ \text{ exists and satisfies } \ v^0(x^+) \leq v^0(x). \end{aligned}$$

Recall that

$$e^{\alpha t} Q_t[v^0](x) = P(t)[v^0](x) + \int_0^t P(t-s)\big[f_\alpha\big(s,w(s,x,v^0(x))\big)\big] \ \mathrm{d}s.$$

Functions $x \mapsto v^0(x-h)$ et $x \mapsto v^0(x+h)$ are respectively sub and super solutions of

$$\begin{cases} w_t = D w_{xx} + f_\alpha(t,w) \\ w(0,x) = v^0(x) \end{cases},$$

with $w(t,x) := e^{\alpha t} v(t,x)$ where v is solution of

$$\begin{cases} v_t = D v_{xx} + f(t,v) \\ v(0,x) = v^0(x) \end{cases}.$$

Hence, for all solutions w, w_d, w_g such that

$$w(0,x) = v^0(x), \quad w_d(0,x) = v^0(x+h), \quad w_d(0,x) = v^0(x-h),$$

the maximum principle asserts that

$$w_d(t,x) \leq w(t,x) \leq w_g(t,x), \quad \forall t \geq 0, \, \forall x \in \mathbb{R},$$

which implies

$$e^{\alpha t}Q_t[w_d^0](x) \leq e^{\alpha t}Q_t[w^0](x) \leq e^{\alpha t}Q_t[w_g^0](x).$$

Taking the limit $h \to 0$ and using Lemma 6 iii), we have

$$\lim_{h\to 0}\Big(e^{\alpha t}Q_t[w_d^0](x)\Big) \leq \lim_{h\to 0}\Big(e^{\alpha t}Q_t[w^0](x)\Big) \leq \lim_{h\to 0}\Big(e^{\alpha t}Q_t[w_g^0](x)\Big)$$

Hence, we have

$$e^{\alpha t}Q\big[\lim_{h\to 0} v^0(x+h)\big] \leq e^{\alpha t}Q\big[\lim_{h\to 0} v^0(x)\big] \leq e^{\alpha t}Q\big[\lim_{h\to 0} v^0(x-h)\big]$$

and eventually

$$e^{\alpha t}Q\big[v^0(x^+)\big] \leq e^{\alpha t}Q\big[v^0(x)\big] \leq e^{\alpha t}Q\big[v^0(x^-)\big]$$

As a conclusion,

$$\lim_{h\to 0} w_d(t,x) := w(t,x^+) \leq w(t,x) = w(t,x^-) := \lim_{h\to 0} w_g(t,x). \tag{3.1}$$

We have proved that Q_t maps the set of nonincreasing and left continuous with a right-handed limit functions to itself.

To conclude, since the semiflow (Q_t) satisfies assumptions $(A1) - (A5)$, we can assert that our cooperative system in the case where $b > m$ has traveling waves whenever $c \geq c_+^*$ where c_+^* represents the minimal wave speed.

References

[Dun83] Steven R Dunbar. Travelling wave solutions of diffusive lotka-volterra equations. *Journal of Mathematical Biology*, 17(1):11–32, 1983.

[FZ14] Jian Fang and Xiao-Qiang Zhao. Traveling waves for monotone semiflows with weak compactness. *SIAM Journal on Mathematical Analysis*, 46(6):3678–3704, 2014.

[HCD+16] Frédéric M Hamelin, François Castella, Valentin Doli, Benoît Marçais, Virginie Ravigné, and Mark A Lewis. Mate finding, sexual spore production, and the spread of fungal plant parasites. *Bulletin of mathematical biology*, 78(4):695–712, 2016.

[LWL05] Bingtuan Li, Hans F Weinberger, and Mark A Lewis. Spreading speeds as slowest wave speeds for cooperative systems. *Mathematical biosciences*, 196(1):82–98, 2005.

[LZ07] Xing Liang and Xiao-Qiang Zhao. Asymptotic speeds of spread and traveling waves for monotone semiflows with applications. *Communications on pure and applied mathematics*, 60(1):1–40, 2007.

[Thi79] Horst R Thieme. Asymptotic estimates of the solutions of nonlinear integral equations and asymptotic speeds for the spread of populations. *J. reine angew. Math*, 306(94):21, 1979.

Phénomènes de propagation de champignons parasites de plantes, par couplage de diffusion spatiale et de reproduction sexuée.

Résumé

On considère des organismes qui mixent reproduction sexuée et asexuée, dans une situation où la reproduction sexuée fait intervenir à la fois de la dispersion spatiale et de la limitation d'appariemment. Nous proposons un modèle qui implique deux équations couplées, la première étant une équation différentielle ordinaire de type logistique, la seconde étant une équation de réaction-diffusion. Grâce à des valeurs réalistes des différents coefficients, il s'avère que la deuxième équation fait intervenir une échelle de temps rapide, alors que la première fait intervenir une échelle de temps lente. Dans un premier temps, on montre l'existence et l'unicité de solutions au système original. Dans un second temps, dans la limite où l'échelle de temps rapide est considérée infiniment rapide, on montre la convergence vers une dynamique réduite d'état d'équilibre, dont les termes correctifs peuvent être calculés à tout ordre. Troisièmement, en utilisant des propriétés de monotonie de notre système coopératif, on montre l'existence d'ondes progressives dans une région particulière de l'espace des paramètres (cas monostable).

Mots Clefs : systèmes de réaction-diffusion, ondes progressives, vitesse d'onde, reproduction sexuée, effet Allee, système coopératif, système monostable.

Abstract

We consider organisms that mix sexual and asexual reproduction, in a situation where sexual reproduction involves both spatial dispersion and mate finding limitation. We propose a model that involves two coupled equations, the first one being an ordinary differential equation of logistic type, the second one being a reaction diffusion equation. According to realistic values of the various coefficients, the second equation turns out to involve a fast time scale, while the first one involves a separated slow time scale. First we show existence and uniqueness of solutions to the original system. Second, in the limit where the fast time scale is considered infinitely fast, we show the convergence towards a reduced quasi steady state dynamics, whose correctors can be computed at any order. Third, using monotonicity properties of our cooperative system, we show the existence of traveling wave solutions in a particular region of the parameter space (monostable case).

Keywords: reaction-diffusion systems, traveling waves, wave speed, sexual reproduction, Allee effect, cooperative system, monostable system.